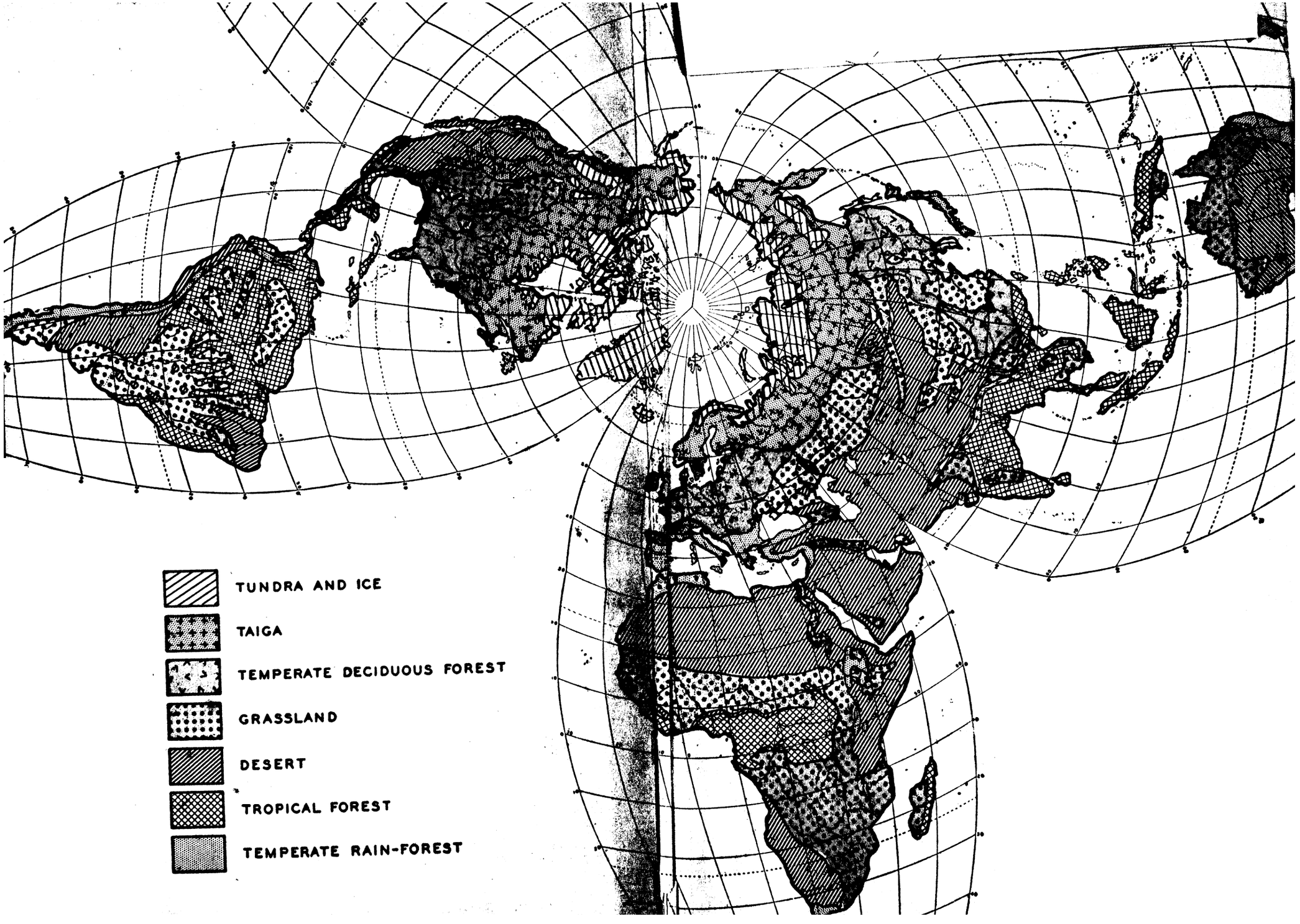
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Ecological Animal Geography

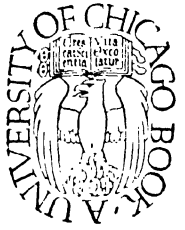
Ecological Animal Geography

SECOND EDITION

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Head Professor of Biology
University of Florida

Chief Curator of Zoölogy
Chicago Natural History Museum



AN AUTHORIZED EDITION, REWRITTEN AND REVISED
BASED ON *Tiergeographie auf oekologischer Grundlage*
By the late RICHARD HESSE

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THE AMERICAN EDITION

is dedicated to two inspiring teachers:

THE LATE DAVID WORTH DENNIS
of Earlham College
and
JAMES G. NEEDHAM

Preface to the Second American Edition

The preparation of a comprehensively revised edition of our *Ecological Animal Geography* of 1937 converts the work into a book still more independent of the German original. The 1937 text, though based on a close translation, had already been much revised by changes, deletions, and additions from Richard Hesse's pioneering *Tiergeographie auf oekologischer Grundlage* of 1924. Even so, large blocks of the original remain, and we have preferred to retain Professor Hesse's name in association with ours, the more so as he himself welcomed the idea of an edition in English. When the junior author called on Professor Hesse in Berlin in 1932, the somewhat diffident suggestion that considerable revision of the German text was planned for the American edition was received with wholehearted enthusiasm. Indeed, Professor Hesse remarked that anything added or any changes made by us would be scrutinized by himself for a projected second German edition.

The result of the incorporation of fourteen years' accumulation of further changes and additions is an essentially new work. Those who might wish to read the book in order to discover or interpret what Hesse wrote or meant in 1924 must be warned that this is not the function of the work envisaged by us. We have hoped to make the book more readable, more accurate, and more nearly abreast with current knowledge; but we have frequently found Hesse's basic data and references of 1924, from much older literature, difficult to replace. The new material is thus quite inextricably interwoven with the old, and we make no apology.

The following subjects illustrate the nature and scope of our revisions and additions: aerial transport in distribution; bioluminescence in marine and cave animals; Bergmann's, Allen's, and Rensch's rules; the concept of the biome, with a schematic map showing the biomes of the world; bipolarity in marine animals; coral reefs and islands; the Hawaiian fauna; intertidal zonation; the limnology of Lake Baikal and of Lakes Tanganyika and Nyasa; the Panamanian land bridge and the Tertiary Panama strait in relation to the marine faunae; the phase theory with regard to grasshoppers and swarming locusts; savanna,

steppe, and desert communities; territoriality; water masses in the oceans; winglessness in beetles; and "zigzag" adaptation. These items are not sharply set off either in importance or by length of treatment from many other changes scattered throughout the book.

Revision of data concerning the number of species in different regions has given particular difficulty. It is hard to find new information of this character for many localities, and the regions more recently surveyed may well have different boundaries from those discussed in our text. In specific instances, when new and comparable data were found, the significant proportions remained much the same as those derived from older lists, though there have been shifts toward both increase and decrease with the changing evaluations of the species category. We have modernized such lists whenever possible. When we found no new comparisons available, dates have frequently been introduced into the text so that the date of the reported survey meets the eye.

Chapter bibliographies have been expanded to include pertinent new publications. A few references were dropped or replaced. Some of the more obscure items and some long series of citations of data are retained by citing the original German edition, i.e., Hesse (1924). Much documentation has been preserved when the items bear early dates. Age alone is little indication of the value of a given report; in fact, in the field of animal geography, older papers may have special value when they accurately describe conditions of existence as they were seen years ago. Titles have been added to all bibliographic items, and the details of citation have been checked for accuracy as far as possible. The revised bibliographies are arranged alphabetically by authors in the hope that this will facilitate their use. The main burden of amplification of the bibliographic references has been borne by the junior revisor, and in this the aid of his colleagues, especially Dr. Fritz Haas, Robert F. Inger, Marion Grey, and Robert Kanazawa, and of Alan Solem, is gratefully acknowledged.

A few figures have been replaced and a few have been added. The treatment of the phenomena of the ecological distribution of birds has been changed in several places, often as a result of constructive suggestions by J. J. Hickey of the University of Wisconsin. Dr. Austin L. Rand, Curator of Birds at the Chicago Natural History Museum, has also been especially helpful in this connection. Statements about mollusks and certain other invertebrates have been scrutinized by another colleague, Dr. Fritz Haas, Curator of Lower Invertebrates. Other colleagues of the junior author at the Chicago Natural History Museum, especially Colin C. Sanborn, Loren P. Woods, Rupert L.

Wenzel, and Henry S. Dybas, have been helpful in suggesting additional matter and correcting nomenclature. Dr. Alfred E. Emerson has been consulted about termite distribution, and material concerning the zoögeography of India was read critically by Dr. Muzaffer Ahmad, now of Lahore, Pakistan. The senior revisor's students in successive classes in animal geography at the University of Chicago have frequently rendered aid in pointing out obscurities and in making pertinent suggestions.

In the complicated preparation of the revised manuscript, the aid of Miss Margaret J. Bauer, secretary of the Department of Zoölogy at the Museum, Miss Laura Brodie, in charge of illustration in the department, and Miss Margaret Bradbury, departmental artist, has been invaluable, as was the assistance of Mrs. Margaret Schultze, secretary to the senior revisor. Miss Patricia Grubbs, Antioch College Assistant at the Museum, bore the brunt of the preparation of the index.

We are thankful to the late Professor Richard Hesse, to English-reading college and university students throughout the world, and to more mature scholars for their cordial reception of the first American edition of what we still think is a great book. We especially appreciate Professor Hesse's approval of our unsupervised revision of his work. He offered only one major criticism; and that concerned our shifting the main emphasis in the final chapter from the long-established interrelations of modern man with the environment and with other animals in Europe to the more recent and dramatic impact of the white man's civilization upon the American scene (see p. 651). After reconsideration, we have retained our former emphasis, although with added discussion, in the final chapter and elsewhere, of the world-wide need for conservation of natural resources, documented by citations to recent pertinent books.

The present revision was carried forward in close connection with the closing stages of the preparation of the *Principles of Animal Ecology*, by W. C. Allee, Alfred E. Emerson, Orlando Park, Thomas Park, and Karl P. Schmidt (1949). Although the two books are concerned with different problems, preoccupation with the formulation and documentation of ecological principles and with the recent literature in that field made it easier to revise and modernize *Ecological Animal Geography*.

Gainesville, Florida
Chicago, Illinois
June, 1951

W. C. Allee
Karl P. Schmidt

Excerpts from the Original Preface

When I finished my essay on "The Ecological Foundations of Animal Distribution" which appeared in Hettner's *Geographische Zeitschrift* (1913) I had thought to turn to other work, but this material had fascinated me and I could not leave it. So, after twelve years of steady work, which was not completely interrupted by twenty months of army service, I offer this book to the friends of zoögeography, hoping for a favorable reception.

For the first time an exposition of animal geography is presented which gives approximately equal space to the animal life of the sea, of fresh water, and of land. There is an understandable demand for such treatment, but the material to be mastered before this is possible is very extensive. Since the founding of the Zoölogical Station at Naples, there have been opened an increasingly large number of marine biological research stations, and the great expeditions for the exploration of marine life in which almost all civilized nations have participated have resulted in the collection of a mass of material almost too great for mastery. Researches upon animal life in fresh water have also come into the foreground in all civilized countries. These sources have yielded results of practical importance for the promotion of fisheries as well as of significance for theoretical biology.

Ecological animal geography is a young science, and its presentation cannot result in so clear a picture as, for example, the classical "Lectures on Comparative Anatomy" of Bütschli. In this new field the fundamental questions are yet to be formulated in order that a rich phase of biology may be opened for further work. I hope this book may be thought of as such an attempt; it deals largely with problems which are taken up separately and arranged in order, and but relatively little space is given to presenting satisfactory solutions. Such treatment does show that the problems of ecological animal geography are capable of exact solution and indicates further in what direction, through observation and experimentation, the solution is to be sought. I hope that this treatment will stimulate further expeditionary researches in this field. We have had an oversupply of travel which yielded animal pelts and alcoholic material; we need rather

observations on the relations between animals and their environment.

I have been almost frightened by the accumulation of animal names in the text. They are not given as faunal lists in which the species are grouped with no other connection than that they come from the same locality; rather the species are given as examples for the formulation of general laws. In the naming of species I have followed Grobben's revision of the *Textbook of Zoölogy* of C. Claus (third edition, 1917). In special cases I have followed other sources; e.g., for palaearctic birds, I have used E. Hartert's comprehensive work. Since the different parts of the book have been taken from work done at widely differing times and since there are different names for many species, my knowledge has not always sufficed to guarantee a correct name, so much the less since, despite all reforms, zoölogical nomenclature is still full of contradictions. Because the use of Latin names for common animals is bombastic in many cases, I have frequently given the common name only.

Inasmuch as the facts used must be drawn from a rich literature, I have tried to bring together the most useful sources and have appended a selected set of references to each chapter. I have not cited all references that have been used, since that would have lengthened the list unduly, and I have restricted myself mainly to summarizations and to books.

All measures and weights are given in the metric system, and other data have been changed to this when necessary. Temperature is given in degrees centigrade, and the designation "C." is usually omitted.

Bonn, Germany R. Hesse
Late March, 1924

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Part
1
The Ecological Foundations of Zoögeography

1. *The Problems and Relations of Ecological Animal Geography*

ZOÖGEOGRAPHY IS THE SCIENTIFIC STUDY OF ANIMAL LIFE WITH REFERence to the distribution of animals on the earth and the mutual influence of environment and animals upon each other. This branch of science therefore forms a department of both zoölogy and geography. Zoögeography corresponds to phytogeography and with it forms the single science of biogeography. These divisions of biogeography are very unequally developed. Phytogeography, in general, has dealt mainly with the distribution of the vascular plants, and zoögeography, in this respect, rests upon a broader basis, since all groups of animals, from protozoans and coelenterates to vertebrates, have been included, though very unequally, in zoögeographic studies. On the other hand, phytogeography has been the subject of active research for a much longer period and has accordingly been much more intensively studied in special fields. Modern work in plant geography continues in both historical and ecological aspects.[2, 7, 10, *]

Among plants, the relations with the total environment are much more direct and obvious than among animals. The capacity for motion from place to place makes animals to a degree independent of their environment; the majority of them are at least able to move towards water, food, or warmth in new localities, and thus they become exposed to new conditions. The formation of spores or seeds, effectively protected from unfavorable influences and easily distributed passively, favors the wide distribution of plants, enabling them to cross barriers with less difficulty, so that limitations of the distribution of plants in accordance with their ancestral history are very much less evident than among animals. Many physiological problems have thus been

* Superior numbers refer to the respective items in the bibliographies at the end of each chapter. See p. 14.

more clearly defined for the plant geographer, and their solutions more easily attained. Zoögeographers have been able to examine many phases of animal distribution in the light of phytogeographic studies. Zoögeography is made difficult by the great complexity of the controlling factors and by the great diversity of reaction to them among the varied types of animals. The solution of zoögeographic problems is not therefore less attractive or important.

The gradual development of the study of animal geography makes it possible to distinguish a number of diverse lines of research that appeared one by one with the advance of this department of science. The origins and foundations of zoögeography lie in the accumulation of faunal lists, in which the animal populations, whether for single groups or *in toto*, are enumerated for specified areas of varying extent. This is the function of "faunal zoögeography," which goes hand in hand with the identification of animal species and in general with the accumulation of collections. These studies are not equally advanced in the various groups of animals. Classes and orders whose representatives are notable for their beauty, brilliant coloration, or diversity of form, or whose simplicity of preservation encourages collecting, such as birds and mammals, beetles and butterflies, and snails and mussels, have always been more intensively collected and studied than such groups as the hydroids, mayflies, springtails, squids, or earthworms.

Faunal zoögeography, in identifying animals and putting in order a wealth of data, forms the basis for every further development of the subject. Extraordinary advances have been made in this direction during the last century. Important scientific expeditions have brought together great numbers of museum specimens from distant countries and seas, and these have been described and classified. The record, however, is far from complete for the smaller, less conspicuous forms, even in the most highly civilized countries.

Animal life is very unequally distributed in any considerable area. Various habitats, or *biotopes*, can be distinguished, according to soil, vegetation, and climatic conditions, each inhabited by a definite and well-characterized animal community. The determination of well-defined biotopes and their dominant species or "indicators," plus the intensive study of the associated animals, constitute another main series of problems for faunal zoögeography, which will require much further study.

In addition to determining the species of animals for a given region, the specific areas, or ranges, of the individual species must be exactly

defined. The ranges of species that occur together in a given locality may be entirely unlike. Giraffes, rhinoceroses, zebras, and antelopes are found together in the steppes of central Africa. The giraffe ranges from the Orange River to the Zambezi, but apparently never occurred south of the Orange. It is absent in part of Mozambique and only reappears to the north of Rovuma, extending thence to Senegambia. The black rhinoceros originally ranged to the extreme south of Africa. Its southward range is now much restricted, and it extends no farther west than the Niger. Zebras also formerly ranged to the Cape, but did not go so far west as the rhinoceros. The giraffe appears to be absent in British Central Africa, whereas the zebra is present. The eland extends beyond the Zambezi-Congo divide; most of the savanna mammals do not. Buffaloes are absent in Somaliland, lions in the Cameroons.[4] A vast amount of detailed study remains to be done on the definition of the ranges of individual species, and exact knowledge of these is required to complete the foundation for zoögeographic investigation. It is evident that crucial ecological studies must be made at the bordering limits of geographic ranges.

The principal avenue of approach to faunistic zoögeography is systematic zoölogy. Intensive systematic studies have unearthed new problems for zoögeography. Of prime importance is the recognition of the fact that many widely distributed animals have a different appearance in the different parts of their range and are divisible into geographic subspecies by means of constant minor differences, in spite of their general agreement in important characters.[11,12] Some comprehensive species of this type are the wall lizard *Lacerta muralis*, the African lion, the puma, the wild turkey, the song sparrow, the king snake *Lampropeltis getulus*, and, among butterflies, the yellow swallowtail *Papilio turnus*. Subspecies of such species may be sharply defined; but they may also be united by intermediates so that the practiced eye of a specialist is sometimes required to distinguish them. The recognition of these minor geographic differentiations is of importance in the study of the influence of external conditions upon animals. Many detailed studies of this type have been made, especially for birds and mammals, and the work of the systematists in this field, although frequently regarded as trivial, is especially valuable. It is, of course, to be desired that a uniform nomenclature and a definite characterization of these geographic subspecies be introduced. This is furnished by the trinary system of nomenclature; among song sparrows, for example, the listing of *Melospiza melodia melodia* and *Melospiza melodia atlantica* makes it immediately evident

that the forms mentioned belong to a "Formenkreis." The term Formenkreis has become current to distinguish series of allied forms whose distinction is geographic and whose origin may be supposed to be entirely or primarily accounted for by geographic isolation.

The definition of subspecies as geographically representative forms, regardless of contiguity of range or of intergradation, preserves the useful trinomial grouping. In fact, it brings the definition of species and Formenkreis into essential congruence. The definitions are sharpened by Mayr,[9] who introduces the useful terms *allopatric*, for forms not found in the same territory and thus geographically representative, and *sympatric*, for forms (now species) that remain distinct in spite of overlapping distribution.

The data accumulated by faunal zoögeography must now be sifted and ordered. The natural laws that lie hidden must be established, and their interrelations studied. Building material is necessary to erect a building, but a heap of bricks is not a structure, and an accumulation of unrelated basic data is not a science. There is interest and even fascination in the recording of observations, but only the hod carriers of science could be content with the mere accumulation of facts. Faunal zoögeography, therefore, leads directly to classification of the facts of distribution; this classification may proceed in various directions.

Comparative zoögeography attempts to classify animal distributions according to their resemblances. This comparison may be made from different viewpoints. Homologies, or inherited resemblances, and analogies, or acquired resemblances, are distinguished in comparative anatomy, and a similar distinction applies to animal distributions. When different faunal lists are compared with reference to the natural relations of their components, faunae may be distinguished whose distribution does not agree with the present geographic divisions of the earth. Such animals of North Africa as the snails, insects, birds, reptiles, and amphibians are much more closely related to the animals of the corresponding groups in southern Europe than to those of Africa south of the Sahara. The fauna of southern Asia is more closely related to that of trans-Saharan Africa than it is to the fauna of Asia north of the Himalayas. Many groups of North American mammals and birds differ more widely from the corresponding groups in Central and South America than from those in Europe and northern Asia. The most obvious faunal boundary between the animal life of North America and that of South America lies somewhere in Mexico and not at the dramatic Isthmus of Panama. The homologies among

such comparable faunae are based upon the blood relationship of their components and upon a common evolution in time and space. The larger faunae of this kind characterize the faunal regions and their subdivisions, within which the animal inhabitants are homologously comparable. For example, the representatives of natural groups in South America, such as the iguanid lizards, the ovenbird family, and the rodents, are interrelated and of common origin whether they inhabit the forests, the prairies, or the mountains.

Closely related species of animals will in general have adjacent ranges, since it is to be assumed that the area in which they developed from their common ancestors was the common origin of their distribution. We observe in this respect that related human stocks in general have a continuous distribution. Two factors mutually condition the distribution of a species: the means of dispersal available to the animal, and the existing physical or biotic barriers to such dispersal. As a consequence of the differences in the means of dispersal in different natural groups of animals, the external barriers affect the different groups in diverse ways. Water animals are limited in their spread by land, and land animals by water. Land animals are often unable to pass mountain ranges, while flying animals are least affected by barriers of any kind. Climate, the lack of suitable food, or the presence of more successful competitors or of enemies may present barriers to the dispersal of any group.

The means of dispersal remain unchanged through long periods of time; they are as old as the principal subdivisions of the animal kingdom, such as the echinoderms, fishes, insects, or birds, and approach uniformity within the group. The position of the more important barriers to dispersal, however, alters with geologic changes in the earth's surface, and these alterations occupy much shorter periods of time than are required for changes in the means of dispersal through organic evolution. We know that many places now occupied by land were formerly covered by seas, that rivers had other courses in former times, that high mountains may be raised anew while others are eroded away, that areas formerly well watered may now be desert, and that ice sheets extended over previously inhabited regions, which were repopulated after the withdrawal of the ice. It is highly probable that land connections formerly existed between certain regions now separated, such as North Africa and southern Europe, and North America and Eurasia (*via* Alaska). Through changes of this nature the ranges of related animals, formerly continuous, may be separated, and regions may be united whose faunae were only distantly allied.

The older a natural division of the animal kingdom, the more such changes of barriers will have occurred during its history, and the more opportunities for dispersal will have been available to its members. In many instances, the systematic relations are the primary factors, antedating the changes in distribution.

Historical zoögeography in this way attempts to work out the development in geologic time of present-day distribution by studying the homologies of animal distribution. For such studies the starting points may be the systematic groups of related animals. The subject matter will then consist of such problems as the restriction of groups like the penguins, hummingbirds, monotremes, lemurs, or armadillos to specific areas; the absence of otherwise widely distributed forms from certain particular areas (as bears in Africa south of the Sahara or of placental mammals in Australia); and the presence of related forms in widely separated regions, such as the tapirs in tropical America and in Malaysia, peripatus in New Zealand, South Africa, and South America, and the horseshoe crabs on the east coast of North America and in the Moluccas. On the other hand the geographic unit may be taken as the starting point, and the fauna of a given region may be analyzed by studying the distributions of the subordinate faunae of diverse origin represented in the area. In Celebes, for example, Asiatic and Australian elements are intermingled.[13,14] Four immigrations can be distinguished, which entered Celebes at successive periods over four distinct routes. These highways of immigration were: (1) *via* Java; (2) *via* Flores; (3) *via* the Philippines; and (4) *via* the Moluccas.

Ecological communities of animals may be recognized that resemble each other superficially in correspondence with resemblances between their environments. These are analogous rather than homologous. For example, the inhabitants of the rain-forests of the various tropical countries, South America, Africa, and Malaysia, exhibit a whole series of evident resemblances, among which adaptations for climbing and for parachute jumping are especially notable. The animals in mountain streams in all parts of the world have numerous and surprising resemblances in their possession of adhesive apparatus. The faunae of small islands, at considerable distances from the continents, exhibit numerous resemblances in their composition. Beds of moss, from the tropics to the polar regions, are inhabited by communities of animals characterized by the capacity to live in a dormant state for long periods, whether they be protozoans, nematode worms, rotifers, copepods, or tardigrades. These biocoenoses found in a given habitat

have analogous communities in similar habitats in the different faunal regions.

The ecological viewpoint, as contrasted with the historical, regards the analogies between animal communities in similar habitats. Ecology is the science of the relation of organisms to their surroundings, living as well as non-living; it is the science of the "domestic economy" of plants and animals. *Ecological zoögeography* views animals in their dependence on the conditions of their native regions, in their adaptation to their surroundings, without reference to the geographic location of this region, whether in America or Africa, the northern or the southern hemisphere. This phase of zoögeography may also proceed either from a geographic viewpoint or from the animal itself. The geographic questions concern the requirements created by the environmental conditions of a given area for the structure and habits of its inhabitants; the modifications in appearance and habits undergone by the animal population in adaptation to the given conditions; and the selective operation of habitat requirements on the composition of the fauna. If a specified animal is made the starting point for the studies to be pursued, the questions will concern the anatomical and physiological characters that fit it to its surroundings and enable it to compete successfully in the struggle for existence; the peculiarities resulting from the influence of the surroundings; and the reasons for its failure to spread into other environments. In this way an explanation may be found for the convergent evolution of different animals under the influence of similar environmental conditions.

It is only a step from the observation of all such groupings of animals, and from the recognition of the fact that they involve comparable phenomena, to the questions of the causes of the appearance of groups with varying limits or of the causes that condition the characteristics in groups with similar habitats. The answer to these problems is sought by *causal zoögeography*. According as the associations to be studied are homologous or analogous, causal zoögeography studies the historical reasons for the evident differences in distribution of the natural groups of animals, or the ecological relations between an environment and its animal population.

The results of historic and ecologic studies in zoögeography are mutually supplementary, but on account of the differences in their methods the relative value of their conclusions is very unequal. The historic mode of approach deals primarily with the geological history of the earth and with the phylogeny of the animal kingdom. As in human history, the events of geologic history and of animal evolution

are never twice exactly alike, and it has been fruitless to seek in them for universal causal connections, as was attempted by Reibisch and Simroth with their pendulation theory of climate and by Eimer with his orthogenetic theory of species formation. The reconstruction of such past events is consequently uncertain, and the number of erroneous conclusions excessively large. The abundance of incompatible hypotheses for former land connections between continents has been shown graphically by Handlirsch,[5] who figures all the supposed land bridges of Cretaceous and Tertiary time on the same maps; scarcely a bit of ocean has escaped the supposition of having formerly been occupied by land. In an important work on the polyphyletic origin of the large terrestrial birds of the southern hemisphere, Burckhardt [1] has brought out the mistakes produced, in another direction, by false phylogenetic premises.

The ecological method is quite different. Ecology deals with present conditions and phenomena, which are subject to analysis and repeated test. Instead of being concerned with unique events, it studies processes, such as chemical reactions or physical experiments, which can be repeated. It is true that the position occupied by an animal is conditioned by its heritage, but environment also influences the animal, by natural selection if by no other means, and the modifications thus acquired are frequently of an adaptive nature; i.e., they make it easier for the animal to live in its environment.

It is accordingly one of the most important problems of ecological zoögeography to investigate the adaptations of animals to their surroundings. An animal may become adapted to the conditions of its existence by somatic and by genetic processes. The most frequent and most important form of adaptation is somatic, or functional, adaptation. Whether an organ is passive or directly active, its capacity often is increased by use, owing to the wonderful property of living matter to react adaptively. Such processes are necessarily repeated when the same conditions are supplied. The enlargement of the mammalian heart with increased bodily activity, the thickening of the shells of mollusks under the influence of wave action, and the enlargement of the kidneys in fresh-water animals with increased necessity for excretion are examples. Other somatic changes that appear with equal certainty in consequence of environmental stimuli may be of indifferent value to the organism. Examples are the reduction in size of marine animals with decrease in the salinity of the water, and many changes in coloration induced by increased or decreased temperature. Such directly conditioned changes may accidentally prove

to be of value to the animal, and they may then be designated as coincident adaptations. In this way the colors of the most diverse animals lose their brilliance under the dry heat of the desert, become pale and dull, and thereby cause the animals to resemble the desert floor. The darkened coloration exhibited by many Lepidoptera when subjected to cold during pupation may favor the warming of the body of the adult in the northern species. Again, in the small crustacean of saline waters, *Artemia salina,* the relative size of the supporting surfaces is increased with decreasing density (i.e., supporting ability) of the salt solution.

Germinal changes also give rise to new characters in animals. These mutations are for the most part of no importance to the efficiency of the animal; but they may sometimes be of value, and they may be preserved by selection and become more and more widely distributed and then more and more adaptive. We may call attention to the kind of preadaptation that involves change of direction of adaptation and may afford opportunity for a new adaptive radiation. Such "zigzag" evolution is exemplified by the derivation of the rays and skates from the sharks; the flattened plane of the belly of the free-swimming shark, which aids it in maintaining position in the water, is evidently the preadaptation that governs the mode of further flattening in association with bottom-dwelling habits.[16]

Special adaptations, physiological or structural, are the more necessary to animals the further the conditions of their environment depart from the optimum. The study of adaptations is for this reason of especial importance to an understanding of the ecology of animal distribution.

Many processes of this kind can be verified experimentally and may be made the subject of physiological analysis. We are, to be sure, still at the beginning of an experimental ecology, and zoölogists are less advanced than the botanists in this field. Experimental animal ecology is certain to undergo active development, on account of the abundance of interesting results promised. Laboratory studies have been made of the change of form in daphnias under the influence of food and temperature; of the transformation of the salt-tolerant crustacean *Artemia salina* with changes in the salinity of the water; and of the relations between frogs and their water intake. Field experiments have also yielded important results; species of turbellarians have been introduced into the brooks of the island of Rügen, where they were absent, although present in the mainland brooks; a Danish race of *Daphnia cucullata* was introduced into Lake Nemi in the

Alban Hills near Rome; special races of *Peridinia* and of *Anodonta* have been introduced into newly made artificial ponds in order to study the ensuing changes.

Unplanned experiments have been still more numerous, and their results throw light on certain questions of ecological zoögeography. The whitefish introduced into Lake Laach (near Coblenz) have transformed into a new subspecies (*Coregonus fera benedicti*).[17,18] The introduction of English foxes into Australia and of the muskrat into Europe are further examples from the very long list of such natural experiments. The release of the English sparrow and of the European starling into North America (in part by the same person!) are familiar American examples. The numerous foreign insect pests brought into the United States have been much studied. A most illuminating and comprehensive work on this subject is Thomson's *The Naturalization of Animals and Plants in New Zealand*.[19] The possibility of an experimental study of the problem of ecological zoögeography gives to the results obtained a potential degree of certainty quite in contrast with the frequent uncertainty of the conclusions of historical zoögeography.

The aims of historical zoögeography are unquestionably high, and valid answers to its questions would be of great importance. It is remarkable that one is able to find clues to events of the remote past by the analysis of the homologies in animal distribution. Historical zoögeography has been valued highly in the eyes of numerous investigators because of its endeavor "to unravel the history of the colonization of continents, and to discover the highways of distribution and the causes of migration in past epochs."[14] This was particularly true in the half century following Darwin's *Origin of Species*, when the study of homologies overshadowed all other lines of research in zoölogy. During that period, historic zoögeography was enthroned, was actively investigated, and now exhibits in consequence a fine series of well-established and connected results. On the other hand, it must be admitted that more sins were committed in this division of zoögeography than in any other through the proposal of unwarranted and frivolous hypotheses. The data are often meager, geological evidence wanting, and the sources of error great. No uniformity of opinion has been reached in even the most fundamental problems, such as that of the permanence or transitory nature of continents and oceans. Nevertheless, a sound body of historical zoogeography is growing up as paleozoölogical knowledge increases and is brought into harmony with faunal zoögeography.

In contrast with the speculative nature of much historical zoögeography, ecological zoögeography bears the germs of a more truly causal science. Although still in its infancy, it has established some general laws, such as the application of the law of minima to the phenomena of distribution (cf. Chapter 2), Bergmann's Rule (Chapter 20), and the correlation between the weight of the heart and the isotherms of climate. Further active research will produce a blossoming of this science like that of its elder sister, ecological phytogeography, in the past generation.

It must be pointed out that a major divergence in speculations and conclusions has occurred between historical animal geography and historical plant geography. Phytogeographers have sought explanations for large-scale distributional phenomena in east-west or west-east connections between the continents in past geological ages and have postulated the origin in the southern hemisphere of great groups of plants that had subsequent northward dispersal.[3,20] Zoögeographers have by no means been in full accord, but they tend to search for the origins of groups of land animals in the northern hemisphere and to account for their dispersal to the southern hemisphere by existing or known former connections between the continents.[8,15] Phytogeographers have freely invoked land bridges or continental drift. Zoögeographers, after a period of uncontrolled land-bridge speculation and after a thorough review of the evidence from fossil mammals, have mainly postulated stability of the continents. Botanical opinion is reviewed by Just.[6]

By way of review, we arrange the subdivisions of zoögeography, descriptive and causal, as follows:

A. Historical zoögeography.
   1. Faunal, accumulating data from field studies, a by-product of systematics.
   2. Comparative, searching for homologies in the data of faunal zoögeography.
   3. Paleontological, tracing existing distributions into the past.
   4. Experimental, examining capacities for dispersal.

B. Ecological zoögeography.
   1. Faunal, accumulating data from field studies, mostly with new emphases (limnology, oceanography).
   2. Comparative, searching for analogies in the data thus found.
   3. Experimental, with
      a. Examination of introductions.
      b. Experiments on tolerance.
      c. Experiments with populations.
      d. Test of theoretical conclusions.

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2. *The Conditions of Existence for Animals*

OWING TO THEIR RAPID REPRODUCTION, LIVING ORGANISMS ARE FOUND everywhere on the earth's surface in places to which they have access and in which they find the necessary conditions for existence.[3] Animal life is thus very widely distributed, but its abundance and diversity vary greatly from place to place and from season to season according to environmental conditions. There are, in fact, few localities aside from the craters of active volcanoes and recent lava flows where there is no animal life and where life is probably impossible. The Dead Sea merits its name, for no animal is able to exist in its waters, with their great concentration of dissolved salts and the high concentration of chlorides and bromides of magnesium. By contrast, Great Salt Lake, with a salt content almost as great, contains diatoms, blue-green algae, protozoa, and large numbers of the brine shrimp *Artemia* (= *Artemisia*) and of the brine fly *Ephydra*. The depths of the Black Sea, which contain much hydrogen sulphide, are devoid of life. One seeks in vain for animal organisms in springs rich in carbon dioxide, or in fumaroles, and they are exceedingly rare in the ice wastes near the poles (see Chapter 19) and in the depths of moving sand.

A supply of matter and energy is necessary for the existence of life. The substances required for the growth and reproduction of an organism, for the maintenance of its energy, and for the production of secretions are designated as foods. For animals these are primarily organic matter of animal or vegetable origin since, unlike green plants, animals are unable to manufacture food from inorganic substances. Special salts supply needed elements such as potassium, sodium, and calcium, among others, and some of these may be imbibed independently of food. Organic nutriment supplies large amounts of chemical energy, which is released as work and heat in the body of the animal. This energy is developed to best advantage in the presence of oxygen,

which is important for its own wealth of chemical energy. The release of such energy occurs by means of chemical transformations, and as the chemical transformations in question can take place only in solutions, water, as a solvent, is an indispensable requirement for life. Some energy is also directly available to animals in the form of light and heat.

Water

Water cannot be withheld from living organisms for continued periods of time without injury and ultimate destruction. Protoplasm is full of water and suspends its functions when this water is withdrawn. It is true that many animals are capable of existing with a very small water supply and are extremely resistant to desiccation. Some of these, both herbivores and carnivores, obtain water from their food; others secure water—so-called water of metabolism—by the chemical transformation of their food.[1,3,5,15,34,36,38] Meal worms (larvae of the beetle *Tenebrio molitor*) have been known to live in bran dried at 105° C. for more than three weeks, and some have survived the fourth week. The survivors of this experiment contained 65% water, whereas the animals at the beginning of the experiment contained only 61.5% water. Tardigrades, rotifers, nematodes, and other simple types of animals retain their vitality in spite of long-continued drying even in sunlight, and become active with renewed water supply (Chapter 18).

Sufficiency of water is most completely assured to animals that live in it. The waters that collect on the earth's surface are rarely even approximately pure; they usually contain, in solution, greater or less amounts of the salts of sodium, calcium, magnesium, potassium, and other materials. The solubility of inorganic substances in water satisfies one of the primary requirements for the development of life, and of plant life especially, although animals also obtain many salts directly from the water. The larvae of Calcispongia and of sea urchins are unable to develop a skeleton in water free from calcium. Pure water is harmful to organisms. It diffuses into their cells and dilutes the salt solutions of the protoplasm to an excessive degree.

Water containing salts in such concentration that no osmosis takes place between it and the organism, i.e., water isotonic with protoplasm, is the most favorable medium for animal life. These conditions are closely approached by sea water.[29] The investigations of Frédéricq [13] and others have shown that sea water is approximately isotonic with the body fluids of the marine invertebrates, whereas

this is not true of fresh water and its inhabitants. The ocean accordingly affords its inhabitants the most favorable conditions of life, a circumstance that has been explained by the supposition that life originated in sea water. According to this theory all non-marine organisms, both plant and animal, that occur elsewhere must have developed from marine ancestors and freed themselves from the marine habitat in the course of geologic time. This hypothesis is supported by the fact that almost all the main branches of the animal kingdom are represented in the ocean, whereas important groups are wholly absent on land and in fresh water, and no important animal phylum is restricted to these environments. The circumstance that only marine organisms are known from the older fossiliferous geologic strata also speaks for the marine origin of life.*

Salinity

The extent of the variation in salinity that can be borne is very different for different animals. Some, such as reef corals and amphibians, are influenced by slight changes in salt content; others withstand much variation in this respect, as, for example, the annelid *Nereis diversicolor* and among fishes, the salmon and stickleback. The amphipod *Niphargus* occurs in water with 8.7 per cent salt in solution, whereas, as is well known, the brine shrimps of the genus *Artemia* tolerate great changes in salinity.[13] The animals affected by slight changes in salt content may be designated as *stenohaline*, and those that withstand great changes as *euryhaline*.

Humidity

Terrestrial animals cannot dispense entirely with water, but some occur only under very humid conditions, whereas others are partial to dry situations. Animals tied to narrow limits of variation in atmospheric humidity may be referred to as *stenohygric*, and those that can withstand great variations of humidity are *euryhygric*. Worms, most snails, amphibians, and water buffaloes are examples of stenohygric animals in moist situations; the camel is a stenohygric animal of arid country. Euryhygric animals are numerous in many groups, especially among the insects, birds, and mammals.

Temperature

The temperature limits between which animal activity is possible are not very wide. The lower limit is necessarily defined by the

* The opposite theory is maintained by some authors.[10]

freezing temperature of the body fluids, a few degrees below that of pure water. The upper limit of temperature for most activities of living matter lies between 40° C. and 50° C., at which point the dissolved albuminoids probably undergo destructive chemical change. Leathes and Raper [24] made the suggestion that temperature toleration is a matter of the relation of fats rather than of proteins; the more liquid fats occur in animals adapted to lower temperatures, and the more solid fats are found in animals adapted to higher temperatures. The effects of the two temperature limits are widely different. The suspension of the activity of protoplasm produced by high temperatures usually causes the death of the animal; the suspension of activity as a result of low temperatures, on the other hand, is not necessarily fatal, and active life may be resumed with the return of a favorable temperature. Many animals are accordingly able to exist in regions where they are forced to suspend their activities at certain seasons on account of low temperatures.

The upper limit of temperature is approached and sometimes exceeded in hot springs. Encysted forms are more resistant, but active Protozoa tolerate only about 50° C. (54.4° is the highest reported by Brues); [8] for Metazoa, about 55° is also the upper limit. The temperatures tolerated by desert insects and desert lizards correspond closely to those endured by the animals of hot springs.[9, 31]

For individual species, the temperature range is for the most part rather narrow. The range varies for different species but is fairly constant for a given form. The three cardinal temperatures are the maximum, minimum, and optimum; the optimum temperature usually lies nearer the maximum than the minimum limiting temperature. The optimum may be widely different for different animals; it lies between 1° and 4° C. (maximum 12–15° C.) for the eggs of trout; between 14° and 20° for the eggs of carp; about 22° for frog's eggs (maximum 30°, minimum nearly 0° C.); and at 38–39° for fowl's eggs. When the temperature range for a species is wide, the animal is said to be *eurythermal;* when narrow, it is *stenothermal.* Stenothermal animals in turn may be cold- or heat-tolerant. Examples of eurythermal animals are the flatworm *Planaria gonocephala* (limits +0.5° and 24°); the oyster (−2° to 20°); the snail *Limnaea truncatula* (= *Galba truncatula*), which in Germany is found principally in cold springs but lives in warm springs at 40° in the Pyrenees; the sperm whale *Physeter,* which lives in all oceans; and the large predatory cats such as the puma, ranging from Canada to Patagonia, or the tiger,

which is equally at home in the tropical jungles of India, the mountains of Central Asia up to 4000 m., and as far north as Irkutsk at 53° N. latitude. Stenothermal warmth-tolerant animals are represented by the reef corals, which flourish only at temperatures above 20°; the crustacean *Copilia mirabilis* (between 23° and 29°); the salpids, the termites, the carp (which require at least 18° to breed); and most reptiles. Cold-tolerant stenothermal forms are represented by a cave silphid beetle that lives in ice grottoes where the annual temperature ranges from −1.7° to +1.0° C.;[45] the pearl mussel *Margaritifera margaritifera;* the crustacean *Calanus finmarchicus;* trout and whitefish; and many others.

Increase of temperature to a certain point reacts favorably on the life of an animal because the chemical reactions on which the release of energy depends are accelerated by the rise in temperature.[22] This is especially striking in the developmental stages. The rate of development of the eggs of the sea urchins *Sphaerechinus* and *Echinus,* is increased 2.5 times for every rise of 10° between 2.5° and 25°.[32] The following figures apply to the development of the cod *Gadus callarias.*[33]

Temperature, °C	−1°	+3°	4°	5°	6°	8°	10°	12°	14°
Period of development, in days	42	23	20.5	17.5	15.5	12.75	10.5	9.7	8.5

The eggs of the herring develop equally well at +0.5° and at 16°, but require 40–50 days at the lower temperature and 6–8 at the higher. The eggs of the rotifer *Notomma* hatch in 4 days at 15°, in 2 days at 28°. The rate of reproduction for protozoans follows a similar rule: *Paramecium aurelia,* for example, divides once in 24 hours at 14°–16°, twice at 18–20°.[16] The period of pupation in insects similarly depends on temperature. According to Krogh, the meal worm *Tenebrio molitor* requires the following periods from pupation to transformation:

At °C.	13.5°	17°	21°	27°	33°
Hours	1116	593	320	172	134

The rate of animal metabolism, measured by the consumption of oxygen and the production of carbon dioxide, also increases with increasing temperature. The meal worm pupa uses, per kilogram and hour, 104 cc. of oxygen at 15° C., 300 cc. at 25°, and 529 cc. at 32.5°. The carp, per kilogram and day, uses 661 cc. at 9° C., and 1692 cc. at 18.2°.

Several formulae have been devised to interpret these temperature effects.[3] The most widely known is that of Van't Hoff, which is based on the observation that chemical and biological processes, within favorable temperature limits, are increased by an approximate constant (two to three times usually) for each 10° rise in temperature. Ludwig [25] reviews the literature and cites original observations on the rate of development of the egg and pupa of the Japanese beetle *Popillia japonica* which show that the temperature coefficient tends to decrease regularly as the temperature increases. The Arrhenius formula, based upon changes in absolute temperature, better fits the facts in many instances that show such a variation in the Van't Hoff coefficient.[12] Krogh [23] advanced a formula to express the relation between temperature and the rate of development in which the constant is added to the rate at one temperature to obtain the rate at a higher one rather than multiplying the slower rate by a constant, as required by Van't Hoff. Krogh's formula is based on the observation that within normal temperature limits an increase of 1° has as great effect upon metabolic processes at one temperature as at another. The time-temperature curve is, within these limits, an hyperbola, and the rate-temperature curve is a straight line that crosses the temperature axis near the threshold temperature of development. Many experiments show that such relationships hold for medial temperatures but that the rate of development is greater than that called for by this formula at low temperatures near the threshold of development and less near the maximum temperature tolerated.

Within medial temperatures thermal constants of development can be calculated by multiplying the number of degrees above the threshold temperature by the number of hours or days required for the development of the stage in question. The life zones of Merriam, still widely used in biogeographic studies in America despite well-known defects, are based supposedly upon the number of day-degrees available in different altitudinal or latitudinal zones.[3] The temperature relations of terrestrial animals are affected markedly by the accompanying humidity, and the physiological action of both is affected by the rate of air movement.[44]

The relations between temperature and rainfall or temperature and humidity for a given area can be shown by plotting the monthly mean temperatures against mean monthly rainfall or against mean monthly relative humidity. Figure 1 shows two such temperature-rainfall charts in which the vertical axis gives temperatures in degrees Fahren-

heit or Centigrade, and the horizontal axis shows rainfall in inches and in centimeters. The graph at the top of the figure extends along the rainfall axis with only slight temperature variations. This is based

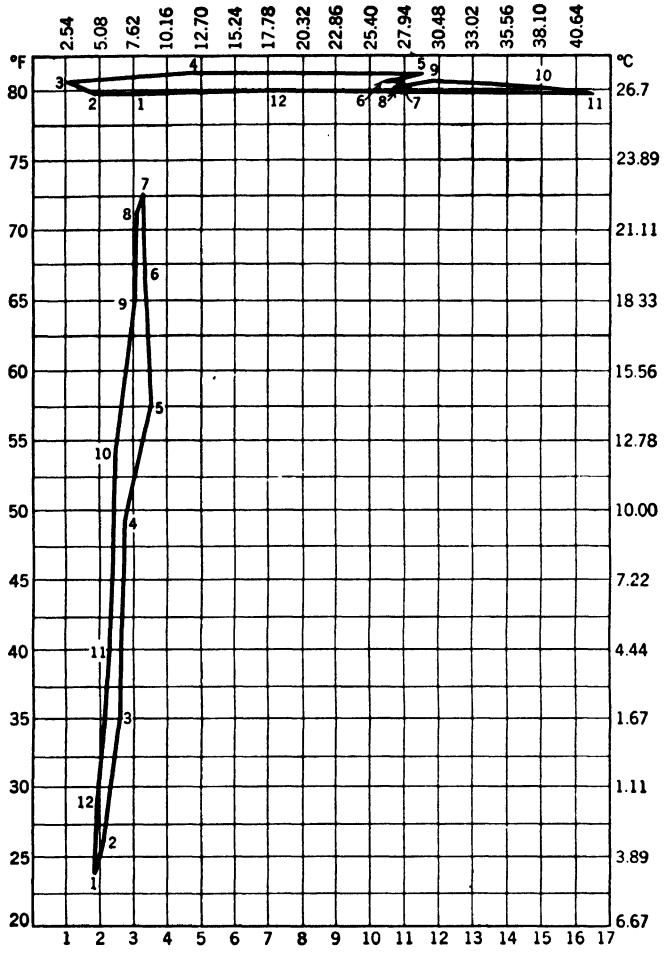


FIG. 1. Graphs showing mean monthly rainfall and temperature for a temperate climate (lower), and for a tropical climate with wet and dry seasons (upper). Temperature is given on the vertical, and rainfall on the horizontal, scale.

on data from Barro Colorado Island in the Canal Zone in Panama. The lower graph extends along the temperature axis with only slight monthly changes in rainfall; it summarizes these two elements of the climate in Chicago.

Light

In contrast with green plants, animals are not directly dependent on light for their food. Many, such as cave dwellers or animals of the oceanic depths, spend their entire life in darkness. At a depth in the sea no greater than 1700 m., a photographic plate remains unchanged after hours of exposure. Arthropods and mollusks, fishes and amphibians, as well as simpler forms of life, are found among the dark-tolerant, photonegative animals. Horses in mines, maintained for years in their underground stalls, show that even the highest forms, which usually live in sunlight, can dispense with light. This is by no means the general rule. Frog's eggs do not develop normally if sunlight is excluded. Gilbert [14] has shown that the green algae found within the egg envelopes of the eggs of certain salamanders appear to have a fixed and perhaps symbiotic relation with the eggs with at least some indication that the presence of the algae accelerates the rate of development of the embryos. Salmon eggs hatch more quickly, and salmon fry are more active, in the light than in darkness, but they grow more slowly.[40] *Mytilus* grows more rapidly in darkness,[17] and light is definitely more injurious to marine plankton from considerable depths than to that from the surface.[18] Absence of light slows up the development of insect larvae that normally live in light, and the presence of light retards the development of insects normally living in darkness.[6]

Ultra-violet radiation reaches the earth's surface in the shorter wave lengths extending about 1000 Ångström units (Å) beyond visible violet. The final atmospheric cutoff for the earth's surface, even under most favorable conditions, comes at about 2900 Å; usually the cutoff occurs nearer the visible violet. Viruses, bacteria, fungal spores, and many microscopic animals, given sufficient exposure, are killed by the ultra-violet radiation of sunlight. These radiations are also important in the synthesis of certain vitamins such as the antirhachitic vitamin D.[3] Knowledge in this field is increasing rapidly.

Experience with short wave lengths for the human skin proves that too much light may be harmful to animal tissues. Pigment layers at the surface of the skin afford effective protection against light. This seems to be the meaning of the dark coloration of animals of high mountains and at times in deserts where there is little protection from the sun's rays. The death of desert reptiles following exposure to the overhead sun appears to be the result of overheating from radiant solar heat and not a direct effect of light.[11,28]

Oxygen and carbon dioxide

Oxygen is of primary importance to life, although a few animals that are able to supply themselves with energy by the decomposition of a rich food supply can live without it; certain annelid worms, fly larvae, and internal parasites are good examples. The ability to live without free oxygen, therefore, scarcely affects the problems of animal distribution except among parasites and in stagnant or polluted waters. Though oxygen is nearly everywhere available, there is a much more abundant supply in air than in water, an important fact for the explanation of the differences between water- and air-breathing animals. Oxygen is absent, or nearly so, in a few aquatic situations. In the depths of the Black Sea and in many Norwegian fiords that are closed by a bar, the evolution of hydrogen sulphide has combined all the available oxygen. In the intermediate depths of tropical seas, where the vertical circulation is very weak, poverty in this gas is the rule. Many fresh-water lakes are without oxygen in their depths in summer. On account of the putrefaction in sewage, the oxygen is often used up in rivers below large cities. The Thames, whose waters contain 7.4 cc. of oxygen per liter above London, has only 0.25 cc. per liter below the city. Only a few animals are able to persist in such situations; these are forms that can reduce their oxygen requirements. Most animals have a large oxygen requirement with a narrow range of variation; these include all air-breathers. In nature there is rarely too much oxygen for animal life, but that given off by aquatic plants has been found to be toxic to certain insect larvae.[26]

In fumaroles, where carbon dioxide escapes from the earth, it may displace the air near the ground on account of its greater density; the Grotto del Cane at Pozzuoli is an instance; the death valley on the Dieng plateau in Java, is another.[30] Such places are closed to animal life. The bodies of small birds and mammals (finches and mice) that have wandered into the carbon dioxide atmosphere are frequently found at the Mofetten on the eastern shore of Lake Laach near Coblenz. The amount of carbon dioxide present in water is apparently an important factor in the distribution of aquatic animals and is associated with the hydrogen-ion concentration (pH) of the water. In the sea and in the deeper lake waters, there is usually an inverse relation between the amount of oxygen and of carbon dioxide present. Fishes avoid waters with a high carbon dioxide tension more actively than they do water deficient in oxygen. The ability of fishes to utilize

oxygen when present in small amounts is decreased with the higher hydrogen-ion concentrations, but in general we may safely conclude that the importance of this factor (*p*H) acting alone has been overemphasized.[2,3] (See also bog waters, Chapter 19, and soil acidity, Chapter 20.)

Pressure

For land animals variation in atmospheric pressure is not an important environmental factor except in mountainous regions, and there the effects of high altitudes are associated rather with oxygen deficiency than with decreased total pressure. For aquatic animals the pressure increases one atmosphere for every 10 m. depth. Even so, surface fishes with the air bladder empty may be subjected to a pressure of 100 atmospheres without harm. This means that under these conditions they can range through the upper 1000 m. without injury. If the air bladder is full, gases enter the blood under the higher pressures. Then, if pressure is suddenly removed, gas accumulates in the blood, causing gas-bubble disease and death. Deep-sea fishes without air bladders may live normally under a pressure of more than 800, and perhaps at 1000, atmospheres. Marine and lake fishes are known to have limitations in their vertical ranges, and these are determined in part by the prevailing pressures.[37,41,42]

Food

Finally, a sufficient amount of organic food is an indispensable condition for the habitability of an area for animals.

The amount of available food is usually the deciding factor for density of life, i.e., for the number of individuals in a given area. In years when there is a richer development of zoöplankton in the English Channel there is a larger mackerel catch.[11] The planting of kale, cauliflower, turnips, and other vegetables in New Zealand was followed by a disconcerting increase in the native insects.[20] In years when mice are abundant, buzzards, owls, and other predators gather in the mouse-infested areas (see Fig. 13). Larger predatory animals are unable to live on small islands, as they cannot find prey in sufficient quantity.

Many animals are not particular about their food and have a large menu; they are euryphagous or omnivorous. The useful contrast between the terms carnivorous and herbivorous may be lost in the various transitional stages leading to the completely omnivorous habit.

Crows and bears are omnivorous. Both carnivory and herbivory may be narrowly specialized or have a wide range; i.e., there may be euryphagous and stenophagous carnivores and euryphagous and stenophagous herbivores. The migratory grasshoppers and some caterpillars are euryphagous herbivores; stenophagous forms are represented by the caterpillars of many Lepidoptera, such as the Apollo butterfly *Parnassius apollo,* which feeds only on plants of the genus *Sedum;* the larva of the zebra swallowtail butterfly, which feeds only upon pawpaw; and the oleander sphinx *Sphinx nerii.* Other insects are limited to related host species such as potato and jimson weed, sometimes sharply to the species of a single genus or other higher category.[27] Euryphagy is general among carnivores, but various insect-eating types tend toward stenophagy, as in the ant- and termite-eating *Myrmecophaga* and *Manis.* Stenophagy tends to limit distribution, euryphagy to extend it. The bird called the nutcracker is limited in Siberia by the occurrence of the nut pine, while the omnivorous raven ranges almost from pole to equator. The distribution of the green sea urchin coincides with that of the hydroids that constitute its principal food.[39] The euphorbia sphinx would have a much wider distribution if its caterpillar were not so strictly limited to a single genus of plants; it was unknown at Göttingen until *Euphorbia* was planted in the Botanical Garden, when it appeared almost at once.[35] Because the snail *Helix aspersa* is euryphagous it has been able to accompany man over the greater part of the earth. The wide distribution of most predatory mammals may be attributed to their euryphagy.

Some plants are protected against being consumed by animals. The mosses and ferns are little eaten; a few snails and insects feed upon them, and a few birds may be driven to eat them in times of famine.[21] Islands with a flora primarily of ferns accordingly have a strikingly poor fauna. Most plants, however, are eaten by animals, and they form the foundation of the food supply of animals, in water as well as on land. The flesh-eaters are thus indirectly dependent upon the plant world, the lion that eats a calf equally with the fly that sucks the calf's blood.

Animals are not restricted in their distribution to the areas where green plants are found. It is sufficient if organic matter reaches their habitat; they may thus occur in caves, in the earth, in ground waters, and in the depths of the sea. If sufficient organic matter (always, in the last analysis, of plant origin) reaches these situations, animals may be abundant in them.

Ecological valence

Animal life is not tied hard and fast to unalterable values of the conditioning factors. Each factor has a specific range, lying between an upper and a lower limiting value. The amplitude of the range of the conditions of life, within which an animal is able to exist, may be designated as the *ecological valence* of the animal. When the limits for the greatest possible number of single factors are widely separated, the species can live in various habitats; when close together, it will be limited to one or a few types of environment. The former have a large, the latter a small, ecological valence. The snail, *Galba truncatula,* which is both eurythermal and euryhaline, or the tiger, which is eurythermal and a euryphagous carnivore, are such adaptable forms. In contrast with these the oleander sphinx, which is stenothermal and stenophagous, is limited in habitat. Species that can adapt themselves to varied environments can naturally be widely distributed. In a few extreme cases animals may be ubiquitous. Habitat-limited species, on the contrary, are specialists and do not appear in many environments. It is entirely compatible with this fact that such species may occur everywhere on the earth where their habitat requirements are found, like the salt-resistant crustaceans of the genus *Artemia* in strongly salt inland waters.

The law of the minimum

The basic habitat requirements together condition the distribution of animals, but the deciding factors are those most subject to variation. Light and oxygen are wanting at relatively few places, but temperature, humidity, and food and water supply vary in a much greater degree, and these factors accordingly are the most important causes of the variation in animal distribution. Liebig found that in the growth of plants the food element least plentiful in proportion to the plants' needs limits their growth. This is Liebig's "Law of the Minimum." This rule may be extended in a similar sense to cover the effect of the environment upon animals since that factor for which a species has the narrowest range of adaptability limits its existence. In other words, the selection of animals in a given environment is determined by the habitat factor that most approaches the minimum. The more closely even a single factor approaches a limiting value, the fewer is the number of species in the situation in question. There may be sufficient oxygen, favorable temperature, and abundant food in a salt pond, but the high salt content permits the

existence of only a few euryhaline animals. A polluted body of water may have a superabundance of food and optimum temperature, but the low oxygen content limits the animals to a few forms such as some Protozoa and the oligochaete *Tubifex*.

Hudson Bay furnishes a striking example of temperature as a limiting factor. All the waters of the bay except a shallow surface layer have a temperature below 1.8° C., even in summer. It supports no commercial fisheries although it lies in the latitude of Iceland, which has notable ones. A fishing expedition in the eighteenth century, with experienced fishermen from Spitzbergen, obtained three fishes with an expenditure of £20,000! [19]

There is another application of ecological valence to the distribution of animals, an extension of the law of the minimum. The continued presence of an animal in an environment depends on that developmental stage in which it has the least adaptability. For example, the lobster *Homarus* does not pass the latitude of the Lofoten Islands on the Norwegian coast because the postembryonic development of the larvae demands an average temperature of 15–16°, which is not reached by the arctic waters; neither the eggs, the segmentation stages, nor the adults are injured by low temperature.[4]

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3. *The Effect of Environmental Selection on Animal Distribution*

THE FACTORS THAT CONDITION ANIMAL EXISTENCE ARE FAVORABLE IN varying degrees at different places on the earth's surface. The most favorable environment of all is afforded by many littoral areas of tropical seas. There the salt content is subject to little variation; the temperature is nearly constant at about 25°, with an annual variation of only 2.3°; and abundant food supply is brought in from the land. The fauna of these seas is richer in variety of form and color than anywhere else. All the phyla of the animal kingdom are represented; unfavorable conditions requiring special adaptations are relatively few; and rank growth with a high tendency to variation combined with the severe struggle for existence between different animals has produced the greatest amount of differentiation. These optimum physiochemical conditions for animal life may be compared with those afforded to the embryos of birds and mammals, which develop in the brooded egg or in the uterus at a constant and most favorable temperature, in an isotonic environment, and are nourished adequately and without effort.

Wherever the environmental conditions deviate from such an optimum, become disadvantageous, and approach any limiting conditions, an impoverishment takes place in the number of major groups represented and the general diversity of the fauna. Many types of organization and many individual species are unable to withstand such deviations or to transform themselves in adaptation to them. Many groups of animals are therefore entirely absent, and others flourish less and tend less toward variation and speciation. Under the stress of conditions that urgently demand adaptation, the number of species diminishes.

Adaptations to similar environmental factors will not, in general,

be able to take many different paths. They will thus produce a certain similarity and will introduce convergent traits in the inhabitants of a given environment, even among those of diverse ancestry. Such common characteristics may result from the direct influence of external factors; for example, the lowering of the temperature results in a darkened coloration in many forms; the absence of light for cave dwellers results in a fauna of creatures without eyes, commonly without pigment, and with a resulting pale coloration. A disadvantageous environment forces common traits upon the inhabitants, and the relation between the type of habitat and the appearance of its fauna becomes more obvious.

Environmental selection of aquatic life

Changes in marine faunae are principally associated with the decrease in temperature with approach toward the poles and with the factors accompanying an increase in depth. In both cases the reduction in variety of animal life is notable. In contrast with the great variety of types of the plankton of warm waters, the arctic plankton exhibits a certain constancy of character.[1] Whereas ninety species of reef corals occur in the Hawaiian Islands,[20] only ten species of Madreporaria are found in the Bermudas, the northern limit of their range. The families of ascidians all attain their greatest number of species in the tropics; [10] the distribution of their 109 genera and of the species is shown in the following table:

	Genera			Species		
Arctic	34 of which	2 (5.9%)	endemic	103 of which	61 (59.2%)	endemic
Subarctic	60 " "	10 (16.6%)	"	432 " "	352 (81.4%)	"
Tropic	71 " "	21 (29.6%)	"	635 " "	563 (88.6%)	"
Subantarctic	49 " "	7 (14.3%)	"	219 " "	173 (79.0%)	"
Antarctic	22 " "	3 (13.6%)	"	42 " "	36 (86.0%)	"

The small number of endemic genera in the Arctic and Antarctic, with a large number of endemic species, attests the effectiveness of the selective process with respect to the higher categories. The number of types that can adapt themselves to the new conditions is relatively small. The Atlantic copepods in 1900 were distributed as follows: [2]

Between Temperature Limits of	Number of Species
27.5–20.3	34
19.6–11.4	19
11.1– 0	8

Among the marine fishes of shallow coastal waters, only a few families are absent in the tropics, while a great number of families are confined to the tropics or subtropics, and a still greater number have the majority of their representatives there. Seven hundred and eighty species of fishes are reported from the coasts of Amboyna in the Moluccas, almost as many as are present in all the seas and rivers of Europe together.

The reduction in total number of species with depth is shown as follows in the *Challenger* collection: [15]

	From Depths of:						
Meters	0–183	183–915	915–1829	1829–2744	2744–3658	3658–4573	Below 4573
Number of species of animals	4400	2050	710	600	500	340	235

A similar impoverishment is caused by any sort of deviation from the optimum. Variation in the salt content of sea water has an especially important influence on marine animals. If this variation is large, great demands are made on the adaptability of the organisms concerned. They must be protected from osmotic changes in the salinity of their body fluids, either by an impenetrable surface or by the ability to eliminate excessive amounts of salt or water through their excretory organs. This form of selection is nowhere better illustrated than in salt pits, in which sea water, evaporated in successive shallow basins, is concentrated for the production of salt. In the salt pits at Bourg de Batz (Loire Inférieur), the channels that conduct the salt water to the pits contain 2 nemertines, 4 lamellibranchs, 9 snails, 6 annelids, 1 crab, and 9 amphipods and isopods; the first evaporation basins contain 3 turbellarians, 3 lamellibranchs, 7 snails, 6 annelids, 1 crab, 1 shrimp, and 7 amphipods and isopods; the second series of tanks (7–8° Baumé sp. gr.) contain 1 turbellarian, 2 annelids, 1 crab, 1 isopod, and 1 amphipod; in the next series of evaporation basins (17–18° Bé) only the turbellarian and one annelid remain; finally, in the salt beds (up to 27° Bé) there is only the salt-tolerant crustacean, *Artemia salina.* The number of species in the fauna is regularly decreased with increasing concentration by the continued selection of euryhaline forms.[7]

The complete elimination of a species is frequently preceded by the production of stunted forms, as in *Cardium edule, Macrostoma hystrix,* and *Nereis diversicolor.* Even *Artemia,* which is especially adapted to waters of high salinity, becomes stunted or defective as the salt content approaches limiting values. Similar phenomena may

be observed wherever the salinity of waters increases, as in salt marshes and in regions without outlet to the sea.

Parallel phenomena appear with decrease of the salinity of sea water. The Baltic offers an excellent example. The salinity decreases from 3% at the Kattegat to 0.8% in the Belt, and sinks to 0.4 and 0.3% in the Gulf of Bothnia (cf. map at the end of Chapter 15). This change has a selective and transforming effect upon the fauna. All the marine fishes, crustaceans, mollusks, and nearly all the annelids are more or less altered forms of North Atlantic species.

The reduction in number of species in such basins as the Baltic corresponds to a still greater impoverishment of the fauna of fresh waters. Leaving out of account the secondarily aquatic forms in fresh water, which have entered it from the land, i.e., all the insects, arachnids, and pulmonate snails, there is a vanishing remnant of originally aquatic forms. A few coelenterates, a small family of sponges, a few turbellarians, annelids, and bryozoans, and a relatively small number of genera of clams and prosobranchiate snails enter fresh water. Fresh-water fishes, protozoans (especially ciliates), rotifers, and gastrotrichs have found the fresh-water environment favorable. Even the fresh-water fishes, however, are far behind the coastal marine fishes in number of species. A modern estimate (Carl L. Hubbs, in lit.) reckons about 30,000 marine and 10,000 fresh-water species.

The size of shad of the lakes of north Italy shows that fresh water is less favorable than that of the ocean. The two forms in the Tessin Lakes are known to the fishermen as the cheppia and the agon. The cheppia (*Alosa finta*) is a migratory fish going up to the lakes to spawn, but otherwise marine. The agon (*Alosa finta* var. *lacustris*) has become permanently resident in the lakes. The cheppia reaches 45 cm., the agon usually only 25 cm.[6]

In fresh waters, the optimum temperatures of the tropics have the same effect as in the seas. Using Günther's figures, the Ganges with the Brahmaputra, draining 1,750,000 sq. km., has 170 species of fishes, while the Mackenzie, draining 1,500,000 sq. km., has about 23. The Indus with 113 species compares with the Saskatchewan with 22, with approximately equal basins. The Nile may be compared with the Obi, both with drainage areas of about 3,000,000 sq. km., the former with 101 species, the latter with 45.[8]

Increase of temperature above the optimum impoverishes the fresh-water fauna in the same way as does decrease.

Additions to the water such as carbon dioxide, humus acids, hydrogen sulphide, iron oxide, etc., require special adaptations and thereby

react selectively upon the fauna. Only a few fishes, such as *Gasterosteus, Cobitis,* and *Tinca,* live in bog waters, rich in humus acids. The carp find these waters less favorable, and pike and trout avoid them. Rotifers, on the other hand, flourish in such water. Of the 186 species of rotifers in Galicia, 100 may be found in bog waters. Admixture of hydrogen sulphide, as in Ritom Lake, Canton Tessin, reduces the number of species. Lakes very rich in iron, in New Caledonia, are inhabited by a fauna dwarfed by the severe habitat conditions; a small fish of the genus *Galaxias,* tiny crustaceans, small snails, and worms are to be found.[17]

Environmental selection of land animals

Terrestrial animal life is also impoverished as compared with marine life, not in number of species or genera and certainly not in the numbers of individuals of special forms, but in types of organization. The number of terrestrial species greatly exceeds those living in water. The great majority of insects are terrestrial, and these alone compose three-fourths of the known species of animals (about a million described forms [16]). The myriapods, arachnids, land snails, land crustaceans, and the reptiles, birds, and mammals, in addition, raise the number of land animals probably to at least four-fifths of the total. In spite of this fact, terrestrial animal life exhibits an impoverishment in wealth and variety of structural types. Not one of the animal phyla is absent in the ocean (even if the Gastrotricha are regarded as of this rank), while protozoans, sponges, coelenterates, ctenophores, nemertians, bryozoans, and echinoderms, and many subphyla are entirely absent among the air-breathers. A still greater number of classes are absent, whereas the only prominent classes entirely absent in the sea are the Onychophora (Peripatus), myriapods, and amphibians.

It is the general rule for air-breathers that their development is favored by sufficient humidity, relatively constant temperature, and abundance of light and food. These conditions are found in optimum combination in the openings in tropical forests like those of the Amazon, the Congo, or of New Guinea. Decrease of moisture and temperature, and especially great fluctuations of these conditions, constantly demand adaptation. As in aquatic habitats, animal life is least abundant on land where the habitat conditions approach the limiting values, as in high mountains, toward the poles, in steppes, or in deserts. The number of species of insects in India is 40,000; [12] Greenland (half as large) has only 599.[11] The number of species of animals decreases

steadily with increasing altitude on the mountains. The size of species that range from the lowlands to the tops of mountains often decreases with altitude. In the tropics and subtropics the average size of cold-blooded terrestrial animals is larger than in the temperate and cold zones. Warm-blooded animals (cf. Chapter 20) exhibit the opposite relation. This size relation applies to ancient as well as to modern groups, whether of insects, myriapods, arachnids, snails, amphibians, or reptiles.[9]

Caves, on account of their relatively low temperature and the absence of light and plant food, support only a restricted fauna, poor in species and individuals, which are reduced in size. They live by eating flesh or fungi, or matter originating outside the caves.

In some places the selective action of the environment leaves species with special powers of adaptation unchanged in their new habitat, or changes them only to a slight degree, into dwarfed forms or phenotypic varieties. For the most part, however, the inhabitants of unfavorable environments are so changed by their physiological and structural adaptations that they are recognized as new species or even as new genera and families. The indirect selective influence of the physical environment upon the transformation of species is extremely effective. Physical factors do not seem to have been the cause of the development of the primary divisions of the animal kingdom, which apparently developed in the same rather uniform environment, i.e., in the lighted zone of the sea. The three principal groups of terrestrial animals, the mollusks, arthropods, and vertebrates, all have representatives in the sea.

The number of species, however, seems to depend on the variety of habitat conditions and on the adaptations required by them and on opportunities for isolation. The herring of the coast, which is subjected to diverse habitat conditions, is much more variable than the oceanic herring that keeps to the open sea except for spawning.

The uniformity of conditions presented by the African grasslands south of the Sahara results in extraordinarily wide ranges of various species of mammals, birds, reptiles, and amphibians; this area may be stated as "Senegal to East Africa and the Cape of Good Hope, exclusive of the rain-forest."[18] Wide ranges throughout the Amazonian and African rain-forests are also the rule. Varied mountainous topography tends to the development of a more varied fauna, often with limited ranges, notably exemplified in the plethodont salamanders of the Appalachian Mountains.[1] Formosa, with a north-south axial mountain range 4000 meters in height, with wooded mountain slopes

and ravines, and coastal plains, is remarkable for the range of its climatic conditions and for a fauna rich in number of species. According to Wallace,[22] it has almost as many species of birds (128) and mammals (35) as Japan (165 birds and 40 mammals).

Adaptive selection

The necessity for definite adaptations acts upon the fauna like a sieve of definite mesh, allowing only more or less similar forms to pass. Thus arise the common characters of animals living under similar conditions, which are the more striking the more closely the environmental conditions approach limiting values. Accordingly, characters common to a fauna are most notable in deserts, in the polar regions, and in inhabitants of temporary pools. Such common traits are difficult to discover in animals of large bodies of water or in the terrestrial animals of temperate zones. In the tropical seas, where optimum conditions reign, such adaptations to the environment are less and less important and are restricted to special habitat conditions, like the floating arrangements of plankton or the adhesive apparatus of the inhabitants of surf-beaten rocks.

Another interesting mutual relation may be explained by means of the factors that condition the wealth of form in a given environment. Where the number of morphologic types is greater, the struggle for existence between the different species of animals will be much more violent than in areas where the fauna is poorer in representatives of diverse structure. In the former case (e.g., in the tropics) there is much more severe competition for the same goal, and the opportunities to get the better of a competitor are much more numerous. Even predatory animals are compelled to protect themselves against enemies of many kinds, and he who escapes Charybdis falls into the jaws of Scylla. Where the struggle with the physical forces of nature becomes more severe, the struggle for existence between animal competitors is reduced, as a result of the reduction in number of types. This is true in fresh water, in the steppes, in deserts, and in the polar regions.

Many animals are able to maintain themselves in physically unfavorable environments after they have given way elsewhere to more modern competitors. Thus the last representatives of the lungfishes persist in fresh water. So do the ganoids, some of which are completely restricted to fresh waters, while others, like the sturgeons, repair to them to spawn. Among the bony fishes the more primitive soft-rayed forms, in competition with the spiny-rayed Acanthopter-

ygii, have maintained themselves everywhere under more adverse environmental conditions, as in the North, in the oceanic depths, and in fresh water, where four-fifths of the physostome species are found.

Although the persistence of some species under increasingly adverse conditions may produce degeneration, as in *Nereis diversicolor* in saline springs or in some protozoans in hot springs, these cases are exceptional. In general, adaptation to an environment enables an animal to flourish under changed conditions that are unfavorable for unadapted animals. Low temperatures are necessary for stenothermal cold-tolerant animals like *Planaria alpina* or the trout.

There are also broad adaptations resulting in increased bodily resistance to adverse environmental factors. *Nereis diversicolor* persists not only in very saline waters but also in almost fresh waters, and *Galba truncatula* occurs in both glacial streams and hot springs.

Numbers of species and of individuals

However the adaptation to adverse conditions may have been reached, the number of competitors for the food supply will be reduced in the new environment, and when a sufficient food supply is available the numbers of individuals of the few adapted species may become enormous. Thus in regions equally well supplied with food, of which one has other environmental conditions favorable and the other unfavorable, the number of individuals of the species will be in inverse proportion to the number of the species present. The brackish-water fauna is characterized by the presence of few species, often of reduced size, but with enormous numbers of individuals.[14] An intensively and scientifically managed fish pond, which is annually drained, plowed, manured, and freed of large plants, is unproductive for a collector, for whom a neglected pond is a rich source of supply of invertebrate forms. For the fish culturist, the unproductiveness in species is more than compensated by the enormous number of individuals of the few flagellates, rotifers, cladocerans, and cyclops that do persist. In salt waters inhabited by *Artemia,* this crustacean is often the only animal of considerable size, perhaps accompanied by the larvae of the brine fly *Ephydra.* The number of individuals in such waters may be so great that the water is a thick broth of *Artemia.* In the tropics the favorable conditions (combined with the intensity of the competitive struggle) permit almost unlimited speciation, but the individuals of many species may not be abundant. During one night in Borneo, Wallace [21] collected 158 specimens of moths, which belonged to 120 different species. Koningsberger [13] states that in Java,

by collecting on the flowers and shrubs of cultivated districts, 100 species of spiders with one specimen each are more easily secured than 100 specimens of a single species. Whitehead [23] never saw the well-known birds of Borneo in numbers and secured only one specimen of many species, though the number of Bornean bird species is almost equal to that of Europe, which is 13 times as large.[3a] The

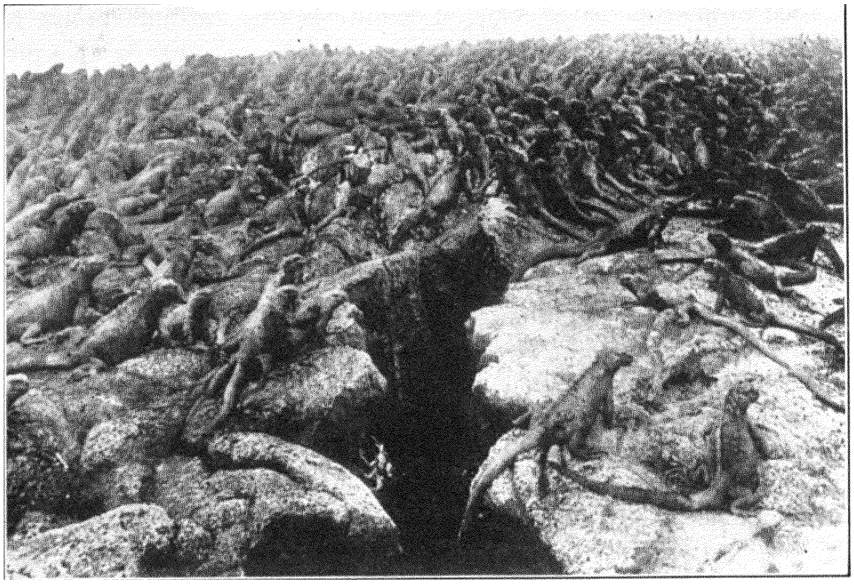


FIG. 2. Aggregation of marine iguanas, *Amblyrhynchus cristatus*, on the coast of Narborough Island, Galapagos Islands. Photo by R. H. Beck. Courtesy of the California Academy of Sciences.

countless numbers of bison that dominated the plains of North America may be contrasted with the great numbers of species of antelopes on the savannas of South Africa, each of which is represented by smaller numbers of individuals. Herbivorous reptiles are not numerous, but of the Galapagos Islands, where they do not suffer from mammalian competition and where the total number of vertebrate species is low, Darwin wrote: "The species are not numerous, but the numbers of individuals of each species are extraordinarily great . . . when we remember the well-beaten paths made by the thousands of large tortoises—the many turtles—the great warrens of terrestrial *Amblyrhynchus* (= *Conolophus*)—and the groups of the marine species basking on the coast-rocks of every island—we must admit that there is no other quarter of the world where this order

replaces the herbivorous mammalia in so remarkable a manner."[3] Similar examples could be increased indefinitely. It must be remembered that a large number of individuals is a correlative of a small number of species only when the conditions of food supply are especially favorable. Thus the number of species of butterflies in New Zealand is only about a dozen, with no especial abundance of specimens.[19]

The relations of numbers of individuals and numbers of species in the tropics may be obscured by the availability of cover. Alfred Emerson, during a six months' stay on Barro Colorado Island, observed only a single specimen of the fer-de-lance (*Trimeresurus atrox*), but a collection from forested Darien made in the course of land-clearing operations produced no less than 407 specimens in 5 years. Analysis of such mass collections of snakes from various parts of Panama by Dunn [5] exhibits proportions of abundant and rare species not very different from those in a collection from a temperate region; about one-tenth of the species make up half of the individuals. On the other hand, the species represented by few individuals are so numerous that one-half of his total list makes up less than a tenth of the individuals.

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4. *Classification of Animals According to the Most General Characteristics of the Environment*

THE OLDEST ATTEMPTS TO CLASSIFY ANIMALS, AS IN THE BIBLICAL ACcount of the creation, are based upon their habitat. Pliny in the first century A.D. divided animals into Aquatilia, Terrestria, and Volatilia. An ecological classification has its justification, independent of morphological taxonomy, in view of the obvious structural adaptations involved. A primary division of an ecological classification of animals separates them into air-breathing and water-breathing forms; internal parasites, whose conditions of life somewhat resemble those of aquatic animals, will not be discussed here in detail.

Another environmental classification is into terrestrial and aquatic animals. All animals whose bodies are surrounded by air, and not water, are in this sense terrestrial; i.e., not only the animals living on the earth's surface, but also the subterranean and wood-boring forms, and the flying groups (insects, birds, and bats), all of which are subjected to the influence of the air with its low density, high oxygen content, and varying humidity. It must be admitted that there are various intermediates between these two groups. Aquatic animals, in a broad sense, include numerous air-breathing types. Frogs in the northern hemisphere are air-breathers in summer but strictly aquatic during their winter hibernation. Many newts are aquatic in summer and hibernate on land. The common earthworms may be entirely immersed in water in the event of continued rains, and some earthworm genera, *Allurus* for example, are true aquatic animals.

The primarily aquatic forms, whose ancestors have always lived in water, are sharply distinguished from secondarily aquatic animals, which have re-entered the water from the land. These preserve

numerous characteristics associated with terrestrial life, in addition to air breathing, as an unmistakable record of their racial history. The primarily aquatic animals, with which we are immediately concerned, obtain their oxygen from the dissolved supply in the water. All are poikilothermal. The greater density of the aqueous medium helps to support their bodies and thus makes it possible to dispense with or to lighten special supporting structures. There are no other positive characters common to all aquatic animals, for all types of structure are represented in the water. Animals with gelatinous bodies permeated with water, Mycetozoa excepted, occur only in water, and such forms are found among the most diverse groups: medusae, ctenophores, worms (*Alciope*) and their larvae, Heteropoda among mollusks, salpae and eel-larvae (*Leptocephalus*) among the chordates. Free-feeding (i.e., non-parasitic) sessile animals are mostly confined to the aquatic habitat, for their food supply consists of suspended organisms brought to them by currents, and they are thus able to dispense with locomotion in search of food.[11] Ant-lion larvae, among terrestrial forms, illustrate an approach to sessile feeding habits. Aside from the arrangements for breathing the oxygen dissolved in water, there are fewer limitations to the organization of aquatic animals as compared with terrestrial forms.

Marine animals

Most groups of animals reach their maximum size in the sea. The giant squids attain a body length of 6 m. with arms of 11 m.; *Tridacna*, with a greatest diameter of 2 m. and a weight of 200 kg., is the giant among bivalves; among arthropods the Japanese crab (*Kaempfferia kaempfferi*) has a limb spread of more than 3 m.; the whale-shark, 10 m. or more in length, represents the maximum for fishes, while the blue whale (*Balaenoptera musculus*) is the largest of living mammals. The unbroken connection of the oceans and the continuous diffusion of the sea water by means of currents, tides, and storms effect a general equality in the composition and amount of the substances dissolved in sea water. Considerable variations occur only in limited areas. This widespread uniformity of conditions is accompanied by an extremely wide distribution of many marine species of animals.

Since the body fluids of marine invertebrates [13] and of sharks are approximately isotonic with the sea water in which they live, special protective structures to prevent the osmotic exchange of substances, by which the concentration of the body fluids might be altered, are not required at the exposed surfaces such as the skin, gills, and mucous

membranes of the gut. Invertebrates in the Mediterranean accordingly have a somewhat higher degree of salinity of blood than those of the Atlantic and North Sea. In the sharks and their allies this osmotic balance between the blood and the surrounding medium is maintained by the admixture of a considerable amount of urea (2–3%) to the body fluids, which have a lower salt content than sea water. In contrast, the bony fishes have a much lower molecular concentration in their body fluids than does sea water, and they maintain osmotic balance by actively drinking sea water and eliminating excess salts. In this respect fishes are independent of the sea water.

Fresh-water animals

The primarily aquatic fresh-water animals are without doubt derived from marine ancestors and must be supposed to have inherited from them a similar molecular concentration of their body fluids. As a matter of fact, among such fresh-water invertebrates as the pond clam *Anodonta* and the crayfish *Potamobius*, the body fluids have a higher osmotic pressure than that of the water in which they live, although not as high as that of sea water. In *Anodonta* these fluids contain ten times as much dissolved material as the surrounding water. A continuous stream of water must therefore diffuse through the semipermeable body membranes, diluting the body fluids, swelling the body, and interfering with the normal functioning of the protoplasm. To enable fresh-water animals to exist, there must be devices that prevent the entrance of water, membranes that have a capacity for change in permeability, or excretory organs that are capable of excreting the water as fast as it enters.

Capacity of the skin to adjust its permeability with respect to the surrounding medium is an anti-osmotic adaptation in some euryhaline animals.[1] In addition to such permeability changes of the epidermis, a mucous covering of the surface of many aquatic forms, such as the snails and fishes, probably protects them against the entry of water. This is the meaning of the gelatinous covering of buds of aquatic plants.[37] The diatom *Thalassiosira* has a mucilaginous covering that protects it against the varying salt content in the water. The removal of slime from the skin of an eel causes the osmotic pressure of its blood serum to vary with changes in the osmotic pressure of the surrounding water more than it does in a normal eel. The mucous coat forms an effective barrier to prevent the exchange of water between the outer and inner media.[28]

Among secondarily aquatic animals, insects and arachnids with

their exoskeleton, and whales and seals with their horny epidermis, have a protection against the influx of water through the body surface, acquired during the terrestrial life of their ancestors.

Adaptation to rapid excretion of excess water is widespread. All fresh-water Protozoa have one or more contractile vacuoles, which constantly discharge water from the body. At 20° C. a paramecium excretes almost five times its own volume of water in an hour. Marine and parasitic protozoans, which live in a medium isotonic with their body fluid, have no contractile vacuoles. Complete proof that the contractile vacuole counteracts the osmotic influx of water is furnished by experiment. If a fresh-water amoeba is introduced into sea water by gradual increases in salinity, it will continue to live, but its contractile vacuole ceases to function and ultimately disappears.[44] Increase in the molecular concentration of the surrounding water slows down the contraction rhythm of the vacuole and lessens the amount of water pumped out. At about 20° C. the following relations exist: [18]

% NaCl in water	0	0.25	0.5	0.75	1.00
Contraction period in seconds	6.2	9.3	18.4	24.8	163.0
Excretion per hour in body volumes	4.8	2.82	1.38	1.08	0.16

In Metazoa the kidneys play the same rôle in removing water taken in by osmosis. In cercaria parasitic in *Galba*—i.e., from snail blood, an isotonic medium—it is usually difficult to recognize the bladder on account of its small extent. When the animal is immersed in tap water, the Y-shaped bladder quickly becomes evident on account of its distention. This shows that the water diffused into the body is being removed by the nephridial system. Isopods, amphipods, and decapods of fresh water agree in having the antennal excretory organ larger than in their marine relatives.[32] Overton [26] has shown that water is absorbed by a frog through its skin and that about the same amount is excreted through the kidneys in a given period. No conclusive data on this subject are available for selachians or bony fishes. It appears that the ability to increase the rate of water excretion would enable a marine animal to enter fresh water, and this primary condition for adaption to fresh water is not equally at the command of all marine animals.

Such marine forms as possess the basic requirements for adaptation to life in less saline water at once find favorable opportunities in brackish water, on account of decreased competition. Relatively few brackish-water forms can make the further advance into fresh water. The relatively small number of species of primarily aquatic fresh-

water forms shows that not many animals are capable of such adaptation. A natural capacity for adaptation to fresh water seems to exist in some genera and families, and representative members have independently accomplished the transition to fresh water in widely separated regions. Examples of such groups among the bony fishes are the genus *Cottus* with its relatives; the Gobiidae; the Elopidae; and the Syngnathidae. Among the higher crustaceans the genus *Atya* (Cape Verde Islands, West Indies, Philippines, and Samoa) and the Palaemonidae (Europe, the Americas, and Africa) may be mentioned. A few important families and even orders of fishes are predominantly inhabitants of fresh waters. Homer Smith,[10] on physiological grounds, and Romer,[33] from paleontological considerations, have concluded that fishes as a whole originated in fresh waters and later invaded the oceans.

Echinoderms and tunicates are entirely absent from fresh waters. The host of sponges is represented only by the small family Spongillidae. Of the coelenterates with their wealth of forms one encounters only a few hydroids, such as *Hydra* and *Cordylophora* (the latter more commonly in brackish water up to 1.3% salinity), but like many fresh-water animals these tend to have a world-wide distribution; and there are a very few fresh-water medusae in widely scattered localities. The flatworms are relatively well represented, with rhabdocoel and triclad turbellarians, but the nemertines are very few. Rotifers and gastrotrichs are present in much greater numbers than in the sea. The fresh-water annelids include a few leeches, the somewhat uniform group of limnicolous oligochaetes (aquatic relatives of the earthworm), and a few quite isolated species of polychaetes. Bryozoa are well represented in a single family of Entoprocta; otherwise the phylum is poorly represented. Crustaceans, especially Entomostraca, form an important element in the primary fresh-water fauna. Despite the presence of these basically aquatic animals, those secondarily aquatic, such as insects, arachnids, and pulmonate snails, dominate the life of fresh water.

Marine invasions of fresh water

The immigration of marine forms into fresh water has taken place for ages and still continues.[27] Fresh-water animals whose close relationship to those in the sea indicates relatively recent entrance into the new habitat are naturally limited in their distribution. Older groups have gained wider distributions. The more or less universal fresh-water forms are usually sharply defined groups, well separated

from their marine relatives. Among such groups, with a long independent phylogenetic history, are the fresh-water sponges, the fresh-water bryozoa, and the Ostariophysi among the bony fishes (characins, gymnotids, cyprinids, and silurids). Where immigration is recent or still continuing, fresh-water groups are related to the inhabitants of the neighboring seas in various degrees. The species may occur in the ocean also; the fresh-water species may belong to genera otherwise marine; or fresh-water genera of families otherwise marine may occur in limited areas. Such relations all indicate recent immigration, ecologically speaking. The newer inhabitants of fresh water have not had time to diverge greatly from their marine relatives.

Numerous examples of regional fresh-water representatives are found among mollusks, crustaceans, and fishes. The marine genus of snails *Tectura* has a single fresh-water species, *Tectura fluminalis*, in the Irrawaddy River. The marine genus *Cerithium* is replaced in the fresh waters of India by *Brotia; Nassa* by *Canidia.*[7] Among mussels, the rock-boring *Pholas* and other marine forms occur in Trinidad 18 km. from the sea, in water entirely fresh, though still subject to tidal movement. The relations are still more evident among the decapods. In the islands of the Indian Ocean[42] only 4 out of 20 genera are confined to fresh water; *Caridina* and *Palaemon* live principally in fresh water but have species that occur in the sea and in brackish water, *Palaemon carcinus* even in all three. Finally, many marine genera * have single species in fresh water. *Palaemonetes vulgaris* is the common prawn of the Atlantic coast from Massachusetts to Florida,[29] while *P. paludosus* occurs in fresh-water streams and lakes as far west as the Chicago area.[30] Among fishes in the Indian Ocean, of 22 species of selachians occurring in fresh water, only 7 are confined to it; the rest live in the ocean as well.[12] A species of bass, *Lates calcarifer,* in southeast Asia, lives in fresh, brackish, and salt water.[14] A variety of the shad, *Alosa finta,* ascending the European streams to spawn, has established itself in the Lake of Lugano. Of the marine genera *Syngnathus, Blennius, Belone,* and others, single species are confined to fresh water.

The immigration of marine animals into fresh water continues in recent time primarily in the tropics. Of the fresh-water selachians, for example, no species is found beyond latitude 35° N. or S., and only a few beyond 30°.[12] The fresh waters about the Gulf of Bengal, the islands of the Malay Archipelago, Madagascar, and tropical America

* *Pseudograpsus, Leander, Penaeus.*

are rich in new immigrants from the surrounding seas. The small variation in temperature of tropical streams probably facilitates the entrance of marine forms. It is also possible that the tremendous rainstorms, which are frequent at certain places and seasons in the tropics, by reducing the salt content of the surface waters, help to select for euryhalinity among marine animals. Temperature may have something to do with the varying behavior of *Alosa finta.* In Scandinavia this species spawns among reefs in the sea; from the North Sea on it occasionally ascends streams to spawn; and about the Adriatic it has become in part permanently at home in fresh waters, in association with its spawning migrations. The presence of large amounts of calcium, characteristic of so-called hard waters, makes the transition to fresh water less difficult.[5,25]

Another process leading to the production of fresh-water forms is the freshening of arms of the sea that become cut off from the ocean. This may occur through changes in the strand line, as in the lakes of Finland and south Sweden, which have been separated from the sea by the rise of the land, or in the lakes of the south Russian steppe, which were left behind by the lowering of the surface of the former Sarmatian Sea. Separation of arms of the sea by tongues of land is frequent along the French Mediterranean coast and in the northern Adriatic. Stenohaline marine animals caught in such basins and thereby subjected to the influence of inflowing fresh water will be destroyed; others, however, will survive and will then remain as forms with marine relations in an association of fresh-water animals. These forms are marine relicts, and such lakes are termed relict lakes.

Lake Mogilnoje on the island of Kildin, on the Murman Coast, Lapland, is a lake of this type in process of formation.[22] Although now without visible oceanic connection, it is still so connected at greater depths by seepage water. For this reason its waters are stratified, with completely fresh water at the surface and to a depth of 6 m.; from 6 to 12 m. there is a rapid increase in salinity; and below this a uniform salt content of 32.5‰ prevails. The lower stratum is without animal life on account of the presence of hydrogen sulphide. The upper stratum contains daphnias and fresh-water copepods, with *Gammarus locusta* (an inhabitant of the marine beach) on the shore; the middle layer contains only marine animals. In 1888, this marine fauna consisted of two or three species of sponges, sea anemones, a few bryozoa, snails and other mollusks, annelids, a sea star, four or five tunicates, codfishes, and *Pycnogonum.* Ten years later a number

of the marine forms were no longer to be found alive, although their remains were still present on the bottom.[31]

Marine relicts in such lakes often become very few in number. In the lakes of southern Sweden, the only forms with marine relatives are *Mysis relicta* and *Limnocalanus macrurus.* In the lakes of the Baltic divide, only *Mysis relicta, Pontoporeia affinis,* and *Pallasiella quadrispinosa* are reported.[34] American examples include *Mysis relicta* in Lake Michigan and a nereid worm in Lake Merced near San Francisco.

The special characters that enable animals to live in fresh water, such as regulative activity of the excretory system, permeability of the body membranes, and mucous covering of the skin, are primary characters of fresh-water animals. A number of additional characteristics of animals in fresh water have probably arisen through the direct or indirect influence of this medium on their organization and may be regarded as secondary.

The first of these secondary features is the smaller size of fresh-water animals compared with their marine allies. This applies to nearly all forms with the exception of the rotifers. Thus the hydroid polyp *Cordylophora lacustris* is smaller and has shorter stalks in fresh water than in brackish. The fresh water *Alosa* of the Italian lakes is smaller than the migratory form. The land-locked salmon of Maine and New Hampshire remains smaller and stouter than the form from which it is derived.[21] The smelt *Osmerus eperlanus* of the North and Baltic seas reaches a length of 30 cm., whereas in the Finnish lakes it grows only to 15 cm. It has been established that the growth of the salmon, in comparison with that of the brook trout, is notably accelerated by its emigration to the sea [8] (Fig. 3). In the bass genus *Ambassis,* all the fresh-water species are smaller than the marine.[9] The causes of this phenomenon are not yet fully known; reduction in size is connected with a departure from the optimum, but that is not an explanation.

The rule has exceptions; the lake trout from the Great Lakes and the huchen of the Danube are as large as any migratory salmonids. The Atlantic salmon *S. salar* is known to have fresh-water colonies that are merely overgrown parr, never more than a foot long; others attain a large size of 20 to 30 lb. The nature and abundance of the food is one of the principal factors responsible for these differences.[30]

Another contrasting secondary character is the decrease in the number of eggs in fresh-water animals. A notable enlargement of the eggs by yolk-masses goes hand in hand with the decrease in number, but

whether this is a cause or an effect is unknown. There are indications that fresh water checks fertility. Thus the flounder *Pleuronectes flesus*, which frequently ascends the European rivers, does not become sexually mature in them. A number of fishes—*Cottus bubalis* and *Gobius niger*, for example—entering the eastern Baltic from the North Sea do not spawn there.[24] The oyster plantations of the river mouths

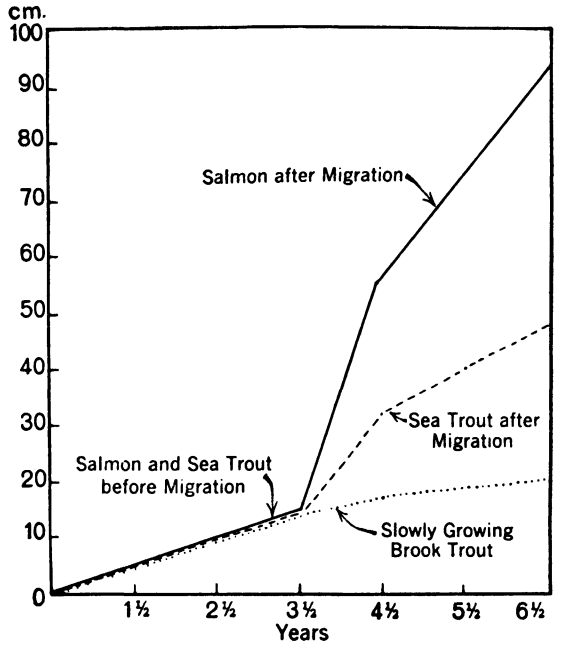


FIG. 3. Growth curves of Atlantic salmon S. *salar*, salmon trout S. *trutta*, and European trout S. *fario*. After Dahl.

of the west coast of France would die out if they were not constantly replenished with spawn from salt water. The brackish-water polyp *Cordylophora lacustris* in fresh water suffers a decrease in the number of gonophores and an approximate halving of the number of eggs in each gonophore.[38]

The fact that egg size increases in fresh water is especially evident in species that also occur in brackish water and in the sea. The small crustacean *Palaemonetes varians* in specimens of equal size (4 cm. length), has 321 eggs, of little over 0.5-mm. diameter, in salt water, and only 25 eggs of 1.5-mm. diameter in fresh water. The egg size is in the proportion of 1:27, and in total mass the fresh-water

form has produced twice as much of egg material as the marine, so that the small number of eggs cannot in this case be a result of general degeneration. In most fishes common to the North Sea and the Baltic, the egg size increases with reduction of salinity of the water; for example, in the flounder *Pleuronectes platessa:*

Salt content	19.45	17.3	15.68‰
Egg diameter	1.876	1.901	1.953 mm.

In the Baltic starfish, *Motella cimbria,* the slight increase in size in the fresher water suggests a mere swelling of the eggs in the weaker salt solution.

The abundance of yolk in fresher waters has the result that the young animals hatch at a more advanced stage, and a free-swimming larval stage is thus suppressed to a greater or lesser degree. In *Palaemonetes varians,* the young zoëa larvae are slender and 4 mm. long at hatching in the marine representatives, and stout and 5.5 mm. long in fresh water.[4] The herring in Schleswig hatches in a noticeably more advanced state in brackish than in salt water.[17] Among fresh-water forms free-swimming larvae are present in the triangle mussel, *Dreissena polymorpha,* and in copepods and polyphemid Cladocera.

Another explanation for the absence of larvae in so many fresh-water animals has been advanced by Sollas. He believes that free-swimming larvae, which are capable of only weak active movements, would always be carried to the ocean by the current of streams that they tried to enter, and that therefore only animals without such larvae, i.e., with large-yolked eggs and abbreviated development, would be able to enter rivers from the sea. These two explanations are not incompatible. The influence of salinity on the amount of yolk simply gives a more intimate explanation of the assumption of Sollas.[11] Entry into fresh water is for the most part preceded by a sojourn in brackish water, and this would affect the eggs as above outlined. According to this supposition, the only animals that could persist in fresh water would be those whose eggs react to reduced salinity as do those of *Palaemonetes.* Animals may, however, be transported directly into fresh water, as happens with *Dreissena,* which is carried by ships; and the yolk content of the eggs of such species can have no significance for the process of acclimatization.

The eggs of fresh-water animals, like the animals themselves, require some protection against dilution and swelling by the inward diffusion of water. Marine forms may have completely naked eggs. Fresh-water animals have eggs with a dense covering, like those of

Hydra or the river crayfish; or the eggs may have a gelatinous covering, like those of snails and frogs; or their eggs may be enclosed in a thick-walled case, as in planarians.

Terrestrial animals

Terrestrial animals contrast with the aquatic forms in many ways. The total inhabitable space available for terrestrial life is much smaller than that at the disposal of aquatic forms. The surface of the oceans and inland waters combined amounts to about 361,059,000 sq. km., whereas the total land surface is only 148,892,000 sq. km. The oceans, with an average depth of 3795 m., so far as investigated, are inhabited by living organisms in one stratum above the other from bottom to surface. On land, ice and desert are nearly or quite closed to life, and as animals are unable to raise themselves permanently in the air, they are confined to a single layer, which even in favorable cases, as in tropical rain-forest, is only 25–70 m. deep. In spite of these spatial restrictions, four-fifths of the known species of animals are terrestrial.

Terrestrial life offers advantages that result in the luxuriance of such animals as are able to adapt themselves to it. The most important of these advantages is the abundance of available oxygen. Less than 7 cc. of oxygen are usually dissolved in a liter of water, whereas a liter of air contains 207 cc. Owing to the rôle played by oxygen in the release of chemical energy, this makes possible an enormously increased rate of combustion for air-breathers if a sufficient food supply is provided. Terrestrial animals accordingly live much more intensively than the primary aquatic forms. Such muscular activity as that of the wing muscles of insects, amounting to 330 contractions per second in the common housefly, is unknown among water-breathers, although extraordinary muscular efficiency is attained by the pelagic fishes.

Many different aquatic animals have at different times become partially adjusted to an air-breathing life. A few of these adjustments have led to the establishment of new and successful groups of terrestrial animals, but for the most part adaptation to air-breathing came to an early stop, without occasioning the complete transformation of the mode of life. Attempts to enter the terrestrial habitat that have met with a limited or partial success are usually confined to isolated genera or to small groups. Invertebrates of this kind are the Onychophora, many isopods and amphipods (*Orchestia*), the terrestrial hermit crabs, land leeches, and land planarians. Among vertebrates a number of fishes from various families and orders il-

lustrate this tendency, as for example *Misgurnus* (Cobitidae), *Saccobranchus* (Siluridae), the eel-like *Amphipnous*, the climbing perch *Anabas*, the mudskipper *Periophthalmus*, and all the lungfishes. The apparatus for air-breathing among these fishes is diverse. That shown by the lungfishes, consisting of a pair of diverticula of the anterior part of the alimentary canal, has proved successful; some such mechanism made possible the development of the air-breathing vertebrates from the parent stock of crossopterygian fishes. The invertebrate groups that have solved the problem of air-breathing, and have undergone a renewed evolutionary development in consequence, are the pulmonate snails among the mollusks, and the myriapods, insects, and arachnids among the arthropods.

In consequence of its low density, air offers much less resistance to motion than water, and the presence of the solid earth as a basis also favors more rapid motion than is possible for aquatic animals. In spite of the low density of the air, a number of diverse types of animals have independently acquired the power of flight. In view of the unbroken extent of the atmosphere, flight is the most perfect form of locomotion. It has been mastered by insects, reptiles (in extinct forms), mammals (bats), and birds.

Another advantage gained by adoption of the terrestrial mode of life was the enormous amount of previously unavailable plant food. Land plants, which attained a high development before the appearance of terrestrial animals, afforded a food supply for which there were at first only a few competitors. The number of herbivores among insects and myriapods, which may perhaps be regarded as the earliest terrestrial animals, is still large. Herbivorous insects include cockroaches and grasshoppers, termites, earwigs, most true bugs, many beetles and Hymenoptera, many Diptera, and most Lepidoptera. Pulmonate snails, also, are almost exclusively herbivorous. The grazers, an ecological division of snails, feed especially upon mats of algae and attached diatoms.[2] The success of the herbivores in the terrestrial habitat made possible the entrance of carnivores, such as arachnids and vertebrates, and favored the development of carnivores among insects and myriapods. The earliest tetrapod vertebrates to enter upon terrestrial life, the Amphibia, are still largely insectivorous. Herbivores appear among vertebrates at a later stage in their phylogeny, and include a few reptiles, a few birds, and a large proportion of mammals.

The advantages afforded by terrestrial life are counterbalanced by great disadvantages and dangers, which have called forth special

adaptations. The most important difficulty consists in the varying humidity of the air. Humidity reaches the maximum at only a few places and then usually only at special seasons, and is usually far below the saturation point. The humidity of the air, combined with temperature, barometric pressure, rate of wind, and amount of sunshine, conditions the rate of transpiration. Soft-skinned animals, under adverse conditions, will be subject to continued evaporation of their body fluids and finally to the drying up of the skin and the entire body. The skin is permanently injured by drying, its cells are killed, and important functions, such as skin-breathing and sensory and glandular activity, become impossible. The epithelium of the breathing apparatus is especially subject to this danger. The breathing organ must have a large but delicate surface, which will permit the rapid exchange of oxygen and carbon dioxide. Two groups of animals, the arthropods and the vertebrates, were especially suited for terrestrial life by the structure of their skin.

The aquatic arthropods have a solid armor, formed by the thickened outer layers of the skin. This armor serves primarily as a framework for the insertion of muscles, whereby the effectiveness of their action is notably increased, and secondarily as a protection. This exoskeleton overlies the outer surface of the body, which is a vital condition for an effective protection against evaporation. The echinoderms have an external armor that serves as a muscle-supporting skeleton, but in this group the armor is formed by the deposition of lime in the subepidermal layers of the skin, and it is covered outwardly by the epidermis, which is thus unprotected against drying should the animal leave the water. Thus, in spite of the existence of a skeleton, no echinoderm has become adapted to a terrestrial or air-breathing existence. The considerable protection against the drying of the skin, already developed in aquatic arthropods, would have been useless as a step toward terrestrial life without some protection to the breathing organs. A respiratory apparatus, to meet this situation most successfully, should be situated in the interior of the body. Most crustaceans, whose breathing organs take the form of thin-skinned, much-branched evaginations of the body wall, find difficulty in acquiring such protection. Crustaceans with external gills enclosed in a gill chamber by the lateral parts of the cephalothorax can survive in the air for short periods, but only under favorable conditions of humidity such as are found at the seashore, especially at night, in the tropics. Many hermit crabs and other decapods exemplify this degree of adaptation to life out of water. Those that have gone over

permanently to terrestrial life and can thereby move far away from the water, such as hermit crabs of some genera and land crabs (*Gecarcinus,* etc.), have apparatus for moistening the gills and for keeping them from sticking together in the air; or they have supplementary breathing organs, as in the cocoanut crab *Birgus latro,* which has enlarged inner surfaces of the gill chambers, with reduced gills (Fig. 4). The terrestrial isopods (Oniscoidea) are widespread, with a considerable number of genera and species. They usually occur in damp places, where the gill apparatus on the underside of the ab-

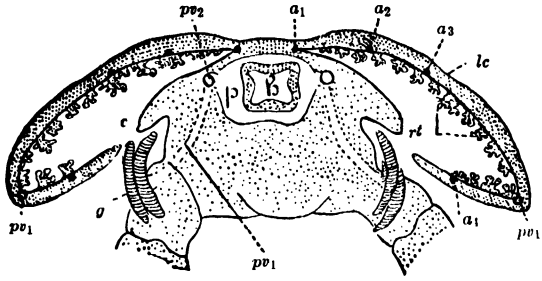


FIG. 4. Cross-section through *Birgus latro: lc,* branchial or lung cover; *h,* heart; *g,* gills; *rc,* respiratory cavity; *p,* pericardium; *eg,* branchial blood canals leading to the heart; a_1–a_4, lung or shell vessels leading from the heart; *rt,* respiratory tufts; pv_1, pulmonary vessels leading to the heart; pv_2, the same near their entrance into the pericardium. After Lang.

domen is not in danger. Among some genera of isopods, as in *Porcellio* and *Armadillidium,* an internal breathing organ, comparable with the tracheal lung of spiders, supplements the gills. The first pair of abdominal legs, which form a cover for the delicate gills, acquire an invagination in the outer skin of their terminal branches, forming a much-subdivided breathing chamber visible externally as a "white body" (Fig. 5). The second or even all five pleopods may sometimes also be so modified. Such isopods predominate in dry situations.

The protection of the breathing organs is most complete in myriapods and insects, with their tracheal systems. Independently of these, arachnids have evolved the so-called fan tracheae or tracheal lungs. A less perfect tracheal system has also made possible an air-breathing existence in moist situations for the more annelid-like *Peripatus* and its allies.

Vertebrates are protected against drying by the stratified structure of their skin, and this is already developed in fishes. In contrast with that of many invertebrate animals, the epidermis of vertebrates is

composed of successive cellular layers. The outermost of these layers undergoes adaptive changes even among fishes. The cells die off with an accompanying development of horn and form a protective covering for the remainder of the skin. In terrestrial vertebrates the number of layers of cells is increased, and the horny stratum, still single in amphibians, is formed of more numerous layers of small cells. Protection against evaporation in both terrestrial arthropods and vertebrates is based on structures already available.

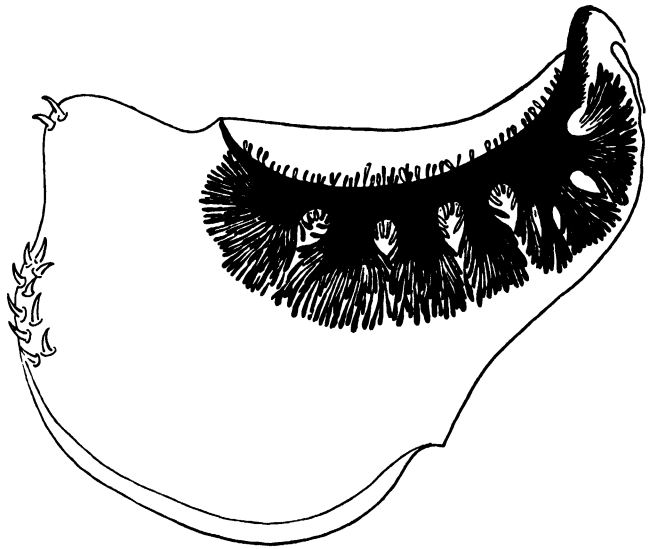


FIG. 5. Outer branch of the first abdominal appendage of the land isopod *Armadillidium nasutum*, with much divided respiratory cavity. After Herold.

Complete transition to an air-breathing existence became possible to the vertebrates, as to the invertebrates, by means of changes in the breathing apparatus. The gills of fishes, not unlike those of the higher Crustacea, afford a sufficient surface only in the water, as their branches cohere in the air. Of the various types of air-breathing organs developed among fishes, lungs proved most successful. These originate as a sac-like evagination of the anterior part of the alimentary canal, just posterior to the hindmost pair of gill clefts.

A third phylum, the Mollusca, has developed another large group of terrestrial forms, the land snails.) These are composed of two convergently developed series that are evidently separate in origin. The majority of the land snails in our zone are pulmonates, hermaphroditic forms without an operculum and sometimes, secondarily, entirely

without a shell. Toward the tropics land snails of the prosobranchiate group become progressively more numerous. These are operculate snails with separate sexes. Like the crustaceans, the aquatic gastropods possess a protective structure, the shell, as a preadaptation to protection against evaporation for the forms taking up terrestrial life. Although it is usually possible for the snail to withdraw entirely into its shell, a part of its body must be stretched forth for creeping and other activity, and this naked part of the animal is protected against evaporation primarily by a coat of mucus. Land snails are thus radically distinguished from arthropods and vertebrates, in which the entire body is covered by the protective layers.

Snails may pass through periods of drought by closing the shell with the operculum, when an operculum is present; the non-operculates may secrete a film of mucus that serves the same purpose; others adhere by means of the foot to a stone, a tree trunk, or a leaf. In dry regions snails usually come out of their shell only during the fall of dew at night or during and after rains. Land snails differ from their aquatic relatives in the position and number of their skin glands. The gland cells are superficial in the prosobranchiates, within the epidermis; in the pulmonates they are sunk deeper into the subepithelial layer and open externally only by means of narrow canals,[19] which reduces the loss of water by evaporation. Their breathing apparatus is formed by the mantle chamber, which is closed outwardly except for a relatively small opening and whose inner surface is only slightly increased by the projecting walls of the blood vessels. The breathing surface of the lung is notably smaller than that of the much-feathered gills of the marine water-breathing snails. The richer oxygen content of the air makes it possible for pulmonate snails to exist with a reduced breathing surface, but in correlation with its small extent their activity and energy development are scarcely greater than those of marine snails.

Many pulmonate snails have lost their shells in the course of their evolution, in spite of the fact that the shell forms so favorable a protection against evaporation. However, by this loss and by the smoothing out of the visceral sac, which was formerly contained in the shell, the slugs have gained a more slender form and are thus better able to avail themselves of existing retreats in which they find protection against evaporation. Their mucus (in *Limax maximus*, for example) is often tougher than in the shell-bearing snails and affords a more effective protection.

Other animals that have accomplished the transition to land life

are a few forms with incomplete protection from evaporation, such as land planarians, nematodes, earthworms, and a number of leeches.

Protection against desiccation is extremely unequal in the various groups, and their capacity for life in the air is equally variable. One may find every transition, from aquatic animals that can exist for a short time out of their native element to forms that live continuously under conditions of extreme dryness without drying out. Even though a sharp line cannot be drawn between them, it seems useful to classify air-breathers into hygric, mesic, and xeric forms on the basis of the extent of their tolerance of aridity.

Hygric animals include land planarians, earthworms, land leeches, *Peripatus,* and the air-breathing crustaceans. All these are found, with few exceptions, in situations with very humid air. They protect themselves against temporary drought by retreating into holes in the earth or beneath stones or logs or similar objects, and, in so far as they are not protected by a dermal armor, by the production of mucus in their skins. Isopods, such as *Armadillidium* and *Porcellio pictus,* that live in drier places, are less subject to evaporation on account of having fewer glands.[20] The air-breathing snails also belong to this category. They are able to come out of their shells only in moist air, but they can penetrate into relatively dry regions if the air reaches the necessary degree of humidity from time to time, as they are able to retire into their shells and close them off during the dry periods. The thicker their shell and the greater their capacity for existing in a state of suspended animation without food, the more possible it becomes for them to inhabit arid situations. Thus in Germany, *Helix* (*Xerophila*) *ericetorum* lives on dry and sun-burned slopes, and elsewhere desert snails extend as far into the steppe and desert as does the occasional deposit of dew. These animals can exist for great periods of time without sign of life, in a state of aestivation. While the German grapevine snail *Helix pomatia* can live at most a year in such a condition, steppe and desert snails, such as *Helix* (*Eremina*) *desertorum,* have been known to revive after more than four years of suspended animation.[7a]

Of the terrestrial vertebrates, the amphibia belong to the hygric group. But these, too, are insured against injury by drought by means of special adjustments that enable them to spread into dry regions with only occasional humid periods. Some are able to save up water in their bladder for times of drought. It has been noted above that frogs excrete the water taken up by their skin through their kidneys and collect it in their bladders. This water contains only very small

amounts of urea and is almost pure. Thus in the Australian deserts, when the frogs bury themselves after the close of the short rainy season, their whole body is swollen by the distended bladder, and they survive twelve and even eighteen dry months in this condition. There is a dearth of exact information about the desert toads and spadefoot toads of North America with respect to the physiological aspects of their aestivation. Xeric animals are represented on the one hand by myriapods, insects, and arachnids and on the other by reptiles, birds, and mammals. These groups are by no means excluded from existence in humid regions. Some, however, probably in consequence of specific adaptation to arid conditions, as in steppe animals like the camel, are unfavorably affected by higher humidities and amounts of rainfall. Since humid regions and situations are relatively few, the xerocoles in general have a wider distribution than the hygrocoles.

The capacity to withstand dry air without danger appears in all gradations. Many myriapods such as *Lithobius* are inadequately protected against evaporation. Many relatively soft-skinned insects avoid direct sunlight and are active only in moist air, in the twilight, at night, or after dewfall or rain. These include mayflies and stoneflies; young mole crickets, which may easily be killed by the sun's rays; mosquitoes, which swarm only in moist air and otherwise remain in hiding in places sheltered from the sun and wind; and most termites, which carry on their building activities and foraging expeditions only at night or in humid weather, as before rainstorms.[35]

Most insects are creatures of the sunlight. They are protected against loss of water by their dense body covering and have few or no skin glands. Nor does the excretion of waste require much water, as a part of the excretory products is stored in the fat-body. Finally, the tracheal breathing relieves the blood of an important function, by carrying the oxygen directly to the points of consumption, so that smaller amounts of blood can care for the distribution of nourishment and for the removal of excreta. How small the need for free water may be in insects is best shown in the forms that can live on very dry food, such as the larvae of meal worms (*Tenebrio*, see p. 16); of boring bettles (*Anobium*), which eat the dry wood of old beams and old furniture; or of the skin beetles (*Attagenus*) and clothes moths (*Tineola*), which live in wool and hair. These insects are able to use metabolic water [3] and can further conserve their water supply by excreting their nitrogenous wastes in solid rather than in liquid form. Many desert-inhabiting animals may be cryptic and nocturnal in habits, and consequently actually hygric rather than xeric.

The air-breathing vertebrates are xeric in very different degrees. Amphibia with their glandular skin protected only by a thin horny layer were characterized above as specifically hygric. They exist in even moderately dry regions only by means of special physiological and ecological adjustments. The three remaining classes, reptiles, birds, and mammals, are also diverse in this respect. Reptiles and birds are in general much better designed to withstand dryness than are most mammals. They may be contrasted as water-savers and water-spenders. Reptiles and birds have an advantage over mammals in their complete lack of skin glands, which promote evaporation. Besides this, they economize on water because their excreta are not evacuated in a dissolved state, but as crystalline uric acid; the solution waters are reabsorbed in the kidneys. The ostrich is an exception, excreting urea in solution.[6]

Mammals, by contrast, give off a good deal of water, through their skin glands and their excrement. There are great individual differences, and skin glands are very unequally developed in the various mammals. When they are present in abundance, as in men, apes, and horses, the loss of water is naturally larger than in forms in which they are nearly or entirely absent, as in most rodents and certain ruminants. Between these extremes are such forms as the hedgehog and squirrel, with skin glands sparingly scattered over the body, and the carnivores, for the most part with a small number of skin glands. A man gives off more than 1.5 liters of water per day through his skin by insensible evaporation, i.e., without noticeable perspiration. When skin glands are transformed into genuine sweat glands,[36] and thus take part in the regulation of body temperature by giving off large amounts of water, the losses of water are notably larger. In dry seasons, a man requires 5 to 8 liters of water daily; in the desert he may sweat at the rate of a liter per hour, or even three times as much.[10] At high temperatures and in dry air the lack of water for more than 24 hours may endanger the life of a man. On the other hand, many mammals can hold out for months without drinking, getting along with the water taken with their food and with the water of metabolism,[3] as do mice and porcupines, hyraces, aardvarks, and many antelopes and gazelles.

Evaporation through the lungs, concentration of the urine, and water content of the excrement are important factors in water economy, but our knowledge of them is as yet inadequate. The importance of these relations in the geographical distribution of vertebrates has not been sufficiently studied. It must be admitted that regulative

adaptation to special conditions may take place within the same species. Thus cattle, with their numerous skin glands, their saliva-dripping mouths, and their soft excrement, are great expenders of water, and as a consequence most of them live in humid regions, and many forms, such as water buffaloes, are swamp dwellers. This group of animals is little represented in steppe regions, though the bison of North America formed an exception. Domestic cattle, however, have become adapted to going without water for several days at a time in the arid peninsula of Lower California.[16]

The physical character of the air as a surrounding medium conditions certain peculiarities of structure in terrestrial animals, and certain features that were excluded by the nature of the aquatic habitat become possible.[11] On account of its low density, the air does not assist in supporting the body as the water does. This necessitates a general stiffening of supporting structures. Forms with a gelatinous body are excluded from terrestrial life, except the Mycetozoa, for which the decaying wood in which they live furnishes support. The soft-bodied terrestrial forms are compelled to rest the whole extent of their bodies on the earth, but these too are firmer in structure than their aquatic relatives, as the land planarians, earthworms, and snails demonstrate. A greater degree of independent motion is possible only when an internal or external skeleton is well developed.

Raised from the earth by means of stiffened limbs, the body offers much less friction when in motion, and at the same time the air offers less resistance than water. On the other hand, the loading of the limbs limits the size of the body, since in consequence of the laws of statics, doubling the size of the body will require more than a two-fold increase in the strength of the supports. Hence the air-breathing, skeleton-bearing forms of mollusks, arthropods, and vertebrates fall behind their water-breathing relatives in maximum size. Even the largest land snail of the genus *Achatina* does not reach the measurements of the marine *Tritonium*. The giant insects and arachnids such as the Hercules beetle (*Dynastes hercules;* 15 cm. long) and some grasshoppers (e.g., *Palophus,* 25–30 cm. long) are much smaller than the lobster *Homarus,* the rock lobster *Palinurus,* or the giant crab *Kaempfferia kaempfferi.* Compared with the blue whale of up to 30 m. in length and a weight of as much as 108,000 kg., the elephant, 3.5 m. long and 4000 kg. in weight, is a dwarf, and even the weight of the giant extinct saurian *Brontosaurus,* 20 m. long, which is estimated at 38,000 kg., is only one third as great. The terrestrial ani-

mals without a skeleton, such as the land planarians and earthworms, are less different in size from their aquatic relatives.

The low density of the air is also accountable for the fact that (parasites aside) there are scarcely any sessile terrestrial animals, in contrast with aquatic animals, among which sessile forms are common. To be successful, the sessile habit depends on an abundant food supply, since small animals and organic particles may be passively suspended in the water and be brought to the animal by the creation of a current, but the air can bear larger particles only in the less frequent instances when it is in rapid motion. The lack of a plentiful supply of air-borne food particles also contributes to the necessity for large-yolked eggs among terrestrial animals, since the delicate larvae hatching from small-yolked eggs would not be able to feed themselves. Only when care of the young takes place and the embryos are supplied with food in the mother's body can the eggs be small and poor in yolk, as in some *Peripatus* and in the viviparous mammals.

Fertilization is internal in all air-breathing forms with the exception of frogs and certain salamanders, which in this respect still behave like aquatic animals and normally resort to water at breeding time. Internal fertilization may take place in aquatic animals, but it is invariable in the fully terrestrial ones. An arrangement like that of wind-fertilized plants, i.e., the random transport of male sex cells to the eggs by means of air currents, is conceivable; but this possibility has never been realized. The fertilization of the eggs is usually accomplished by means of a copulation. This means a great saving in materials on the part of the males, as compared with the free emission of sperm into the water, which is so common a process in aquatic animals.

A higher development of the organs of sense is a general accompaniment of the transition to terrestrial life. On account of the greater transparency of the air as compared with that of the water, the eye increases in importance, though no new types of eyes have been evolved. In terrestrial vertebrates eyes capable of accommodation are adjusted for distance when at rest, and are actively focused for near objects. In squids and fishes, when at rest, the eyes remain adjusted for near objects and accommodate actively for the more distant ones, which present faint and indefinite images in water.

The chemical senses of aquatic animals are developed in the air-breathers into the senses of taste and smell. By this division of labor, the one is stimulated by liquid substances, the other by gaseous ones,

which, however, must become dissolved to be perceived. The sense of smell acquires a great importance in some air-breathers (many insects and most mammals) for general orientation and may even replace vision in importance. It is of special consequence to nocturnal and cave animals. This importance of smell depends in part on the tendency toward uniform diffusion of gases and the resulting wide and uniform distribution of odorous substances in the air. As the organs of taste and smell must have cells of living protoplasm at the surface, they are especially subject to the danger of drying. In the air-breathing vertebrates they are protected by being placed in special cavities or chambers and are there kept moist by means of glands. In aquatic animals, even in fishes, the organs of chemical sense may be distributed over the whole surface.

Organs of hearing are enormously more developed among terrestrial animals. These are found in terrestrial vertebrates, in insects, and perhaps among arachnids. They are wanting in primarily aquatic animals except in fishes. Sense impressions at great distances, as in terrestrial forms, are not possible for aquatic animals. The males of many Lepidoptera are attracted by the odor of the females from distances of several kilometers. Some steppe mammals catch the scent of freshly fallen rain many kilometers away; vultures see their carrion from an extraordinarily great distance; and the cries of parrots lead monkeys from afar to isolated trees with ripe fruit.

The much lower conductivity of the air for heat, as compared with that of water, has made possible the appearance of homoiothermal animals among terrestrial forms. It is true that some homoiothermal animals are found in the sea—penguins, whales, and seals, for example—but they are secondarily aquatic forms with especially well-developed insulation.

Warm-blooded animals are rendered independent of external temperatures, within certain limits; this makes it possible for them to live in zones and at seasons when other animals are dormant on account of cold. Uniform optimal internal temperature produces, in addition, acceleration of nerve impulses, shortening of the latent period in muscle contraction, and acceleration of digestion; all of which result in an intensification of life processes.

All these factors work together to raise terrestrial animals to a level of more intense activity and more diversified behavior than that of aquatic animals. This higher level also finds expression in the frequent development of a more complex central nervous system and in the attendant phenomena of instinct and reason. Among primarily

aquatic animals, only cephalopods, crustaceans, and fishes are in any degree comparable to land animals along this line, and social life, in the strict sense, such as appears among insects, birds, and mammals, is less perfectly developed among the primarily aquatic forms. Thus, although the sea is its original home, animal life reaches its highest development on land.

In contrast with the great uniformity of habitat conditions in the water, especially in the sea, there is a much greater diversity and variability in the conditions to which terrestrial animals are subject. In the sea temperature variation has an amplitude of only 26°, and only 20° at any one place. On land the temperature may go far below zero and may rise to more than 70° C. The differences in humidity are, of course, excluded in the aquatic habitat. The great differences in the nature of the soil deeply affect animal life. The influence of topographic relief, on account of its climatic results, is more impressive; and finally, the separation of land areas by water stands in sharp contrast with the much greater continuity of the oceans. All these factors together result in more diversity and complexity of adaptations and of directions of evolution, and favor to a high degree the transformation of forms both in space and time. This explains the much greater number of species of terrestrial as compared with aquatic animals remarked upon above. It also explains the fact that genera of aquatic animals extend so much farther back in geologic time, which is a correlative of the more rapid evolution among land animals and the shorter duration of the life of a species among them. The oldest genera of animals now living are aquatic forms—witness the brachiopod *Lingula* (Cambrian to Recent) and the gastropod *Pleurotomaria,* which originated in the Silurian period. The origins of our present-day land snails date from the Eocene, those of the freshwater mollusks from far back in the Cretaceous.[23] Of arthropods, many genera of Crustacea can be traced back to the Mesozoic. Among modern cirripedes, *Pollicipes* appears in the Jurassic, *Scalpellum* in the Cretaceous. Among decapods *Callianassa* also appears in the Jurassic, and *Palinurus, Nephrops,* and probably *Homarus* are known from the Cretaceous.[43] In contrast with these, the genera of insects range only into the Tertiary, and the genera and for the most part even the families of the Jurassic are extinct.[15] This is even more notable among the vertebrates. The genera of fishes have changed relatively little since the Cretaceous; *Ceratodus* known from the Triassic is very close to the living *Neoceratodus;* many modern genera of selachians are known from the Jurassic and Cretaceous; teleosts like

Clupea and *Beryx* appear in the Upper Cretaceous, and many other existing genera in the Eocene. In contrast with these, the reptiles have undergone great changes since the Cretaceous, and the genera of mammals rarely extend as far back as the Miocene.

Thanks to the advantageous characters acquired in connection with terrestrial life, the water affords a new sphere of action for air-breathers in which they have no competitors on their own evolutionary level. This explains the readaptation to life in the water by terrestrial forms, which thus become secondarily aquatic animals. In the ocean it is chiefly the vertebrates that have returned to aquatic life, in part poikilothermal forms, such as the sea turtles and sea snakes, in the warmer seas, and in part homoiothermal animals, such as auks and penguins, sea otters, seals, whales, and sirenians. Marine arachnids are limited in number, and almost no insects are truly marine. One small family of water striders, the Halobatidae, spend their whole life on the surface of the sea, often far from land. The dipterous family Chironomidae has a few larvae that live below the tidal zone. In fresh water, contrariwise, great numbers of insects have taken up their existence, either for their entire life or at least for their larval period, together with some spiders, all hydrachnids, and many pulmonate snails. The fresh-water inhabitants also include a number of reptiles (crocodiles, turtles, and numerous snakes), numerous birds, and various mammals, such as the otter and beaver. However, the breathing of air, which is the chief source of advantage for the terrestrial forms, is always retained in the secondarily aquatic vertebrates. Only the water mites and insect larvae with tracheal gills reacquire the ability to obtain oxygen from the water. Others are in the transition stage; witness *Limnaea* from the deeper waters of Lake Geneva and the aquatic turtles with accessory anal breathing organs. The larvae of amphibians are gill breathers, and in the axolotl and the perennibranchiate salamanders they reach sexual maturity without metamorphosis. It is perhaps a question as to whether these larvae are secondarily aquatic in a strict sense. Sometimes, as in the sea snakes and sea turtles, there is a superficial network of blood capillaries in the mouth and on the jaws.

With the exception of a few viviparous animals such as sea snakes, whales, and sirenians, the secondarily aquatic vertebrates above the Amphibia retain their terrestrial breeding habits. Crocodiles and turtles lay their eggs on the shore, the penguins lay and brood their eggs on land, and even such thoroughly aquatic mammals as seals seek the land at the breeding period.

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5. *Barriers to Distribution and Means of Dispersal*

THE EXTREMELY RAPID REPRODUCTION OF LIVING ORGANISMS CAUSES THEM to spread in every direction, constantly tending to enlarge the area which they inhabit, so that no place in any way capable of supporting life remains unoccupied.

When a catastrophe such as a flood or a volcanic eruption destroys life at some place, it is soon replaced. On August 26, 1883, the small volcanic island of Krakatoa, 41 km. east of Java, was the scene of a tremendous volcanic explosion, which destroyed it in part and covered the remainder so thickly with ash and pumice that no plant or animal was left except, perhaps, a species of earthworm. After only three years the soil was thickly covered by blue-green algae, thereby being prepared for the advent of higher plants; 11 species of ferns and 15 flowering plants were found. A visit in 1897 showed further progress, with 12 ferns and 50 flowering plants established. In 1906 a new examination yielded 114 species of plants, and the composition of this flora was notably different from the earlier ones. Animals had promptly followed the plants. Even in 1889 there was a whole list of arthropods: spiders, flies, bugs, beetles, butterflies, and moths; and even a species of lizard (*Varanus salvator*) was present. A visit in 1908, 25 years after the eruption, yielded a collection of 263 species, of which 240 were arthropods; 4 species of land snails were found; 2 species of reptiles and 16 birds composed the vertebrate element. Investigations in 1920–1921 yielded 573 species of animals, among which were one snake (*Python reticulatus*), 26 breeding birds, and 3 mammals (2 bats and *Rattus rattus*). Comparison with neighboring islands shows that the fauna then had about 60 per cent of the expected number of species.[12] Approximately 90 per cent of the plants and animals present could have arrived by air transport. The rats and

lizards probably came on driftwood or boats.[63] Rhizopods, rotifers, and tardigrades were found on Krakatoa in 1928.[23] By that date, 45 years after the disaster, the 47 species of vertebrates on the island included 3 species of bats. The rat present was represented by 2 subspecies and therefore probably came from two different sources. There were 36 species of birds, 5 of lizards, and a crocodile, in addition to the python previously recorded. The crocodile, and perhaps the python, could have swum. The nearest island not destroyed by the eruption, Sibesia, is 18.5 km. away, so that the new inhabitants must have come from at least that distance by means of wind and waves and other agencies of "fortuitous dispersal."

The possible distribution of plants and animals, however, is not unlimited. Dispersal does not take place with equal success in all directions, and in different organisms the capacity for dispersal is also very unequal. Definite limits are set by the physical and organic environment and by the constitution of the organisms themselves. The possible distribution of existing species accordingly depends upon the barriers present, upon the means of dispersal at the command of the organism in question, and on its vitality and adaptability. Thus definite patterns of distribution appear, and well-marked highways may be found by which dispersal has taken place. These highways are not common to all animals. They are conditioned by and change according to the ecological valence and the means of dispersal, according to the classes and orders, and even to the genera and species to which the animals belong. Barriers and means of dispersal are fundamentally different for aquatic and terrestrial animals; and among the aquatic animals, in turn, the relations tend to be different for marine forms and for fresh-water species. The distribution of genera, families, and higher categories generally involves the historical factors, with interrelation of paleogeography and evolution.

Barriers and means of dispersal for marine animal life

The oceans form a single vast continuous mass of water, only partially separated into divisions by the continents, so that these divisions have no sharply defined limits. A few basins, such as the Mediterranean and Baltic seas, are connected with the open ocean only by narrow straits and are thus rather well delimited. Barriers to dispersal are fewest for marine animals, and those that do exist are more or less intangible. A world-wide distribution among mammals is found only among some marine whales, such as the sperm and the killer whales.

Land masses inserted between the oceans naturally form insurmountable barriers to aquatic animals, even when the land masses are narrow, like the Isthmus of Panama or of Suez. Strong swimmers and other widely distributed pelagic forms, can, of course, pass around the continents to the north or south unless prevented by some other factor. The irregularities in the topography of the ocean floor, such as ridges, deeps, and channels, are much less marked than on land, but nevertheless may form effective barriers in some places for the bottom-inhabiting animals although, in themselves, they afford no hindrance to the spread of pelagic forms.

Temperature sets a limit to the distribution of many stenothermal marine animals. The warm parts of the oceans are separated from each other by cold regions at the poles. The Indian and Pacific oceans are continuous in the warm zone; the Atlantic is separated from them by colder waters. In consequence, the uniformity of the marine life, from the east African coast through the entire Indian Ocean and far into tropical Polynesia, is very striking among both fishes and invertebrates. Most genera of mollusks, for example, and a great many species have this wide range and differ strikingly from the fauna of the Atlantic.[30] Of the 160 species of the genus of crabs *Cyclometopa* in the Red Sea, only two occur to the west, while the others extend for the most part far into the Pacific.[31] Cold- and depth-tolerant animals have a wholly continuous habitat. The temperature drops rapidly with increasing depth, and below 2000 m. rarely is above 3° C., even in the tropics, so that the cold oceans of the two poles are united by the cold waters of the oceanic depths.

The greater oceanic depths form a barrier to the spread of such animals of the littoral region as are confined within a narrow variation of depth. Such animals may be called *stenobathic*. They can migrate only along the coast. If they meet a thermal barrier, their distribution may be limited. With the exception of a few pelagic animals, a few of brackish water, and a few of the deep sea, scarcely a species of the marine Metazoa is common to the east and west coasts of tropical Africa.[48] On the other hand, eurythermal pelagic forms are restrained by no barriers, and some of them are accordingly found in all seas. Such forms include the schizopod crustaceans *Euphausia pellucida* and *Eucopia australis*, the whale shark, and the above-mentioned whales.

The salinity of ocean water, in general, varies only between narrow limits. Where arms of the sea have an abundant inflow of fresh water, and are consequently less saline, many inhabitants of the

neighboring ocean are excluded. The freshening of the surface water near the mouths of large rivers may be a barrier to the spread of littoral forms in shallow waters. For example, none of the species of sea urchins of the Patagonian coast are found north of the mouth of La Plata.[45]

There are fewer methods of distribution for marine animals than for terrestrial forms. There are no true flying forms. All are dependent on movements within the water or on the movement of the water itself. But even in the water, many animals are restricted in position, either completely sessile on the bottom like the corals, bryozoans, or oysters, or very limited in their power of movement, like sea anemones and some mollusks. Many marine animals such as worms or snails, which creep, and crabs, which walk or run with more or less speed, are restricted to the bottom. The majority of these have free-swimming larval stages. The greatest degree of freedom is enjoyed by those that can rise freely in the water, whether in suspension or by active swimming. The greater the capacity for swimming, the fewer are the effective barriers. By contrast, the suspended plankton is dependent on passive dispersal by currents.

Passive dispersal of marine animals is almost confined to the surface forms. The Florida current, which north of Cape Hatteras is known as the Gulf Stream, is relatively shallow, with a depth of about 800 m. Similarly, its counterpart, the Kuroshio of the West Pacific, is also somewhat shallow, reaching down about 700 m. The level of no motion varies and, although usually nearer the surface, lies at 3000 m. in the westward-bound north equatorial current in the Atlantic.[65] Most wave motion tends to be negligible below about 100 m., but it may extend deeper than 150 m., and storm waves have disturbed sand nearly 400 m. below the surface.[49] This type of movement of the water operates to distribute the weak swimmers and especially the plankton, which is composed of plants and animals that do not swim independently of the motion of the water. Much plankton is thus transported by the Gulf Stream from the warmer parts of the Atlantic to the coasts of Europe and even to the neighborhood of Spitzbergen. Such animals may escape the current by downward vertical movement, or, by rising, may become subject to its motion.

The oceanic currents are of especial importance to the distribution of sessile marine forms that have a free-swimming larval period. Littoral animals may be carried in this way to places where the depth is too great for them to develop further, and so be destroyed. The eggs and larvae of many animals of the depths rise to the surface,

undergoing their development in the light. Many crustaceans (Euphausidae, Penaeidae) and deep-sea fishes (Muraenidae and Scopelidae) afford examples.[36] This procedure is naturally effective for the distribution of these forms because the larvae come within the influence of the currents. Among the brachiopods, only *Discina atlantica* has a world-wide distribution. This is explained on one hand by the rise of its free-swimming larvae to the surface and on the other by the fact that this species is distinctively a form of the greater depths, so that the mature larvae find suitable habitat conditions almost wherever they sink to the bottom.[4]

The distances traversed depend upon the rate of movement of the current in question and the duration of the free larval period, which varies greatly among different forms. The larva of the brachiopod *Terebratulina septentrionalis* attaches itself after 10 to 12 days; the zoëa stage of the decapods continues for 25 to 30 days; and echinoderm larvae may drift for periods of 20 to 60 days before metamorphosing. The larval life of the trochophore of annelids and mollusks seems to be much shorter (4–5 days), as does that of the planula larva of corals and sea anemones and the Müllerian larva of turbellarians.[16] Almost all the Crustacea of the group Stomatopoda, whose adults are slow-moving bottom dwellers, are widely distributed because they have a long larval life with exceptional powers of suspension; *Gonodactylus chiragra* occurs in all oceans, and *Squilla cruposa* on the coasts of North America and Africa.[7]

Even the adult stages of sessile forms may be transported by currents if they attach themselves to a moving object. Barnacles (*Balanus* and *Lepas*) are found on driftwood and on actively swimming animals including whales, turtles, and even sea snakes. The bivalve mollusk *Dreissena* attaches itself to wood by its byssus; and even reef corals (*Pocillopora*) have been found attached to a floating piece of pumice.[57]

Transport by other marine animals may also occur. The ten species of sucking fishes (*Echeneïs, Remora*), which attach themselves to whales and to sharks and other fishes by means of their large sucking disks, are distributed to all tropical and warm seas by this means, though their own swimming powers are slight. Many marine forms are transported by shipping. Thus the American sea anemone *Sagartia luciae* was carried along the coast from the south to New Haven and Boston and thence reached Europe, arriving at Plymouth in 1896 and at Büsum in 1920.[50]

Barriers and means of dispersal for fresh-water animals

Conditions for direct dispersal are decidedly less favorable for fresh-water animals than for marine forms. All permanent fresh-water basins are separated by land of greater or less extent. River systems are sometimes connected because one stream pirates the headwaters of another. Rivers for the most part flow into the sea, but migration from one river system to another is not facilitated by this means, since the sea offers as effective a barrier to most fresh-water forms as does the land. Fresh-water animals that can enter the sea may thereby have a very wide range. Nearly all the genera of fresh-water fishes of Africa are different from those of South America, and only those like *Arius* [6] whose representatives enter the sea, are common to the two sides of the Atlantic. Neighboring river systems are often decidedly different in their fauna on this account, especially if they flow into different oceans, and the watersheds then form the dividing lines between such faunae. Thus the Danube basin is distinguished from that of the Rhine by the difference in the migrating fishes, with different species of sturgeon and salmon,* and the presence of eel and shad in the Rhine, which are absent from the Danube. The absence of the sticklebacks (*Gasterosteus*) in the Danube and the presence there of numerous eastern fishes such as *Abramis sapa, Gobio uranoscopus,* and *Perca volgensis,* which are absent in the Rhine, differentiate the Danubian fauna still more. The homing instinct of salmon, which brings them back to breed in the streams of their nativity after their sojourn in the sea, tends to prevent a mixing of the salmon populations of adjacent river systems. Conversely, although the Atlantic breeding grounds of the European and American eels overlap, the species are distinct.

Remarkably long distances by water connect portions of different drainage basins separated by only a few miles of land. Thus in New York, Lake Chautauqua of the Mississippi River drainage is about 125 miles from Lake Seneca of the Atlantic drainage, yet to go from one to the other by water would require traversing thousands of miles, almost half of which would be through salt water. Before the opening of the Chicago Drainage Canal in 1900, the water journey from Lake Chautauqua to Lake Erie, which lie eight miles from each other, would have been even longer.

Dispersal within a body of quiet water meets with little or no

* *Acipenser ruthenus* and *Salmo hucho* in the Danube, *A. sturio* and *S. salar* in the Rhine.

hindrance. In running water, the current has an important influence. In strong currents upstream dispersal is made difficult; bottom forms like snails and eels or powerful swimmers like the Salmonidae are able to cope with a current most easily. Suspended animals are affected by even a slight current; thus in the Havel lakes near Berlin the lower lakes have a larger number of the cladoceran *Bosmina coregoni* than the upper, since they can spread with the current but not against it.[55] Waterfalls and rapids accordingly form well-marked barriers to dispersal. The salmon is unable to pass the falls of the Rhine and is therefore absent from Lake Constance. Above the Trollhättanfall in Sweden there were formerly no eels, either in Lake Venern or in the streams draining into it, because the young eels were unable to pass the fall; [66] with the building of locks at the beginning of the nineteenth century this condition was changed.

Passive dispersal plays an important rôle in inland waters. Fishes, which are the only active swimmers in fresh water, frequently serve other animals as a means of transport. Thus the larvae of river and pond mussels (*Unio* and *Anodonta*) clamp themselves to the fins or gills of various species of fishes, living on them for a short time as parasites, during which period they are transported by their hosts. The marine fishes that enter the rivers of Malaysia bring their parasitic isopods with them. Thus *Rosinella typus*, a cymothoid, is reported from the Gulf of Bengal, the Capuas River in Borneo, and the Sea of Sinkarah. This isopod is known to leave the fish, maintain itself for a time on the bottom, and then attach itself to another fish, which may be a fresh-water species. The isopods of the family Bopyridae parasitize marine crustaceans (*Palaemon* and others) and are carried into rivers by their hosts, where they establish themselves.[69]

The passive distribution of fresh-water animals by flying forms is more frequent and effective. Birds are the principal transporting agents. Eggs and forms in a dormant state become attached to the feet, bills, feathers, and tongues of swimming and wading birds. Such transport has been confirmed by direct observation for rhizopods, statoblasts of bryozoans, winter eggs of cladocerans, threadworms, rotifers,[73] and eggs of snails. Frog spawn may be kept in the air for considerable periods (up to four days), if the weather is cool and damp, without losing its vitality.[35] The conditions for its transport are therefore favorable. Bivalves occasionally clamp themselves to the webs of ducks' feet and may be transported, if they are not too large.[39]

Transport of tiny animals from one body of water may also take

place through the agency of insects. The larval stages of hydrachnids parasitize aquatic beetles and bugs and are carried away by them on their aerial journeys. Snails of the family Ancylidae have several times been seen adhering to the wing covers of beetles.[28] *Dytiscus marginalis,* a water beetle with strong flight, has repeatedly been found with the small bivalve *Sphaerium* clamped to its legs,[30] and *Pisidium* has been found attached to a water bug. The small ostracod *Cyclocypris laevis* is transported in this way by flying insects.[74] Such means of passive transportation are of little consequence to marine animals, with their continuous habitat; but they are important to fresh-water animals, on account of the discontinuity of theirs.

Fresh-water animals may be carried up by tornadoes and deposited at a distance. Gudger [19] has given an excellent résumé of authentic "rains of fishes." Other animals such as tadpoles, frogs, salamanders, and mollusks are transported in this way.

Barriers and means of distribution for terrestrial animals

Barriers to distribution are of especial importance for terrestrial animals. Whereas the oceans are connected, the principal land masses are separated by sea water into three hugh blocks, Eurasia and Africa, the Americas, and Australia. In addition, there are a great number of islands of all sizes, entirely separated from other land masses. The oceans are thus the principal barriers to the free dispersal of land animals. These separations are bridged at only a few places in the polar seas, where ice may connect various islands; Sakhalin and the polar islands of North America have thus been connected with the mainland. In general, however, a separation by the sea conditions the distribution of animals, and narrow straits may separate very distinct faunae, as does the Mozambique Channel between Madagascar and Africa, which is only 400 km. wide.

Rivers may effectively limit the dispersal of animals but more frequently have only minor significance as barriers. Great streams like the Amazon and its tributaries may limit the range of many forms of forest mammals, birds, and butterflies. The ant bird *Phlegopsis nigromaculata* furnishes a dramatic example. It occurs along the entire south bank from the Atlantic to the Andes and has not become established on the north side of the river.[42] The La Plata estuary forms the southern limit of the range of the capybara and the northern limit for the viscacha.[37] The south Russian Dnieper separates ranges of the spermophiles *Citellus suslica* and *C. citellus.*[25] For lower animals, however, rivers often have more importance as a connection

than as a separation. There is no noteworthy difference in the mollusk fauna of the north and south banks of the Amazon, or of the Ganges. Floods cause shifting of the stream-bed and create and destroy islands. Pieces of woodland may be passively transferred from one bank to the other, and with them their fauna. The Hwang Ho, for example, has completely changed the lower part of its course nine times in the past 2500 years. Floating trees and roots afford a means of transport to many animals for an unplanned crossing of the river.[75,76] The Mississippi at New Orleans is not a barrier to distribution, in a region in which an increase in height of land of about 20 feet at the northern side of the coastal swamps divides two distinct sets of communities and limits the distribution of many species and subspecies of land animals. Small rivers and lakes are of no importance as barriers.

Mountains and deserts may be placed with the oceans as barriers of importance; in some respects they are even more effective, partly because of intimately associated climatic changes. The sea, if the body of water is not too broad, does not present a barrier to flying animals; it equalizes temperature differences and nowhere forms a sharp climatic limit. In contrast, a mountain range of considerable height not only forms a barrier to movement by its steep slopes, but also prevents many animals from reaching or crossing its passes on account of the reduced temperature and lowered atmospheric pressure. The faunae on the north and south slopes of the Himalayas or on the east and west sides of the American Cordillera are quite distinct. The fauna of Africa south of the Sahara exhibits a striking uniformity, for no high mountain chains are present that are comparable with the Himalaya in Asia or the Cordillera in America. In consequence the principal groups, and even a great number of species, have an unusually wide range both from east to west and from north to south. This is equally true of reptiles, birds, mammals, insects, and land isopods.[8,14,58]

Mountains of even moderate height may form effective barriers for certain species or even for whole faunae. The starling, introduced into New Caledonia in the 1870's, has increased on the west coast to such a degree as to be a pest; but it had not crossed the mountains and was absent on the east coast in 1917.[56] If the mountain range in question is older than an associated marine strait, its effectiveness as a barrier will be apparent by comparison. Sumatra is traversed for its entire length by a mountain range that separates a northeastern and a southwestern coastal strip. The fauna of the northeastern strip is in

the main like that of the Malay Peninsula and to a lesser degree like that of Borneo; the endemic species of Sumatra are found south of the mountains, and the difference between these two parts of Sumatra exceeds the difference between its northeast slope and the Malay Peninsula.[32] The fauna of Victoria south of the Great Dividing Range is much closer to that of Tasmania than to the fauna north of the range, which agrees with that of New South Wales.[64] Mountains, if sufficiently high, form more effective barriers to the distribution of snails than do straits.

The direction of mountain ranges has an important influence on their attendant climatic effects. When they parallel the lines of latitude, they coincide in general with climatic limits and intensify them. In some, such as the Himalayas, the cold north is directly juxtaposed to the tropical south, and faunae of diverse composition may then be brought into immediate contact. If, on the contrary, they extend from north to south, they form veritable highways upon which polar or temperate forms may extend far toward or even into or through the tropics. In America, with its cordillera extending from Canada to Chile, the puma has been able to spread from Alaska to Patagonia. In Eurasia the principal mountains, the Pyrenees, Alps, Carpathians, Caucasus, Hindu Kush, Himalaya, Tien Shan, and Altai, extend from east to west. They thereby provide definite east-west or west-east lines of dispersal for many animals, and prevent crossing from north to south.

Deserts make a sharply defined boundary for all terrestrial animals, as distinguished from flying animals, especially when they are a nearly continuous series, as from Senegal to Mongolia. The Sahara forms the faunal division between north Africa and central and south Africa, and only interchange occurs in the Nile Valley. This interchange is limited by the narrowness of the valley and does not affect the essential distinctiveness of the two faunae. The fauna of the Cape is also separated from that of central Africa by the Kalahari Desert, and contains a number of endemic genera, such as, among the tiger beetles, *Manticora, Dromica,* and *Myrmecoptera.*[33]

Biotic barriers are also important even on a geographic scale; witness the effect of the tsetse fly carrying trypanosomes in restricting the range of domestic ungulates in Africa. Wallabies have, practically speaking, vanished from the drier parts of South Australia, except for a very occasional rock wallaby in the hills, as have all the interesting little marsupials such as the jumping mice and the rabbit bandicoots or "bilbies." The bilbies were apparently ousted from the country,

actively and literally, by rabbits. These invaders now occupy the old bilby warrens; and very useful they must have found the ready-made burrows, for the open country has a good deal of limestone in the soil either as rubble or as a solid sheet, which must make burrowing painfully hard labor.[54]

The means of dispersal for terrestrial animals are very varied and of unequal effectiveness. Active motion appears in the most complete gradation. Leaving out of consideration the sea birds, for which the power of flight is of greater importance than swimming as a means of distribution, relatively few terrestrial animals can swim any considerable distance. The crocodiles are among the best swimmers, ranging to the Solomon and Fiji Islands; two individuals of *Crocodylus porosus* are known to have withstood the 900-km. sea journey to the Keeling Islands.[29] Many snakes also swim well. Snakes have repeatedly been washed up on the Keelings, usually arriving dead or dying, but some survive the journey. The European water snake *Natrix natrix* is a good swimmer. It has been found in the sea off the Finisterre coast, 5 km. from land.[20] It is thus somewhat curious that snakes tend to be absent or few in species on oceanic islands. The hippopotamus and polar bear seem to be the best swimmers among the terrestrial mammals. The hippopotamus swims the strait between the mainland and Zanzibar, a distance of 30 km.; a polar bear has been observed swimming in the open ocean 30 km. from the nearest resting place. Reindeer also swim well and readily enter the water; they are said to have been taken by ships on frequent occasions, far from land.[44] Twenty kilometers seems to be the maximum distance that can be negotiated by the red deer.[9] Conversely, the Palk Strait, 30 km. wide, has kept the tiger out of Ceylon. Amphibians are killed by salt water, though a very few may adjust to brackish water.[51]

The speed of movement on land is relatively unimportant for the distribution of animals on account of the amount of time available. Although earthworms and snails move slowly, they have occupied all the area in northern Europe that was covered by the ice sheet since its retreat. Effective and active wandering by land snails is attested by the occurrence of the photopositive helicid snails on isolated areas of Muschelkalk and Cretaceous rocks in the North German Plain [32] and by the relatively rich and uniform snail population of the scattered ruins in the Black Forest, which are otherwise poor in snails.[5] In the United States the colonies of the introduced *Helix* (*Cepaea*) *hortensis* expand rapidly.[32] Introduced European earthworms have displaced the native forms near the cities in California, Chile, Aus-

tralia, and elsewhere, and have spread a considerable distance inland. Almost nothing is left, on the Antilles, of the native oligochaete fauna.[43]

Mountains and deserts form climatic barriers, and greater powers of motion do not necessarily enable animals to cross them. When connections, such as ice masses, are temporary, powers of rapid motion may enable animals to spread from the mainland to otherwise inaccessible islands and from island to island. Thus the caribou have spread from the Melville Peninsula to Baffin Island and farther northward, the reindeer from the mainland to Nova Zembla, and the wolves have followed them. The arctic fox seen by Nansen more than 100 km. north of Sannikow Land in the New Siberia Archipelago illustrates the distances to which swift runners may travel over the ice.

Flying animals are least limited in dispersal by physical factors. The air offers no barriers; only the low temperature and lessened density at high altitudes may affect flight. Deserts, mountains of moderate height, and seas of not too great extent are not barriers for good fliers. However, there is great variation in the power of flight in different groups of flying animals.

Among insects, forms with limited flight are usually restricted in range. The number of genera of limited distribution, inhabiting at most two faunal provinces, is very large in the caddisflies (Trichoptera), and this may safely be ascribed to their weak flight.[68] Flightless grasshoppers have smaller ranges than winged species. Thus 6 fully winged species of the genus *Platycleïs* and 12 with vestigial wings occur in Austria and Hungary. Of the 6 species with complete wings, 2 range over all of Europe and 4 into the Mediterranean province, while of the 12 flightless forms, 5 are restricted to Dalmatia and one to the Swiss Jura.[72]

Of 45 species of Orthoptera common to the desert and steppe faunae of central Asia and South Africa, not one has both sexes flightless, and only a few have weakly flying females. The mantid species ranging farthest to the east in the Polynesian Islands belong to the relatively small group without notable wing reduction in the females.[70] The great power of flight of the hawk moths (Sphingidae) makes possible a wider distribution of their species than of other Lepidoptera: *Celerio cingulata* has a vast distribution, and the morning-glory sphinx ranges throughout the Old World. Many individuals make extended flights; the morning-glory sphinx, which is unable to gain a permanent foothold in East Prussia, is constantly maintained there by an influx from the south; the oleander sphinx,

whose pupa succumbs to the winter in central Europe, is caught from time to time in north Germany and even in Russia, and such specimens must have flown from points south of the Alps; the death's-head has flown to St. Helena. The large American noctuid *Erebus odora* has been taken on Tristan da Cunha, about halfway between Montevideo and the Cape of Good Hope, and is occasionally seen on ships not far from the European coast.[60]

Some species of butterflies have a well-developed flocking instinct, and large flights of such forms have been observed. Among these are the thistle butterfly (*Pyrameis cardui*), which is absent only in South America, and the common monarch butterfly, which has spread across the Pacific *via* the South Sea islands to Australia since 1890 and is now the most abundant butterfly at Sydney. The latter species has also appeared at various places in India and Europe and on the English and Spanish coasts.[59] A flight of more than 20 *Papilio hector* came aboard the *Novara* 300 km. from Ceylon.[15] Dragonflies also include powerful fliers. *Pantula flavescens* sometimes appears in numbers on the Keeling Islands, and dragonflies were observed daily above the water on a journey made from Singapore to Sydney during calm weather.[29] Great swarms of dragonflies frequently appear. Swarms have also been reported for the backswimmer (*Notonecta glauca*). Mountaintops, especially in the tropics, may swarm with flying insects apparently carried up by the winds since they neither develop there nor feed in that zone as adults. They are especially subject to being blown away from such exposed situations.[46] There may be large-scale directed but quite unexplained flights of butterflies as described by Hingston in the Himalayas.[26]

Bats, in consequence of their powers of flight, also exhibit wide distributions of their species and genera. Several genera are world-wide in range or nearly so; thus species of *Myotis* are found in every continent south of the tree limit in the northern hemisphere. Various single species of *Lasiurus* and *Lasionycteris* are extremely widespread in North America. Broad stretches of ocean do not seem to be crossed by bats of their own accord, and most species of fruit-eating flying foxes of Malaysia and Polynesia are restricted to particular groups of islands. The occasionally fish-eating *Noctilio leporinus* appears on all the West Indian islands, without the formation of local races; other species of bats have frequently developed special subspecies on the various islands of the Antilles.[1]

Though flight reaches its highest development among birds, there are great differences in the flying power of various groups. Some birds

of prey such as the sea eagle and the barn owl have an almost world-wide distribution; the stork journeys from East Prussia to Cape Colony and back every year. Many shore birds nest in the Arctic tundra and winter in the temperate zone of the Southern hemisphere. In contrast with these, many other birds are restricted to relatively small areas. The gallinaceous birds, such as the pheasants, which are poor fliers, have relatively restricted ranges. The members of the heavy-flighted auks are so different on the two coasts of North America that, of 17 Pacific and 6 Atlantic species, only three of these are common to both coasts, two of which form separate races.[2] Finally, for some species, such as petrels and gulls, the ocean not only is not a barrier, but actually becomes a source of food and a place to rest. Powerful fliers of these groups are among the most widely distributed birds.

Passive distribution of terrestrial and fresh-water animals takes place in various ways. Storms carry dust, twigs, and leaves many miles, and thus transport not only resting stages of Protozoa and small Metazoa, but also small snails, myriapods, insects, spiders, and their eggs. The "Pampero," a southwest wind from the Pampas, brings a veritable rain of insects to Buenos Aires and Montevideo. Many insects are blown up to the glaciers in our high mountains; large larvae of a goat chafer (*Aegosoma scabricorne*) fell to the ground during a thunderstorm in Basel.[17] Rains of caterpillars which were brought by storms are reported in south Russia, and rains of springtails (*Collembola*) in Balwyn, Victoria. Spiders with their flight threads have blown onto rigging of ships 300 km. from land. Only free-living spiders are transported by this means, and these accordingly are the only kinds of spiders found in the Hawaiian Islands; the few cryptozoic spiders found there were introduced by man.[53] Flights of continental butterflies, such as *Plusia gamma* and *Psilura monacha*, have often been carried by the wind to Helgoland and even to England.[17] The possibility of population of more remote islands by aerial transport is much better than was formerly realized. An analysis of the West Indian insect fauna by Darlington clearly indicates wind dispersal as an important element in the origin of the fauna.[13] Even tiny snails can be carried thus and may then give rise to a diverse snail fauna by radiative evolution.[21]

It is well known that birds are frequently transported by windstorms. Sea birds from both the Atlantic and Pacific have been recorded in Wisconsin. The accumulated records of accidental occurrence of European birds in North America north of Mexico, cited by

the *Check List of North American Birds* (1931), include 44 species.[2] No less than 11 of the 16 land birds in this list, however, have been recorded only from Greenland, leaving five "accidentals" from Europe for the North American continent. Examination of the best comparable list of British birds[71] discloses records of 14 land birds of American origin, and of 25 aquatic species. The British coast line is only about one-tenth the length of the North American, and if this is taken into account the disproportion between the two lists becomes still greater. This clearly exhibits the influence of the prevailing westerly winds of the north Atlantic.

Flowing water often serves as a means of distribution of terrestrial animals. A number of Alpine species of snails have been brought down to the plains and have established themselves on the river banks: thus *Cochlostoma septemspirale* on the Danube at Kehlheim and *Helix* (*Cepaea*) *silvatica* from western Switzerland to Karlsruhe and Worms.[10, 18] The woods bordering the La Plata have a fauna very different from that of the neighboring pampas, especially snakes, amphibians, and brilliantly colored insects of northern origin. Large streams at flood time carry driftwood, tree trunks, and even whole floating islands, and thus transport not only many small forms but a few large animals. The Paraguay occasionally brings large snakes, crocodiles, and jaguars to the neighborhood of Buenos Aires.[27] Spix and Martius report a number of monkeys on a floating log in the Amazon, a squirrel on another, and a tiger cat and a huge caiman on another.

Branches and trees and large rafts are carried out to sea by the rivers and are then carried farther by currents and winds. Masses of driftwood and rafts up to a length of 30 m. have been observed at the mouths of many tropical rivers, such as the Amazon, Congo, Ganges, and the Indo-Chinese rivers. In the summer of 1892, a floating island of about 1000 sq. m. extent was sighted repeatedly in the Gulf Stream between latitude 39.5 and 45.5 N. and longitude 65–43 W.; even large animals may be transported for long distances in this way. A boa constrictor was washed up on the beach of the island of St. Vincent coiled around the trunk of a cedar; it at once attracted attention and was killed.[38]

It must be recognized, however, that the actual establishment of a species of mammal or reptile in a new territory or island, in consequence of this sort of transport, could take place only under especially fortunate circumstances. If the sea journey lasts more than a few days, mammals, and especially small ones, will die of starvation;

reptiles might fast for longer periods. In a strong wind, which is necessary for rapid flotation, the waves would break over the floating object and endanger the travelers; and driftwood often is pounded for days by the surf and only rarely carried directly ashore. Even if the traveler has successfully reached the land, colonization can take place only if both sexes of the species in question or at least a fertilized or pregnant female have completed the journey. The ability to continue will even then depend on the habitat conditions afforded by the new locality. Thus the chances for the colonization of new territory in this way, especially by mammals, seem at first glance to be slight.

Matthew [41] and Barbour [3] have critically examined the possibilities of colonization by rafting. Barbour does not believe that rafting furnishes a feasible explanation of such distribution, while Matthew thinks that it does. Employing Matthew's estimates of the probabilities of dispersal by rafts, correcting the arithmetic of the original analysis, and allowing for the increased estimates of the duration of Cenozoic time, calculated in 1947 as 75,000,000 years (Knopf, in Simpson [61]), the number of probable successful Cenozoic colonizations of oceanic islands by mammals by this means amounts to 25,000. This is an embarrassment of riches to account for the relatively few mammals found on truly oceanic islands.

The chances are much better for forms with a dormant stage or with eggs that may be carried on these natural rafts. The eggs of reptiles might come ashore unharmed in the roots of trees or in holes or crevices in their trunks. The geckoes lay hard-shelled eggs, attached to the bark or trunks of trees, which require many months for development, a period ample for transport to great distances.[62] Insects may be distributed in their pupal stages, especially wood-eating forms which pupate within the trunks of trees. This may explain the preponderance of snout beetles on St. Helena, where they compose more than half the native beetle fauna. Snails, with and without opercula, are good subjects for this form of transport. The experiments of Darwin and Aucapitaine have shown how resistant they are to sea water; of 100 snails kept under sea water in a perforated box, 27 were still alive after 14 days, among them 11 out of 12 species of *Ericia*. In addition to arboreal snails, the strand-inhabiting Auriculacea are especially exposed to such transport.

In any case, the assumption of a large rôle for such rafting in the colonization of a given territory must be made with reservations. In general, the chance nature of raft transport would result in a varied assemblage of animals, unrelated except for the common adaptation

for this means of dispersal. Pilsbry [52] and Crampton [11] regard the land snails of the Pacific islands as spread by land connections rather than by fortuitous dispersal, on account of the common primitive characters of kidneys and genital organs of the genera *Tornatellina, Gastrocopta, Partula,* and others. Some authors similarly regard the placental fauna of Australia, with the exception of the dingo, as non-fortuitous, since there are 16 endemic genera of rodents with numerous species.[67] The presence of 16 genera does not necessarily imply 16 landfalls, since a group of related genera may evolve from a single successful emigration. The absence of other forms is then exactly in accord with the requirement of a "chance" assemblage by fortuitous dispersal.

The dispersal of small non-parasitic terrestrial animals by temporary attachment to flying forms is of sufficiently common occurrence to be distinguished as a special mode of commensalism under the term "phoresy." [24] Pseudoscorpions, for example, have been found attached to flies, craneflies, beetles, and bugs; it is highly unlikely that they are in any way parasitic, and it may be supposed that in some instances they had attached themselves in search of parasitic mites. It is, of course, entirely natural for parasitic forms to be carried in this way. The nest parasites of swallows and swifts, for example, are transported by their hosts, and still more the feather and hair mites, and lice, fleas, and parasitic Diptera. The same is true of the minute external parasites of bees and ants.

Intentional and unintentional transport by man has carried great numbers of animals to countries where they were originally absent. Domestic animals were taken with him, and then frequently became feral; horses and cattle in the various parts of South America did so, as did cattle in Australia and pigs and goats on many islands. Primitive peoples caused this as well as civilized man. The wide distribution of pigs in the South Sea Islands is explained in this way, and the presence of the dingo in Australia is also attributed to the agency of man.[64] Seafarers have often left domestic animals on isolated islands as a source of food for later visitors. By this means cattle were introduced on St. Paul, rabbits on Porto Santo and Kerguelen, and goats on Juan Fernandez.

Game animals have been similarly transported and established in new localities. The fallow deer was introduced in central Europe from the Mediterranean province. There has been a great waif transportation of different sorts, like that of the banana waifs to the United States and the dyewood waifs to Hamburg. The majority of such

waifs fail to become established, but if they do, being released from the biotic pressure of their native land, they may develop into economic pests. This whole subject of man's influence upon ecological zoögeography will be considered in the final chapter.

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75. Idem, 1917, "Die Tierwelt der Umgebung Basel nach neueren Forschungen." *Verhandl. naturforsch Ges. Basel,* 28, pt. 2:28–65 (p. 60).
76. Idem, 1919, "Der Rhein als Bahn und als Schranke der Tierverbreitung." *Ibid.,* 30:137–188.

6. *The Effect of Geographic Isolation*

THE AREA INHABITED BY A SPECIES IS IN GENERAL SURROUNDED ON ALL sides by barriers preventing its further dispersal, and the species is thus limited in its range. As we have seen, the nature of these barriers may be very diverse. Barriers of different kinds combine to produce an isolated area, as is done by the mountains and ocean on the west coast of South America, or the desert and sea in North Africa. Cave animals are isolated by their negative reaction to light and by cave walls. The border of the range of a superior competitor or of an enemy or of a rich fauna may form a limiting barrier. Climatic barriers also exist, and these usually show a less definite boundary than do physiographic barriers. A fairly marked climatic barrier is furnished by the 20-inch isohyet in the United States, which approximately coincides with the hundredth meridian.

Barriers to dispersal have a twofold effect. In the first place, they may separate closely related forms on the two sides of the barrier and thus prevent interbreeding. This makes possible independent differentiation of the two groups, since newly acquired characteristics will be restricted to that one in which they appear and will not become the general property of both. The earlier belief that variations would be suppressed by crossing with invariant individuals, i.e., that "panmixia" would entirely nullify variation, has become very questionable with the growth of our knowledge of heredity. In two isolated related groups, however, the individuals within each group will, in general, resemble each other more than they will members of the other group. Thus arise subspecies, and, with continuing isolation, species. In the second place, the presence of barriers operates to protect species within their isolated ranges from competition of rival forms or enemies that might be dangerous to their survival, and thus enables protected forms to take full advantage of all opportunities presented by their environment.

There is both direct and indirect evidence of species change associated with geographic isolation. The experience of animal breeders shows that, even without intentional selection, isolated groups of domestic animals develop in different directions in a relatively short time, and that the prevention of free crossing is an important element in selective breeding. The development of the dairy breeds of cattle on the islands of Jersey, Guernsey, and Alderney illustrates both of these principles. The chief evidences of the importance of isolation in the origin of species are derived from the study of the geographic distribution of animals. Wagner [89] was the first to emphasize, from the evidence of distribution, that geographic isolation must have an important effect upon the transformation of species and the formation of subspecies. He even believed that this was the only way in which one species can become differentiated from another, failing to take into account the other means of preventing interbreeding. The most important of the latter are, first, "physiological isolation," brought about by a change in the bodily and instinctive characters connected with reproduction itself, whereby the appearance of distinct groups within a species is possible without any geographic isolation,[68] and, second, ecological isolation, which similarly enables related forms to exist side by side in the same area though in different habitats or with different habits. This matter has been reviewed by Mayr,[52] who concludes that even physiological and other differentiation arise first in geographic isolation.

The transformation of a species may take place by germinal changes or mutations, either large or small, and by environmental selection of such favorable mutations when they do appear. Such mutational change proceeds slowly. Geographic isolation particularly furthers the appearance of new adaptive modifications when the habitat conditions in the isolated area differ from those in the original home of the species, but isolation may further the development of new races based on non-adaptive characters even though the habitat conditions do not differ essentially. Isolation, if it removes a group of animals from enemies, may make possible the development of structures or colors that would otherwise be eliminated. Potent selective agents include climate, soil, food, and competition. The varying effectiveness of barriers in separating interbreeding communities is of greatest importance to evolution, which occurs most rapidly when relatively isolated populations are interconnected by emigration.[1]

If individuals from another area can enter a partially isolated group, their effective mutational changes will be brought with them, and

the differentiation of the group from the ancestral form may be thereby retarded or hastened; this relation will tend to be reciprocal. With complete isolation, the groups differentiate first into subspecies, and then, with longer periods of time, into wholly distinct species and even into new genera and families. Such new forms are confined to the isolated area in question, since it is in the highest degree improbable that identical mutations should become established in a species independently. The isolated evolved form is endemic. The longer the isolation continues, the larger is the number of mutations and the greater becomes the divergence from related organisms in other regions. The systematic value of these endemic forms—subspecies, species, genus, family—consequently makes possible a conclusion as to the duration and completeness of the isolation. Thus, of the animals that have colonized Krakatoa since 1883 from the neighboring islands, not one is endemic. The native fauna of the Hawaiian Islands, by contrast, is largely composed of endemic species, with numerous endemic genera and even families.

Physiologic isolation most frequently results from mutations of the generative organs of such a nature that two groups lose their mutual fertility. Infertility has thus come to be a criterion of specific distinctness. When, however, the differentiation into distinct species is caused by geographic isolation, mutual fertility need not be lost. The geographic races of the lion or of the zebra are completely fertile, and this is also true of such completely distinct forms as the various pheasants, the red deer and wapiti, and the European and American bisons.[37]

These theoretic considerations on the rôle of geographic isolation in the evolution of species are amply supported by the facts of animal distribution. If we take a given species in a specified area as a starting point, we do not find its nearest relative in the same district, nor in a distant one, but in an adjacent area separated by some barrier. This is *Jordan's Rule*,* which seems to hold rather generally for expanding dominant groups of vertebrates but does not hold, of course, for ancient relict groups. The whole body of research on geographic variation, which is now being carried out in detail for birds and mammals and some groups of insects, continues to confirm this rule, and for examples it is sufficient to refer to any systematic work dealing with a large region, such as Hartert's *Birds of the Palaearctic Fauna.* There are certain exceptions in which intimately related forms occupy

* The use of the term "law" for such ecological generalizations does not seem advisable.

the same area. Thus Dunn [17] regards the four species of Jamaican tree frogs of the genus *Hyla* as related stocks that have diverged into species sorted primarily by size at transformation. Among fishes, the gobiid *Eviota* and the blenniids *Enneapterus* and *Salarias* are represented by closely allied pairs of species in the coral reefs of Samoa.[40] This is not surprising, in view of the possibility of physiological isolation. That these cases must be cited as exceptions speaks for the high degree of importance of geographic isolation.

Isolation is also to be seen in related forms that inhabit the same region but occur in different environments and have different habits or are sexually mature at different seasons of the year. Such differences constitute ecological isolation. This is illustrated by two closely related crayfishes that occur together in southwestern Pennsylvania. One, *Cambarus monongalensis*, is confined to springs with clear water; the other, *C. diogenes*, lives in marshes and other stagnant waters.[57]

Closely related forms that now inhabit the same area may of course have originated in separate areas and have come together by emigration. They will then remain separate if a sufficient degree of bodily or instinctive differentiation to prevent interbreeding has arisen during their separation. The animals of the Chicago area, for example, have entered from three different directions since the glacial period; southwestern (Sonoran), southeastern, and northern elements are distinguishable. The fauna of central Europe has a similarly diverse origin, and Taylor writes of its grasshoppers: "This circumstance explains some cases in which two or three very closely allied forms inhabit the same area and occur in the same habitat. They have originated in three distinct areas from a preglacial common ancestor, and have reached their present common area of distribution only after postglacial migration." [92] The European wheatear, a characteristically Eurasian thrush, ranges through most of Eurasia and has entered North America from two different directions. *Saxicola oenanthe leucorhoea* reaches Labrador *via* Greenland, while *S. oe. oenanthe* has reached Alaska from the Chuckchen Peninsula.[81] It is a matter of only a relatively short time until the two forms may be expected to meet in Arctic America.

The same barrier may be of very different effectiveness for different species. The powers of dispersal of an animal species may be summed up as its "vagility." The less the vagility of a species, the less it is able to overcome barriers, the more numerous are the areas that afford the condition of geographic isolation for it, and hence the more numerous the opportunities for independent variation. The degree of

vagility of different groups of animals is in inverse proportion to the number of geographic races presented by a given area.[13] The crested lark *Galerida cristata,* a strictly resident bird that rarely ranges far from its home, forms an unusually large number of local races. The gray sea eagle scarcely varies with a nearly world-wide range. Widely distributed cirripedes tend to break up into local races, unless they lead a planktonic existence by attaching to floating wood and pumice, like most species of *Lepas* and *Conchoderma.*[63] In the same area a species of high vagility may be represented by a single form, while

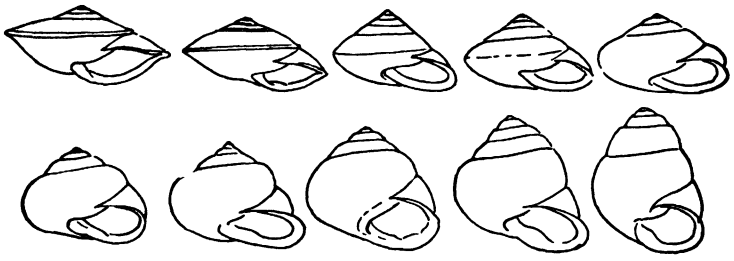


FIG. 6. Series of forms of *Helix* (*Murella*) *scabriuscula* (1–2), *globularis* (4–8), and *sicana* (9–10), from the mountains of Sicily, arranged in a geographical series from west to east. After Kobelt.

another with low vagility may be split into numerous local forms. Thus species of birds are often represented in Germany each by a single subspecies, whereas certain flightless ground beetles have numerous subspecies, and snails, especially aquatic snails, vary almost from station to station. With a low degree of vagility mere distance becomes a sufficient barrier to prevent interbreeding. All the conditions are favorable to the formation of local forms among the reef corals, whose vagility is restricted to a brief larval period; with the manifold conditions of their environment, their variability is very great, and even neighboring reefs may be different;[14] in part, however, this is because of their plasticity of growth form, a plasticity that obscures taxonomic characters.

When there are no impassable barriers, neighboring geographic forms may be connected by intermediates, as are the subspecies of the wide-ranging puma or those of the snail *Murella* (Fig. 6) in Sicily. The presence of such transitional forms is the most usual criterion for subspecific classification. Transitional variation may be wanting at the boundary between the ranges of vicarious forms, which are then regarded by many authors as specifically distinct. Occasional

hybridization, as in the crows *Corvus corone* and *C. cornix*, does not appear to correspond to subspecific intergradation. We agree with Mayr in a much broader interpretation of the subspecies concept, reserving the term species for the grade of differentiation at which reamalgamation with the nearest related form has become impossible, or apparently so.

An excellent example of the effect of geographic isolation within a restricted area is supplied by the Achatinellidae of the Hawaiian Islands. These arboreal snails have speciated into a great number of forms, apparently in association with topographic features. Zimmerman [93] lists 42 species and 75 subspecies of the genus *Achatinella* from the island of Oahu alone. The extreme fragmentation of the land snails of Hawaii and other South Sea Islands into species and subordinate forms has been ascribed to isolation of wooded valleys by bare treeless ridges, which would form a barrier to the dispersal of strictly arboreal animals. In a conference with Messrs. Zimmerman, Bryan, and Kondo, on the occasion of a visit to Honolulu in 1949, it was pointed out to one of the authors (Schmidt) that the supposed isolating ridges are at most secondarily bare, and that the original condition in Oahu, and in Tahiti as well, consisted in a continuous blanket of forest. In a search for other effective isolation factors, it was suggested that the lava flows of earlier eras of more active vulcanism may well have isolated numerous areas of forest of varying size, which became reconnected only with the successional development of soil and forest on the aging lava. We believe that isolation by mere distance must have operated as an important factor in the speciation of these snails. The importance of this distance effect even in so widespread and active a form as the leopard frog of eastern North America has been shown by Moore.[56]

Extreme geographic fragmentation is much more common among land and fresh-water animals than among marine animals, whose continuous environment reduces the effectiveness of such barriers as exist. This is one of the reasons for the great absolute and relative preponderance of the terrestrial forms in number of species.[13]

The same barrier may separate a whole group of forms from their relatives. The two faunae then have a great similarity of composition, without being exactly identical. The corresponding species of a genus or the subspecies of a species represent each other in the corresponding environments of the two areas, without occurring anywhere together. They "vicariate." Such vicariation takes place on a large scale between the mammals of Eurasia and North America, where

the European and American beaver, the red deer and wapiti, the European elk and the American moose, the reindeer and caribou, the wisent and the American bison, and the European and Canada lynx replace each other. The bird faunae of the north and south islands of New Zealand exhibit the same relation. The mammals of Kilimanjaro and Kenya exhibit a similar vicariation; monkeys, lemurs, shrews, squirrels, various mice, hyraces, elephants, river hogs, and antelopes are represented on the two mountains by corresponding species or subspecies.[50] Such vicariation is demonstrable in eighteen pairs of forms, among which are included:

	Kenya	Kilimanjaro
Monkeys	*Colobus abyssinicus kikuyensis*	*C. a. caudatus*
Lemurs	*Galago kikuyensis*	*G. panganiensis*
Squirrels	*Heliosciurus keniae*	*H. undulatus*
Hyraces	*Procavia crawshayi*	*P. valida*

The same phenomenon, referred to by Jordan under the term "geminate species" is conspicuous on the two coasts of Central America (see Chapter 7).

Adaptive radiation

When the barrier is an old one and the isolation has been long continued, mutational changes accumulate, and animals of the same origin become so different that they live in wholly different environments. Thus the different habitats come to be filled by related animals, and the whole fauna in such an isolated region exhibits an intimate phylogenetic relationship that is wanting in areas that have been open to continued dispersal, with their fauna accordingly subject to progressive extinction. In the isolated area, the different habitats are filled with animals of a single stock, but these are so transformed by adaptive radiation that they resemble the forms of diverse groups that fill corresponding niches in the environment elsewhere. The Australian region affords an excellent example. Except for monotremes, a number of rodents, and the dingo, the mammals are all marsupials, and these occupy the most diverse habitats. The wombat takes the place of the marmots; the Tasmanian wolf, that of the wolves; the dasyures, the civet cats; flying phalangers replace the flying squirrels, and the kangaroos fill the place of the larger herbivores. The resemblance is not only one of habits and in part of outward appearance, but may include details of structure, such as the form of the teeth, and is sometimes so great that one may speak of convergence.

Thus the resemblance between the mole-like marsupial (*Notoryctes*) of Australia and the placental golden mole (*Chrysochloris*) of Africa, related to their common adaptations for burrowing, is so great that Cope assumed a direct relationship between the two forms.[47]

Adaptive radiation frequently produces ecological equivalents. Closely allied vicarious forms are likely to inhabit the same ecological niche; the concept of ecological equivalence, however, may properly be extended to include the presence of taxonomically unrelated animals in remote parts of the world but in similar habitats, as the moles just cited. Such forms as the plains-dwelling kangaroos may be regarded in this sense as ecological equivalents of the horses, though without morphological resemblance. The characins include about one-third of all the fresh-water fishes of South America, and this single family has representatives of all types, from the herbivorous forms to the predatory ones, corresponding to our carp, whitefish, trout, pike, and catfish, which belong to as many different families. Among the South American birds the ovenbird family (Furnariidae) shows a similar adaptive radiation, replacing birds of the most diverse families in other parts of the world; they live on the ground, burrow in it, live in bushes, or climb like woodpeckers; they inhabit the rain-forests and hot dry valleys, the banks of mountain streams, or the pampas; they reach the high mountains, and small *Synallaxis* are found in the most barren parts of Patagonia; they feed on seeds, or insects, or worms and snails; they are correspondingly varied in appearance, and differ in size, in the form and size of bill, in length of limb and toes, and in the length and form of the tail. Fifty-five genera of this family are now recognized, with hundreds of species.[33] Darwin's finches, 14 species in all, members of the sparrow family (Fringillidae), have undergone similar adaptive radiation on the Galapagos Islands.[46]

The auks and penguins are analogous groups in the arctic and antarctic seas. The extinct great auk, the dovekie (*Alle alle*), and razor-billed auk (*Alca torda*) are the northern forms, the emperor and adelie penguins and their relatives, the southern. They resemble each other greatly in habits, somewhat less in general appearance.

Bodies of water isolated for long periods may acquire a similarly radiating fauna. The crustacean suborder Cumacea is represented in the Caspian Sea by the single genus *Pseudocuma*, which is rare in the ocean, whereas in the Caspian it has 13 very diverse species. These are especially remarkable in paralleling other distinct *genera* of the oceanic Cumacea; thus, among other examples: *Pseudocuma diasty-*

loides resembles the genus *Diastylis; P. abbreviata,* the arctic *Eudorellopsis deformis; P. campylaspoides,* the genus *Campylaspis.*[70]

Geographic isolation in the ocean

The degrees of isolation in the ocean vary in its different parts. The open ocean has few barriers. The continents separate it into several major divisions, but within these the only surface barrier on a geographic scale is that of temperature, whose effectiveness depends upon the eurythermal or stenothermal character of the animals concerned. Thus the Gulf Stream forms a temperature barrier that divides the species of craspedote medusae into two groups.[82] Generally speaking, however, the actively swimming pelagic species tend to be world-wide in their distribution. In the tropics the Indian and Pacific faunae agree closely, whereas the Atlantic differs from both; the pelagic forms of the Pacific that are absent in the warmer parts of the Atlantic are for the most part merely replaced by allied forms.[11]

The conditions are different with the inhabitants of shallow water. Their distribution is limited by more numerous barriers, such as oceanic depths, peninsulas, nature of the bottom, freshening of the water at river mouths, as well as the temperature factors. The ranges of species are consequently smaller, often very small, and the number of species in each genus is larger. Geographic species and subspecies that replace each other in adjoining areas are frequently developed. This applies particularly to forms with slight vagility, which are especially numerous in coastal waters. The sessile actinians, for example, frequently form endemic species; all the actinians of the New Zealand coast are endemic, and their distribution is dependent on the nature of their larval stages. Those with ciliate larvae are widely distributed, while those that have no free-swimming stage are restricted to special areas, in which they may be extremely abundant.[20] Of the 10 actinians on the coasts of the Canary Islands, 3 are endemic. Connected marine coasts form highways of distribution for such forms. Of 52 actinian species on the east African coast, 63% are endemic; 21% occur also in the Red Sea, but only 2% are Indian and 5% Indo-Pacific.[58] Ascidians are represented on the east and west coasts of northern North America by parallel series, whose members correspond exactly but are distinguishable specifically.[32]

The construction of ship canals at Suez (1869) and Panama (1914) has not opened free channels of communication for marine organisms across these isthmuses to the extent that might be expected on first thought. The Panama Canal is not at sea level, and the fresh water

of Gatun Lake kills most animals attached to ships during the several hours required for its passage. The tarpon (*Tarpon atlanticus*) has completed transit from the Atlantic to the Pacific. It is a member of one of a small group of families found nearby inhabiting salt, brackish, and fresh water more or less indiscriminately.[35] The Suez Canal is at sea level; it is not, however, a thoroughfare for marine organisms. The factors that tend to prevent ready passage of the Suez Canal include: (*a*) Plankton-bearing currents are deflected from the Mediterranean entrance at Port Said, and for ten months of the year differences in water level and the prevailing winds cause currents in the canal to flow northward from the Bitter Lakes. (*b*) There is oil contamination at the Red Sea entrance. (*c*) The canal passes through the Bitter Lakes with heightened salt content. In Great Bitter Lake, the bottom mud is devoid of life; this lies directly over an ancient salt bed which is gradually being redissolved and presumably will vanish by the end of the present century. The high salinity of these lakes probably acts as a barrier even though bryozoans and isopods are carried through their waters on the bottoms of canal barges. (*d*) A further obstacle to free passage is presented by Timsah Lake, the salinity of whose waters varies enormously from hour to hour. The extent to which animals pass through the Suez Canal, despite these obstacles, has not as yet been carefully determined.[21,26] A ctenophore was recorded from the Palestinian coast in 1942. Ctenophora were supposedly absent from the Mediterranean, and this one may well have come through the Suez Canal. It resembles those found in the Red Sea.[30]

Restriction to coastal waters leads to specific transformation in the fishes also. Littoral sharks and rays are scarce about New Zealand, but form a number of endemic species.[19] Out of 65 of the marine fishes of St. Helena, 17 are confined to the island littoral.[9] The coastal fishes of Micronesia and Polynesia are closely allied, while those of the Hawaiian Islands are mostly specifically, though not generically, different, evidently on account of the isolation of the latter group.[40] The littoral fishes of the Antarctic Ocean form groups of species in definite areas, like Tierra del Fuego, the Falkland Islands, South Georgia, South Shetland, and Grahamsland, in which the same types appear as vicarious subspecies.[19]

Even mere lack of vagility, for sessile or mainly sessile animals, without any special barriers, may afford sufficient isolation for the divergence of species. In the flounder *Pleuronectes flesus*, which still possesses a considerable degree of freedom, the specimens from the

English coast (at Plymouth) run 30% "left-sided," whereas on the German coast opposite, the "left-sided" forms are only 5%.[16] In the starfish *Solaster papposus* of the northern seas the number of arms varies from 10 to 14; but specimens from a given locality have an almost uniform number of arms. In some places the 10-armed form predominates, at others the 11-armed, the 12-armed at Tenby on the English coast, the 13-armed on a stretch of the Greenland coast, while those of the Kattegat are 14-armed; the specimens from given areas agree also in other characters, such as the development of the dorsal skeleton and number of paxillae.[13]

The starfishes of the genus *Pentaceraster,* ranging through the entire Indian and Pacific oceans, present a great variety of form, but so many transitional and intermediate types are present that from a conservative standpoint they all belong to a single species, *P. mamilatus.*[15] The same phenomenon is true for some sponges whose vagility is slight, their opportunities for dispersal being for the most part confined to a short larval period. Thus 32 supposed species of *Spirastrella,* a widespread genus in the Atlantic, Pacific, and Indian oceans, have been united into a single protean species by the demonstration of transitional forms.[87] Reef corals are famous for their diversification and adaptability, and their environmental conditions have such great variation that each individual branch may be subject to special conditions, and there are almost as many modifications as branches.[14]

Geographic isolation in inland waters

Geographic isolation of small areas is especially characteristic of inland waters. A lake, pond, inland swamp, or a pool is surrounded by land as an island is by water. The great majority of inland lakes are small; less than 30 exceed 1000 sq. km. in extent, and many are very small. Rivers are separated by land at their sources, by the sea at their mouths, equally effective barriers for their fresh-water inhabitants. The environmental conditions, especially in standing waters, are extremely variable: the daily and seasonal temperature range; the dissolved substances, organic and inorganic; the kind of bottom; the vegetation of the shores; all combine to give an individual character to almost every body of water, in sharp contrast with the uniformity in the sea. The theoretic conditions for the transformation of species in fresh water are accordingly extremely favorable. The variability of the wide-ranging inhabitants of fresh water is great, but is controlled in part by the transgression of barriers at times by either active or passive transport.

Examples of the multiplicity of variations in fresh-water animals are striking. Thus the genus of mussels, *Anodonta,* represented by 2 species in middle Europe, according to Clessin, was divided into 26 species by Kuster, while French students later recognized more than 200 for the same area. The forms differ in outline, size, thickness of shell (Fig. 7), and in the coloration of their outer and inner surfaces, but they are completely united by intermediate specimens.[7] Haas [29] reduces the hundreds of named forms of palearctic unionids to 20

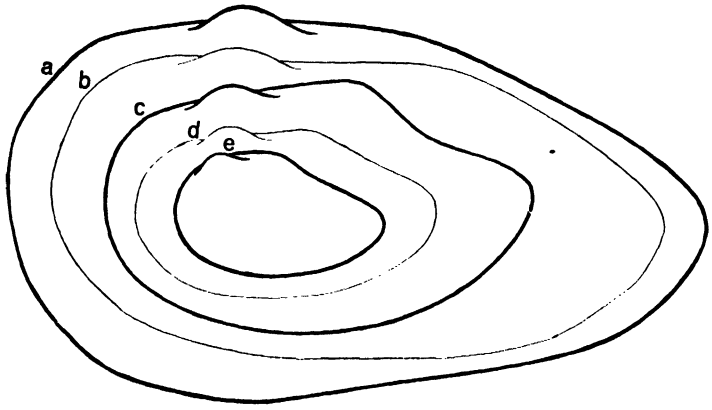


FIG. 7. Outline, average size, and shell thickness (heavy contour = thick shell) of five forms of *Anodonta cygnea* at their centers of distribution: *a, forma typica; b,* var. *cellensis; c,* var. *piscinalis; d,* var. *anatina; e,* var. *lacustrina.* After Buchner.

species. The genus *Pisidium,* the appropriately named *Dreissena polymorpha,* and the snails of the families Lymnaeidae and Planorbidae exhibit a similar variation. The lakes of the glaciated area in Europe are inhabited by fishes of the salmonid genus *Coregonus,* whose variability is such that each well-isolated lake is inhabited by well-defined subspecies of one or more forms, the degree of divergence being roughly proportional to the distance between the lakes. The species of cladocerans, especially of the genus *Bosmina,* vary in form from lake to lake [69] (Fig. 8). Each of the Great Lakes of North America except Lake Huron has its own form or forms of one or more species of lake herring or cisco, salmonids of the genus *Leucichthys.* Lakes Huron and Michigan share three such forms that are not found elsewhere. Many smaller lakes of that region also have their own species or subspecies; thus the species *L. bartletti* is known only from Siskowit Lake on Isle Royale in Lake Superior.[36]

Variation in the environmental conditions is in general less exten-

sive in flowing water, though some important variation in the composition of the water of brooks and rivers does occur and affects the faunae concerned in the same way as in lakes. The black-water rivers of South America, with their high content of dissolved humus materials, differ in the composition of their faunae from the neighboring streams. The bog-fed brooks of Scandinavia lack the alpine turbellarians. These are exceptions.

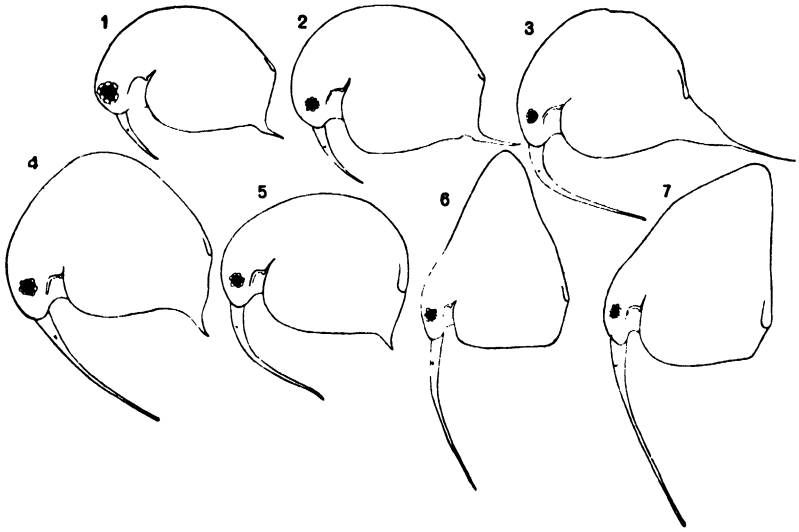


FIG. 8. Summer forms of *Bosmina coregoni* from various Baltic lakes: 1, Lake Paarstein; 2, Lake Rzumo; 3, Lake Wolzig; 4, Lake Luggewiese; 5, Lake Steinkrug; 6, Lake Dlusitsch; 7, Lake Wolzig. After Rühe.

The effect of isolation in preventing interbreeding is more marked in the rivers than in lakes. The different large drainage basins of Germany have different species and varieties of mussels.[13] The well-isolated rivers of Patagonia, flowing into the Atlantic and separated by semi-arid plains, are inhabited by distinct faunae of fresh-water mollusks.[62] The widespread fresh-water crustacean *Caridina niiotica*, found in Africa, Bengal, and Celebes, has 8 different subspecies besides the one in the Nile. The fish genus *Rhamdia* (*Pimelodus*) has split into at least 15 species in the rivers of Central and South America, south of the La Plata, a species for each river system.[39] In North Africa each river is inhabited by different species of *Barbus*,[28] and in the Rocky Mountains each river system tends to have its own species or subspecies of trout.

In spite of the vastly increased opportunities for isolation in fresh water, the great number of species that might be expected from the abundance of isolated areas is not realized in fact. The modifications of mollusks, crustaceans, and fishes cited above are in part transitory, arising from the direct influence of the given external conditions, and are not genetically permanent species characters. Many invertebrate fresh-water animals have a world-wide distribution. The animal species of fresh-water plankton are to a large extent cosmopolitan (copepods, for example, but with the exception of the Centropagidae, and cladocerans).[22] Of bottom-dwelling forms, Protozoa and rotifers are very widespread. Thirty-six species and varieties of rhizopods from the region of Lake Tanganyika [72] contained only 3 new forms, and of 213 rotifers from the same territory only 21 are endemic.[10] The fresh-water sponge *Ephydatia fluviatilis* occurs in Europe, North America, South Africa, Australia, and in the Malay Archipelago, and most sponge genera have a very wide range. All the fresh-water coelenterates and sponges of Australia belong to European genera. Two species of *Hydra* and three of *Spongilla* are regarded as specifically identical with the European forms.[18] Many of the rhabdocoel turbellarians of fresh waters are very widespread.[25] These are all, to be sure, adapted for wide distribution by their resting stages, which protect them against the drying up of their habitats.

Even the snails and mussels of inland waters have surprisingly large generic and even specific ranges, though they are incapable of active migration across land barriers. The families Lymnaeidae, Planorbidae, Physidae, Ancylidae, and Unionidae have a world-wide range. Even the exceptionally isolated New Zealand, with its highly specialized fauna of eleven genera of fresh-water mollusks, has only one endemic genus.[66] The same phenomenon characterizes fresh-water insects. The tropical and temperate representatives of the Dytiscidae are more alike than in any other family of beetles. Among species, the dytiscid *Eretes sticticus* is present on five continents, and *Cybister tripunctatus* has a range nearly as extensive.[14] Some genera of water bugs, such as *Ranatra* and *Notonecta*, also have a wide distribution.

There is thus a contradiction between the high degree of isolation of bodies of fresh water and the low degree of differentiation of their faunae. The presence of the same species in the tropics and in the temperate zones is not explainable by a greater uniformity of environment in fresh waters as compared with terrestrial environments.[55] A satisfactory explanation of this contradiction was presented by Thomas Belt, who called attention to the transitory nature of lakes

and streams in terms of geologic time.[5] Ponds and lakes in general have a short life; a number of factors combine to destroy them. Rivers and brooks fill the lakes in mountainous regions with detritus. Lake Constance is constantly being filled by the Rhine, and it is estimated that this process will be completed in 12,500 years; the life of Lake Geneva, Switzerland, into which the Rhone brings an annual sediment of 2,000,000 cu.m., is reckoned at 45,000 years, and that of Lake Lucerne is placed at 23,000 years. Shallower ponds and oxbows, whose banks are covered with vegetation, gradually disappear as the result of the encroachment of the vegetation; plant remains raise the level of the bottom; marsh and bog plants grow out farther and farther toward the middle and limit the open water until it is finally entirely gone. The process of extinction proceeds rapidly in a senescent lake when once a bog margin and false bottom have been established.[38]

Many lakes and rivers fall victims to drought, and, as they dry up, their faunae are destroyed. During a part of the Quaternary, the desert valleys of the Great Basin in North America were lake basins of vast extent, known to geologists as Lake Bonneville and Lake Lahontan. The surface of the latter at its maximum was 167 m. above that of the present Pyramid Lake.[24] Lake Ngami in Bechuanaland was a real lake only 50 years ago; it is now a marsh in process of disappearing. Many Siberian lakes are in process of drying up; the Sary Kupa, for example, at 50° N. latitude, formerly an elliptic basin with a longer diameter of more than 100 km., was later broken up into 20 considerable lakes.[60] With the disappearance of such waters, their faunae must be extinguished, at least such elements as were effectively isolated and hence on the way toward changing to new species. The frequent intercommunications between river systems, including the well-known phenomenon of stream piracy, have also operated to break down the isolation of their faunae and to further the general phenomenon of wide distribution in fresh-water animals.

There are, however, a number of large fresh-water basins in which the faunae differ strikingly from the usual fresh-water aspect and exhibit the results of long-continued isolation. They have numerous endemic species and genera, and their genera are strongly differentiated into species adapted to the various habitats available. All these basins are characterized by large size and considerable depth. The principal ones are Lake Baikal (35,000 sq. km., 1706 m. deep);[90] the three central lakes of Celebes (Posso, 420 sq. km., 440 m. deep, Towoeti, 160 sq. km., 203 m. deep, and Matano 800 sq. km., 590 m. in

depth);[45] and the Great Rift valley lakes, Tanganyika and Nyasa, each with an area of about 35,000 sq. km. and depths of 1435 m. and 800 m. respectively.[4] Recent studies of the fresh-water fauna of Lake Ochrida in the Balkan Peninsula show that it is to be added to this list, probably with some other Balkan fresh waters.[65, 80] (See Chapter 18.)

In faunal composition the Caspian Sea, with a surface of 439,000

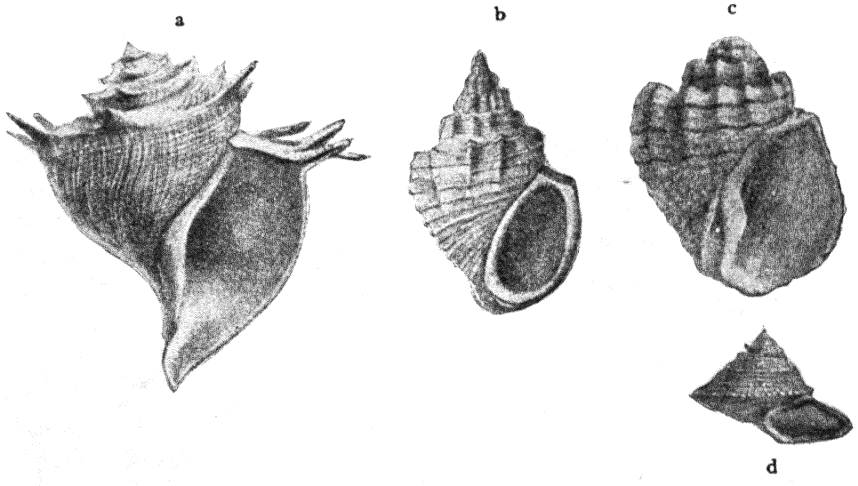


FIG. 9. Tanganyika snails: *a, Tiphobia horei; b, Paramelania damoni; c, Lavigeria diadematata; d, Limnotrochus kirki.* After Lauterborn.

sq. km. and a depth of 946 m., compares more closely with these bodies of fresh water than to any of the partially isolated seas.

Geographic isolation on land

Islands are unquestionably the most effectively isolated of land areas. They are comparable with inland lakes and ponds in being surrounded completely by an effective barrier; but they differ from these bodies of water in their relative permanence. Islands therefore present an abundance of endemic species and genera, and even some endemic families and orders. The amount of endemism is inversely proportioned to the accessibility of the island from other, more thickly populated areas, usually the nearest mainland. The strength and regularity and direction of the wind are also factors in populating islands. Endemism on islands is most frequent in forms for which the difficulty of reaching the island is most extreme, so that new in-

crements of the parent form are unlikely to follow. Endemic species are thus sometimes more numerous among mollusks and reptiles than among insects, and more numerous in the latter group than among bats and birds. The Antilles have a large fauna of fresh-water snails in common, but their land snail faunae for the most part differ from island to island; the eggs of the fresh-water snails are easily distributed by aquatic birds, whereas the land snails' eggs are dependent upon driftwood and storms. The converse relation may appear, as in the Polynesian islands, where there are endemic species of birds although the lizards are identical from island to island. Similarly, in Melanesia fruit bats with powerful flight have formed numerous endemic species in several archipelagoes. Speciation in these flying forms may be explained as the result of isolation made effective by the development of homing instincts.[74]

The duration of the isolation is naturally of great importance for the amount of change undergone by the fauna of an island. Unfortunately this very amount of differentiation is usually the only evidence available for the estimation of the age of an island. In the very recently repopulated Krakatoa no differentiation has taken place. On very completely isolated ancient islands the genera are frequently split up into numerous species.

The amount of endemism on an island may or may not be influenced by the mode of its origin, whether by the breaking up of a former continental connection or by independent development as a volcanic or coral island. The degree of isolation in either case may be the same. The composition of the fauna is different, however—a phenomenon to be examined in more detail later (Chapter 26).

The Hawaiian Islands are the most completely isolated archipelago, more than 3000 km. distant from the American coast and as far from Samoa. They form a group of volcanic islands extending from northwest to southeast for about 475 km., and the individual islands are well separated. Endemic forms consist of large series of species of certain genera and smaller series of related genera, which combine into families. All the species and three-fourths of the genera of land snails are endemic. The family Achatinellidae is especially notable, with only a general relationship to the widespread Polynesian genus *Partula* and with highly primitive characters in its sexual apparatus and mantle.[61] This family, with 12 genera and subgenera and more than 300 species, is confined to the Hawaiian archipelago. Some genera are confined to special islands, *Carelia* to Kauai and *Thaanumia* to Oahu; *Perdicella* and *Newcombia* are found only on Molokai and

Maui; and *Amastra* and *Leptachatina* have endemic species on each of the principal islands. Each of the valleys radiating from the mountains is often characterized by a special series of species.[27,42] Zimmerman in 1948 knew of over 5000 species of Hawaiian insects, of which 3722 were endemic, in contrast to earlier reports in *Fauna Hawaiiensis* * of about 2700 endemic species out of a recorded total of 3325. Important elements of the fauna are not confined to the Islands. Wasps of the genus *Odynerus*, with more than 100 species, exhibit a greater development in Hawaii than in any other area inhabited by this almost cosmopolitan genus.[93] The aquatic birds belong for the most part to widespread species, and only 5 out of 24 species are endemic. Certain finch-like forms that look like thrushes are wholly confined to the islands, and 9 genera with about 40 species form a special family, the Drepanididae. Each island containing a bit of the original forest had its special species of each of the 9 genera, and *Hemignathus* tends to have 2 species, one large and one small, on each of the larger islands.[3]

The Galapagos Islands present similar faunal characteristics. This archipelago is situated on the equator about 900 km. west of Ecuador; two ocean currents flow past them, one from the coast of Peru and one from the gulf of Panama, but they are in a region of relatively little wind. The land snails, whose dispersal may have been favored by oceanic currents, are little specialized; most of the 76 named species are endemic,[12] but the genera are without exception found also in Central or South America. Of the 59 genera of birds, 9 are endemic. These include two water birds, the flightless cormorant *Nannopterum* and the fork-tailed gull *Creagras*, and 7 land birds, the Galapagos ground dove *Nesopelia*, the mocking bird *Nesomimus*, and 5 genera of the endemic family of finches Geospizidae. Sixty-two of the 108 species recorded are land birds, and all these are endemic, except for the bobolink, barn swallow, and osprey. The endemic genera of land birds include 49 of the 59 endemic forms. Some of these species occur on only one island, others on several, sometimes with the formation of subspecies.[83] Their relations are primarily American. The giant land tortoises, from which these islands take their name, are represented by 14 species on the 9 largest islands.[86] The genus of lizards *Tropidurus* is represented by separate species or subspecies on each of 12 islands.[85]

The Azores present a contrast with the above-named archipelagoes,

* See citations by Zimmerman.[93]

as their fauna exhibits much less endemism. This group is composed of 9 volcanic islands 1400 km. from the Portuguese coast. The only lizard is identical with a Madeiran species. Of the 122 kinds of birds recorded, less than 30 breed on the islands, and only 5 of these have become differentiated sufficiently to be recognized as Azorean races.

It may be assumed with certainty that Madagascar, an island almost large enough to be called a small continent, was once united with Africa. Matthew,[51] to be sure, regards Madagascar as an oceanic island never connected with the adjacent continent. The rich amphibian fauna and the diversity of the fauna of lizards and snakes indicate connection with Africa. The Madagascan fauna appears to have had a long and undisturbed period of development in isolation, and the resultant peculiarity of its animal life makes it necessary to place the date of connection far back in geologic time. The dominant genus of earthworms is *Kynotus*, with 10 species, confined to Madagascar. Among snails the genus *Tropidophora* has a great number of Madagascan species, with few elsewhere, while *Ampelita* and *Helicophanta* are endemic. Forty-two of the 46 Madagascar genera in the cetonid family of beetles are confined there. The amphibians and reptiles are represented almost entirely by peculiar genera, some quite without existing related forms in Africa. Two endemic genera of iguanid lizards, the family otherwise found only in the Americas and in the Fiji Islands, and two of boid snakes, either identical with or very closely allied to the American genera *Constrictor* and *Boa*, occur in Madagascar.

Of 28 genera of mammals, exclusive of bats, all but 3 are endemic. Through the long-continued isolation, 3 distinct families have been developed (or preserved). These are the primitive insectivores Centetidae, with 7 genera and 23 species; the rodent family Nesomyidae, with 7 genera and at least 12 species; and the subfamily of lemurs, Lemurinae, with 12 genera and about 50 species. The Centetidae have undergone adaptive radiation; some live like shrews or hedgehogs, others in the water like muskrats, and still others burrow like gophers.

The dependence of the formation of species under isolation upon the vagility of the groups of animals concerned is well illustrated by the fauna of Celebes. Of the species of birds 28% are endemic, of reptiles 36%, of amphibians 40%, of mammals 40%, of land snails 79%, and of land planarians 91%.

Islands close to the mainland are often little differentiated in their

fauna; the genera and often the species are identical with those of the mainland. Trinidad is zoögeographically indistinguishable from adjacent South America; of 65 mammals and 64 reptiles very few are confined to it, and only 13 out of 63 land snails are endemic.[77] It is true that about one-third of the 41 fresh-water fishes are endemic; even so, they are mostly local races of widespread forms, though with 2 endemic genera.[18]

The fauna of Tasmania is closely similar to that of Victoria south of the Dividing Range; the species are identical or in vicarious pairs; there are no endemic genera of vertebrates, disregarding the Tasmanian wolf, *Thylacinus,* and the Tasmanian devil, *Sarcophilus,* which are recently extinct in Australia, or of fresh-water fishes or land and fresh-water snails. The vagility of the respective groups governs the amount of endemism in species; only 10% of the species of birds are endemic, as compared with 81% of the land snails.[79]

Environmental difference in the isolated area is also an important factor for the transformation of isolated species, but isolation operates to produce new forms without differences in habitat. Thus the genus of birds *Coereba* of the family Coerebidae occurs in Central and South America and in the West Indies; with 13 subspecies on the mainland, there are 19 in the Antilles, with an endemic form on each island.[34] In the Rhio-Linga Archipelago, a series of small islands off the east coast of Sumatra, with an area of about $\frac{1}{90}$ that of Sumatra, there are no less than 8 well-distinguished subspecies of dwarf deer, Tragulidae, whereas all the similar deer on Sumatra and on the Malay Peninsula north to Tenasserim belong to a single species, *Tragulus napu.*[54] There can be no question that the habitat conditions on these small islands are less varied than in Sumatra and the mainland area. The islands of the Aegean Sea each have special varieties of the clausilid snail *Albinaria coerulea,* in spite of the great uniformity of the insular conditions. An apparently innate variability has led to extreme fragmentation of the lizards of the genus *Lacerta* into recognizable races, island by island and islet by islet, in the Mediterranean island groups.[41,53]

The mainland does not afford the possibility of such complete isolation as do islands. A few areas are surrounded by mighty barriers, such as the 3600-m. high plateau of Tibet, bounded on the north by the Kwen-lun, Altyn-dag, and Nan-shan and on the south by the Himalayas. The Tibetan mammal fauna is perhaps the most peculiar of any on a continental area; 5 of the 28 genera and 30 of the 46 species are endemic.[6]

The upper levels of high mountains or of mountain ranges that rise from plains to a considerable height are as effectively isolated as islands for stenothermal cold-tolerant animals for which the warmer lowlands are impassable barriers. Mountain faunae accordingly afford numerous evidences of the formation of species and subspecies resulting from isolation. The mountain ranges that extend in interrupted series from the Pyrenees to the Himalayas and toward Syria and Abyssinia have their special subspecies of ibex, distinguished by the form of their horns but otherwise closely similar and still completely fertile with each other.*

The mountains of middle and south Germany have numerous geographic races of the carabid beetle *Carabus silvestris*, usually peculiar to the special districts. Vicarious beetles are known from the mountains of Africa, such as the genus *Carabomorphus* on Kilimanjaro and the Gurui Mountain, and *Arinodromus* on Kilimanjaro and the high plateau of Lisca in Shoa.[44] Mount Kina Balu in North Borneo has a very characteristic fauna. An unusual number of the species collected there by Whitehead in his expedition of 1886 were new to science, and are probably confined to this mountain; of 21 mammals 6 were new; of 161 birds of 128 genera 41 species and 6 genera were new; of 52 amphibians and reptiles 16 were new, with 4 new genera; one of the 4 species of fishes belonged to a new genus and species; and the beetles included also an unusual number of new and remarkable forms.[91]

Valleys are isolated by mountain ranges as mountains are by plains. Thus each of the river basins of Borneo has its special orang, and the beetles of the genus *Carabus* and many Lepidoptera form special varieties in the isolated valleys of the Alps. The well-known isolation of snails in different valleys in Hawaii furnishes a still better illustration of this point.

The photonegative birds of the forest floor in the Amazon basin are effectively isolated by the broad rivers and their overflow areas. Thus, with identical environments, 41 pairs of species are found on the north and south sides of the Amazon.[78]

The isolation of cave animals is effective. As they are photonegative and avoid dry air, they are unable to migrate from one hollow to another unless there are subterranean connections; their habitats are as isolated as ponds for fishes or as islands for lizards. Caves, how-

* *Capra pyrenaica* in the Pyrenees; *C. ibex* in the Alps; *C. severtzowi* and *C. raddei* in the Caucasus; *C. sibirica* and its varieties in Persia, Tibet, and the Himalayas; *C. nubiana* in Sinai; *C. walie* in Abyssinia.

ever, are not so transitory as inland waters, and they afford long-continued uniformity of habitat conditions. A high degree of differentiation into species in cave-dwelling forms is the frequent consequence. The small snails of the genus *Lartetia*, related to the Hydrobidae, are present in numerous places in the Jurassic and Muschelkalk region of southwest Germany. They live in underground waters and reach the surface in springs, in part as empty shells, in part also alive. With great constancy of generic characters, they are very variable in minor features (Fig. 10), and the species fall into geographic groups, each

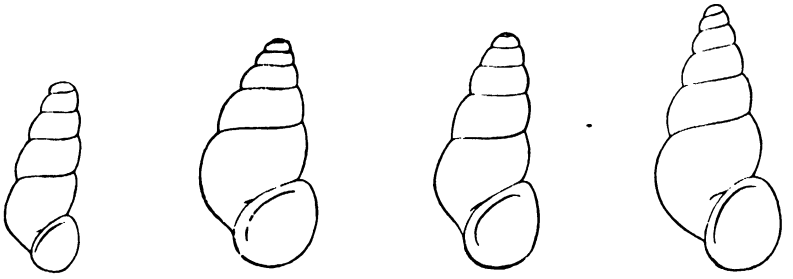


FIG. 10. Various species of *Lartetia*, from left to right: *L. pellucida*, *photophila*, *putei*, and *acicula*. After Brauer.

type of *Lartetia* corresponding to a special type of spring.[23] Of the pulmonate snails the genus *Zospeum* is widely distributed in caves and is broken up into 30 or 40 forms.

Beautiful examples of the effect of isolation in caves are presented by the cave beetles in the limestone caves of middle and south Europe. The carabid beetles *Anophthalmus* (a subgenus of *Trechus*) is represented by numerous species in caves, and these form subspecies confined to a single or to a few neighboring caves. The silphids of caves, subfamily Leptoderinae, are so split up that almost every cave has its special species. These represent a number of genera that are not very sharply differentiated.[73]

Widespread species form local races and subspecies without special isolation. Thus the lions, zebras, antelopes, and giraffes are split into a number of geographic races, which are in part sharply defined and in part connected by transitional forms. The butterflies of Celebes are spread throughout the island, but each of the four peninsulas has its own local forms.[67] There is an endless series of geographic races of the Apollo butterfly *Parnassius apollo*, which ranges from Syria to Finland and from Austria to beyond Lake Baikal. The geographic variation in this butterfly is favored by an extraordinary individual

variability. The situation is similar with the goat chafer *Dorcadion.* Lack of wings and slowness of motion hinder its dispersal, so that numerous local races have arisen; ten varieties of *D. fuliginator* are listed in central Europe.[73] The South American butterflies of the family Erycinidae are extremely restricted to their places of origin by a tendency to avoid flight. The specimens of a given locality resemble each other like coins from the mint, but even the most insignificant change of locality may be accompanied by a slight but constant difference; the geographic races are accordingly innumerable. Other American Lepidoptera, such as *Heliconia, Melinaea,* and *Mechanitis,* have a similar behavior and distribution. The erycinid genus *Calydna* differs from its relatives in the possession of strong powers of flight, and in this genus the individuals of a species, even from widely separated localities, exhibit no appreciable variation.[75] Such geographic races, especially of mammals and birds, frequently exhibit no morphological differences and are distinguished primarily by means of coloration. Constancy of a character in a series of specimens, rather than the degree of difference, forms the basis for the recognition of subspecies in the practice of many American taxonomists.

Isolation and primitive forms

Another effect of geographic isolation is the preservation of groups from destruction by removing them from competition with their more advanced relatives. Of certain species, genera, families, and even orders, which formerly had a wide distribution, some remnants have been able to maintain themselves in isolated areas when barriers prevented the entry of more advanced competitors.

Thus *Lepus timidus,* elsewhere a mountain and arctic form, occurs at all levels in Ireland, where it is free from the competition of the European hare *Lepus europaeus.*[71] In Germany, where the two lizards *Lacerta agilis* and *L. vivipara* occur together, the former devours the young of the latter, and thus prevents its spread. *L. vivipara* is able to maintain itself only in areas where its enemy cannot live, especially in places without suitable sites for egg-laying or where the temperatures are too low to hatch them. Mountains above 1200–1500 m., the arctic territory, and bogs and swamps, even south of the Alps (for example, in Lombardy), furnish these conditions, and these are inhabited by *L. vivipara. Planaria alpina* is in competition with *Planaria gonocephala* and *Polycelis cornuta* wherever the water temperature has a range of variation of more than 6° C. At intermediate heights *P. alpina* is found only in the uppermost parts of spring brooks;

at altitudes where its competitors are excluded by the uniform coldness of the water, it is widely distributed.

Disappearing human groups have been crowded together in much the same way in unfavorable and inaccessible areas. Groups speaking a large number of apparently unrelated languages are found in the Caucasus, languages that seem not only to be unrelated among themselves but also unrelated to other known languages. There seems to be an accumulation of people representative of numerous linguistic stocks in such areas; in some cases, they represent remnants of stocks found nowhere else. Almost all the language groups of North America are represented in the relatively restricted area between the Pacific and the Rocky Mountains. In South America an astonishing number of languages is found on the slopes of the Andes, while the rest of the continent has no more than a dozen language groups.[84]

Australia affords one of the best examples of the preservation of archaic types. It is rightly called the land of living fossils. Here are found the only egg-laying mammals, with two genera, *Echidna* and *Ornithorhynchus;* with their numerous reptilian characters, these are veritable "missing links." With them lives the greater proportion of the surviving marsupials, which formerly ranged over Eurasia and North America but are now restricted to the Australian series, to a few South American genera, and to the North American opossum. The isolation of Tasmania has even preserved two species of predaceous marsupials, *Thylacinus* and *Sarcophilus,* which are extinct on the Australian mainland, where their remains are found in the Pliocene, and in Recent deposits in company with those of the dingo, which has evidently replaced them.[79] Southern Australia and Tasmania harbor survivors of the primitive crustaceans of the family Anaspididae, consisting of 3 monotypic genera: *Anaspides, Paranaspides,* and *Koonunga.* Their primitive character is shown by their relations with the Palaeozoic genera *Uronectes* and *Palaeocaris,* and their intermediate position between the two large and widespread orders, Schizopoda and Arthrostraca.

New Zealand is likewise the home of certain primitive relicts. *Sphenodon* is the sole survivor of a formerly widespread order of reptiles. *Liopelma* represents the most primitive of the families of frogs. The most primitive of all Lepidoptera, the hepialid *Palaemicra calcophanes,* lives here. It is so closely allied to the caddisfly genus *Rhyacophila* that it almost forms a link between the two orders.[76] New Zealand and Australia are the home of the primitive mygalid spider *Hexathele.*[64]

Underground caves are also a refuge for primitive forms. A large proportion of the cave snails of the Balkan Peninsula, including the genera *Meledella, Pholeoteras, Phygas,* and *Speloeoconcha,* is entirely unrelated to the present snail fauna of the surface and represents a remnant of a fauna no longer existent there.[88] Animals of subterranean waters are likely to be peculiar and primitive. The blind cave salamander *Proteus anguinus* has no relatives in Europe. In the same waters in which it occurs are found crustaceans of the genus *Troglocaris,* of a group whose representatives are otherwise absent in fresh waters in Europe. *Bathynella natans,* found in deep wells at Prague and Basel, is the only relative of the above-mentioned Anaspididae found outside Australia.[8]

Fresh water is an impassable barrier for many marine animals and plants. Animals that were able to adapt themselves to fresh water have thus been able to survive in it long after they became extinct in the sea. The simple coelenterates, *Hydra* and *Microhydra* and their relatives, are probably preserved only because of their adaptation to the fresh-water environment. The ganoids that dominated the seas in the Mesozoic survive primarily in fresh waters. The three remaining genera of the extremely ancient lungfishes are fresh-water forms. The more primitive bony fishes, the physostomes, make up a large majority of fresh-water fishes. Relatively few of the spiny-rayed Acanthopterygii have become adjusted to the fresh-water environment. The array of archaic fishes in fresh waters supports the theory that fishes originated in flowing inland waters and later entered the sea.

When such a protecting barrier is broken down, as happens nowadays chiefly through the agency of man, the primitive types are usually doomed. When, by accident or intent, modern animals are introduced in the isolated areas, they promptly demonstrate their competitive superiority over primitive inhabitants. Thus the marsupials of Australia are disappearing before the introduced cattle, sheep, rabbits, housecats, and foxes of the settlers. The endemic birds of New Zealand give way before the buntings, starlings, and goldfinches. In all parts of the southern hemisphere the native earthworms disappear with the introduction of Lumbricidae.

When man himself becomes an enemy, the effects are still more severe. The list of animals exterminated by thoughtless action is long. Steller's sea cow *Hydrodamalus,* the great auk, the dodo, and solitaire on Mauritius and Réunion, the passenger pigeon, the quagga,[2,31] and many more are gone, and still others are in danger

of extinction. Even the composition of the marine fauna is altered by the influence of man. Whales and seals disappear in consequence of hunting, and lobsters and soles are diminished in size and numbers on the fishing grounds. The same phenomenon has taken place with primitive human races, many of which have been exterminated, displaced, or absorbed by European or other dominant peoples. The original faunal conditions are to be found only in distant wildernesses, in high mountains, in tropical forests, and in the sea.

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7. *Historical Zoögeography*

THE DISTRIBUTION OF LIFE IS NOT SATISFACTORILY EXPLAINABLE BY THE present arrangement of barriers and land connections. There are frequent examples of areas formerly connected now entirely separated. North America, for example, has much more faunal resemblance to Eurasia than to South America. The fauna of southern Victoria agrees closely with that of Tasmania and differs markedly from that of northern Victoria and New South Wales. Many such facts are explained by the changes in the earth's surface in the course of geologic time. Stratified rocks, which cover great areas of the existing continents, show that there have been extensive invasions of these land areas by the sea. Conversely, numerous land masses now separated from the adjoining continents, notably Great Britain and many East Indian islands, can be shown to have been joined to them by dry land in the past. It is generally accepted that Great Britain was united with the European continent until recent times, geologically speaking, on the evidence of the presence of submarine continuations of the British and Norwegian river valleys to a depth of 60 m., of the presence of terrestrial deposits at a depth of 200 m. off Bremen, and of the presence of the remains of large land mammals, such as the mammoth and rhinoceros, on the Dogger Bank in the North Sea, where they are frequently brought up by fishermen.[11] The invasion of the continents by relatively shallow inland seas need not affect the general permanence of outline of the great continental blocks, whose limits are defined by the continental shelves rather than by existing shore lines.

The older concepts of the origin and evolution of life, based on the nebular hypothesis, require complete revision in the light of the much more adequate planetesimal hypothesis of Chamberlin and Moulton. Chamberlin's further theories of the larger outlines of geological his-

tory are of special importance to historical zoögeography. According to these theories, the earth has passed through a number of climatic cycles. From the extreme of humidity, warmth, and uniformity, which corresponds to base-level erosion of the continents, accompanied by extensive transgressions of the continental borders by shallow inland seas, the cycle passes to the opposite extreme of cold, aridity, and zonal climates, with accompanying uplift of the continents in adjustment to the isostatic balance and with renewal of erosion. The uniform base leveling corresponds to widespread deposits of limestones, ending in coal formations. The periods of uplift are marked by formations, often red in color, that suggest arid conditions; these periods culminate in great extensions of glaciers from mountains and from the poles.

Permanence of barriers

Mountains have been no more permanent than marine barriers. Some mountain ranges are younger than many types, even than some species, of animals. The very ranges that are now highest and most important as distributional barriers, such as the American Cordillera, the Himalayas, and the whole series of successive ranges from central Asia to the Alps and Pyrenees, were demonstrably uplifted in the Tertiary. Low mountain regions, on the other hand, may often be shown to be the remains of once higher ranges, whose importance as barriers has been reduced by long-continued erosion.

Steppes and deserts also change; they are formed anew or are recaptured for a renewed development of plant and animal life. There are traces of a recent steppe period in central Europe;[31] this was brought to an end by conditions favoring extension of the forests. Present-day records indicate a climatic change to warmer and drier summers, perhaps partially induced by drainage and stream regulation, with disappearance of forests and a return to the steppe in this area.[56] The ruined cities of the deserts in central Asia indicate that this region was inhabited at a relatively recent date. The deserts of the Great Basin in North America are in part the bottoms of extinct lakes. The impermanence of fresh-water basins and of rivers has already been discussed.

Climatic changes have gone hand in hand with the changes in the earth's surface. Should a submarine ridge arise between the British Isles and the Faeroes, the Gulf Stream would be deflected from the Scandinavian coast, and both the land and marine fauna of this area would be powerfully affected. It is legitimate to suppose that the

Tertiary opening of the Central American straits between the Atlantic and Pacific Oceans must have had far-reaching effects on ocean currents and climates. New mountain ranges influence the amount of precipitation in adjacent areas, while their upper levels, with lower temperatures, precipitous topography, less protection from sunlight, and more violent winds, offer wholly new conditions.

Changes in climate have also taken place independently of topographic changes.[8] Fossil remains of dense forests, such as are now to be found in the warmer parts of the temperate zone, are found in the north polar regions, where the length of the winters and the dryness of the air now make tree growth impossible. These remains indicate a warmer and more humid polar climate in the early Tertiary; [18] and similar climatic change in the south polar region is indicated by the discovery of silicified tree trunks in Kerguelen Island. On the other hand, there is abundant and conclusive evidence of the existence of a glacial period at the close of the Tertiary, during which a large part of the northern hemisphere was covered by glacial ice. In Europe the glaciers of the Scandinavian mountains and of the Alps extended far into the plains, and glaciers were present even in the intermediate ranges. The climate of the lowlands was wholly different from that of the present. A large part of North America, at the same time, was covered by a continuous continental glacier. The most recent period of glaciation was divided into interglacial periods during which animals intolerant of cold invaded northern regions, only to be driven out by a new advance of the ice sheet. Traces of glaciations in much more remote epochs may be observed in many regions, even in the tropics. The presence of coral reefs of earlier geological epochs in northern latitudes also indicates a warmer climate of the contemporary seas, for reef corals are now restricted to the tropics and require a minimum water temperature of 20° C. Marine deposits of Iceland and the Arctic of relatively recent periods exhibit a fauna now found only far to the south.

Since barriers are important for the evolution of animal forms and have a direct effect upon distribution, it is evident that the past rearrangements of land and sea and of other connections and barriers must have been of profound influence in the dispersal of animal life on the earth's surface. Satisfactory explanations of present faunal relations may depend on the recognition of the presence of former connections or barriers. Zoögeography must reckon with time as well as with space.[62]

On the basis of evolutionary theory, we must assume that, accidental

dispersal or extreme vagility aside, every natural group, whether species, genus, or family, must inhabit a continuous area, or an area that has at least been continuous or connected at some time during the history of the group. Such continuity is primarily a continuity in time, for the various connections that have influenced the dispersal of the group need not have been contemporaneous. Forms with a common ancestry must of necessity have had a common center of origin.

There are certain modifying corollaries to be added to this basic principle. Wallace states that "two identical species have never been developed independently in widely separated areas"; this statement applies equally to groups of higher rank. In the sense that different ancestral forms could not give rise by convergence to identical descendants, this is unquestionably valid, for the number of separate characters that would have to fall in line is unthinkable. Nevertheless, identical varieties may arise from the same stock in widely separated localities if they arise as modifications dependent on the influence of the same conditions. The widely distributed appendiculate *Frittilaria borealis* appears in the same subspecies (recognized as the *forma typica*) in both the north and south polar seas and may be the persistent ancestral type from which the form in intermediate seas is derived. The contrary hypothesis, that the two populations of *borealis borealis* have been independently derived from the tropical form, is also maintained.[12] Parallel evolution is indicated in some supposed genera. The snail genus *Potamides* of brackish water (India, Africa, California) is derived from the marine *Cerithium*. It is much more probable that different *Cerithium* species have developed into the various *Potamides* species under the influence of brackish water in the different parts of the world than that all the species of *Potamides* are to be derived from a single ancestral form. It would perhaps be better not to speak of the genus *Potamides* but to refer to *Potamides* forms of the various *Cerithium* species.

The center of origin is sufficiently obvious in many groups of animals. Thus the numerous species of snails of the family Achatinellidae are confined to the Hawaiian Islands, and neither living nor fossil forms of this group are to be found elsewhere. It must have arisen here from ancestors related to the Polynesian *Partula*.[37] The same general situation holds for the endemic Hawaiian family of birds, the Drepanididae (cf. Chapters 6 and 26).

Another example of a natural group with continuous range is afforded by the penguins. The sea is not a barrier for them, and, though

their headquarters are on antarctic and subantarctic shores, a few species range north to the southern tips of the three southern continents and to the South Island of New Zealand. One species has reached the Galapagos Islands on the equator, but its northward spread has been favored at this point by the cold waters of the Humboldt Current. Their fossil remains are likewise known only from the southern hemisphere.[25]

Such continuity of distribution is by no means invariable. The ranges of families and genera and even of species are often broken by broad areas in which the forms in question are absent. One may even say that discontinuity is the rule for the higher groups, even perhaps for genera, but certainly for families and orders. The more remote the period of common origin of the related forms, the greater will be the probability of discontinuity of range in the modern survivors. There are numerous instances in which a former continuity of range can be demonstrated to explain the present discontinuity. The range of the Pyrenean shrew *Myogale pyrenaica* is widely separated from that of its relatives in the steppes of southern Russia, but fossil remains of this genus are found in the terrestrial deposits of France, Belgium, England, and Germany, where it has presumably become extinct in consequence of changes in climate and vegetation. The varying hare *Lepus timidus* is represented in Ireland and the Alps as well as in north Europe and Asia; the ptarmigan *Lagopus mutus* has representatives in the Alps, the Pyrenees, and the Caucasus. These instances, in which there are isolated outliers of an otherwise arctic range, are amply accounted for by the southward extension of a cold climate in the glacial period. Subfossil bones testify to the former presence of the ptarmigan and alpine hare in central Europe; with the retreat of the glaciers, they withdrew to the north and to the higher altitudes of the mountains. A whole series of arctic animals (and plants as well) are to be found on Mount Washington in the White Mountains of New Hampshire. Their relatives, usually of the same species, live in Labrador and Greenland.[15] Discontinuity of range is accordingly explained by extinction in the intermediate areas, whether in consequence of altered habitat conditions or specifically through competition with more advanced forms.

The converse reasoning is also possible, and climatic changes may in inferred from the composition and distribution of faunae. The abundance and wide distribution of the remains of steppe animals, such as the saiga antelope, horse, gopher, and jerboa, in alluvial deposits make it probable that a steppe period followed the glacial period

in central Europe, although the evidence for the existence of such a steppe period is far from being as abundant or conclusive as that for glaciation.[31] Such distribution of steppe conditions in the past would explain numerous instances of discontinuous ranges, such as that of the shrew, *Myogale*, mentioned above. In a limited arid area in Moravia, covered only with a little coarse grass and a few stunted bushes, Burr found more than eighty species of Orthoptera that were wholly unlike those of the surrounding territory and exhibited a high degree of resemblance to those of the Volga valley. He explains this area, probably correctly, as a faunal island, a relict of the steppe period.[58] The evidence from reptiles with Great Plains affinities in the central United States indicates a similar postglacial eastward (instead of westward) extension of a grassland fauna in North America.[46]

As has been stated previously, such survivors of a former period, when habitat conditions and faunal relations were different from those of the present, are termed relicts, and one speaks of glacial relicts, steppe relicts, marine relicts, etc. The changed conditions may not be climatic ones, and every kind of habitat factor may be involved. There are relicts from periods when the competition in an animal community was different. The rise of new competitors, better adapted than the older forms to engage in the struggle for existence, leads to the destruction or dispersal of the older forms, and the few that survive, whether by isolation or by exceptional ability to meet competition, appear as anachronisms, i.e., relicts, in the changed environment. This is commonly true of relict forms in the sea, where the physical conditions have undergone relatively little change. The genus *Nautilus*, for example, was a member of a flourishing family in the Mesozoic but is now the sole survivor of the tetrabranchiate cephalopods and occurs in only a few species in the Pacific and Indian oceans. The few modern genera of pentacrinids are confined for the most part to deep seas and represent a group that flourished in the Jurassic and Cretaceous. The few modern ganoid fishes have become adapted to fresh water, where they have escaped the brunt of the struggle for existence with the more modern bony fishes, which have supplanted the ancestral Mesozoic ganoids in the sea. Whatever the reasons for the occurrence of relict groups, they indicate that some sort of change in their physical or biotic environment has taken place.[16]

The satisfactory explanation of the discontinuity of distribution of certain animals by demonstrable changes in the environment, as in the glacial and steppe relicts, makes it possible to conclude that in other instances present discontinuities are based on changes in a former

continuum. One explanation of such discontinuity of related groups is that barriers to dispersal of some sort have arisen, such as mountain ranges, deserts, climatic changes, rise of superior competing forms, or extensions of the ocean. In respect to marine life, bodies of land separating formerly continuous parts of the sea play the same rôle in producing discontinuous or vicariating distributions.

Another explanation of bicentric distribution is found at times in the extinction of forms from the intermediate area. There are at present two distinct populations of the Hudsonian curlew breeding, migrating, and wintering on opposite sides of the Americas. Although these populations seem to have no opportunity to meet and mix, no racial distinction has been detected, and their separation seems to have been comparatively recent. It is possible that the connecting link, a Mississippi valley group, was wiped out, along with the Eskimo curlew, in the period since the early nineteenth century.[57]

The mammalian faunae of Eurasia and North America exhibit a high degree of similarity, in spite of the fact that the parts of the sea that separate them are impassable barriers for the larger animals. The number of genera in common is large, and the species of the same genus are frequently so closely allied that they may be regarded as subspecies of the same form. The beaver, moose, reindeer, and bears are thus closely related, while the wisent and bison, the lynxes, and the various deer are only a little more distinct. This resemblance extends to such Tertiary animals as horses and camels, some of which are now extinct in one or both areas. The supposition that a land connection existed between the two continents in geologically recent times and that such a connection must have existed at various times in the Tertiary thus acquires a high degree of probability.[26] This land bridge probably existed at Bering Strait and across Bering Sea and may have included part of the Arctic Ocean. The shallow seas in this region favor this hypothesis. The great similarity between the fauna of Great Britain and that of central Europe leads to the conclusion that a land bridge existed here also, and this hypothesis is supported by geological evidence.

An example of similar faunal relations is presented by the marine faunae on the two coasts of Central America. Though the isthmus of Panama now forms an impassable barrier, the littoral fauna of the Pacific and Atlantic coasts in this region exhibits a large number of genera of fishes and invertebrates in common, and within these the peculiar phenomenon of "paired species," the *geminate species* of Jordan,[23,35] the direct relative of a given species being one of the

opposite coast instead of some congener on its own coast. Jordan demonstrated at least 100 such pairs of species of fishes, and the phenomenon is clearly represented in various groups of invertebrates. There are, for example, 33 genera of decapod crabs listed by Rathbun as confined to tropical American waters and represented in both the Pacific and Atlantic. The subject is reviewed by Ekman,[12] who joins in the opinion that all this evidence indicates former broad water connections between the Atlantic and Pacific in the Panama region and perhaps also elsewhere across Central America.

This is in full agreement with the explanation of the deep-seated differences between the Tertiary mammalian faunae of North and South America as resulting from long isolation of the South American continent. The two continents are thought to have been connected in the Upper Cretaceous and perhaps in the Paleocene, the connection continuing at most into the early Eocene. Separation extended from early Eocene to Mid-Pliocene, probably to late Mid-Pliocene.[31,51] The geological evidence supports the zoögeographic indications.

These examples show how both periods of union and the appearance of separating barriers may be dated by the comparison of the geologically older elements of the faunae of given areas. Similarity (i.e., homology) of faunae speaks for union at the period of origin or active dispersal of the forms in question; differences may be supposed to have arisen since the date of separation.

The Sarasins[42] analyzed the fauna of Celebes, especially the mollusks, amphibians and reptiles, and birds, with reference to relations with the inhabitants of the surrounding islands. On the basis of their evidence it appears very probable that the present fauna has reached Celebes by four distinct routes since the emergence of this island in the Eocene. The groups investigated, which are taxonomically widely distinct and also have decidedly different ecological relations, exhibit surprisingly comparable relations, which increases the reliability of the conclusion. The groups examined are distributed as follows:

	Widespread Forms and Uncertain Endemic Species	Proportion from the Java Bridge	Proportion from the Philippines	Proportion from the Moluccas	Proportion from Flores
Mollusks	30.3%	21.4 %	23.3%	15.1%	9.9 %
Reptiles and amphibians	17.6	37.95	26.4	11.1	6.95
Birds	28.8	25.6	16.0	19.6	10.0
Average	25.6	28.3	21.9	15.3	8.9

It is similarly evident that a part of the fauna of South America, and of the mammalian fauna in particular, is of much later origin than the remainder. The Tertiary separation of this continent extended through a period of most active evolution of the mammals of the northern hemisphere. The older Tertiary rocks of South America contain remains of marsupials, edentates, hystricomorph rodents, and platyrrhine monkeys, but remains of the present South American carnivores, and of tapirs, peccaries, deer, and llamas, are wanting. It is evident that the latter series emigrated later and arrived after the re-establishment of the connection with North America. An exchange of forms took place at this time, for the armadillos and porcupines of North America are likewise relatively late arrivals, contemporary with an invasion of ground sloths and glyptodonts, which reached Pennsylvania.

Conclusions as to former land connections and former climatic arrangements may thus be based upon zoögeographic data, and, if there is abundant palaeontological evidence, such changes and rearrangements may be established and dated with some degree of certainty. Zoögeography thus becomes an important aid to geology, specifically to palaeogeography, and many have regarded this form of distributional study as the capstone of the zoögeographic structure. The value of zoögeography for the elucidation of former land connections seems to be the higher, inasmuch as geologic evidence in this direction is unavailable at the bottom of the sea. F. Sarasin even refers to zoögeography as a form of submarine geology.[40] Most hypothetical former land connections are based on the present distribution of animals.[52,53]

The probability and possibility of the conclusions derived from these premises must be examined with especial care. Palaeogeographic maps should be based on geological and palaeontological, as well as neozoölogical and neobotanical, evidence, but these three elements are of very unequal value. The geologic evidence of the existence and extent of former seas, which have left their deposits in areas now continental, is most certain. Land connections, deduced from the correlation of stratified rocks in areas now separated by seas, are less convincing. Palaeontology, from the identity or differentiation of fossil faunae, is sometimes able to conclude with a high degree of probability on the nature of the contemporary connections or separations. The data of palaeontology are meager for the most part, so that only rarely, as in the question of the former connection of North America and Eurasia, is this kind of evidence at all adequate.

The principal and often the only source of evidence for the former existence of land connections remains in the data of zoögeography; but this evidence is least reliable and becomes progressively less useful as the period of the supposed connection becomes remote. As accessory evidence, to support and illustrate the conclusions of geology and palaeontology, especially with regard to geologically recent changes, the phenomena of animal distribution have a high value. When employed alone, they are of doubtful importance, and even a large amount of evidence must be interpreted carefully and critically.[48]

Such critical care has only too often been wanting, and this field of zoögeography has become a clearing house for fantastic combinations. From Forbes through von Ihering and Scharff to Uvarov,[59] the tendency to explain facts of animal and plant distribution by assuming the presence of land bridges has been uncontrolled. The unbridled hypotheses concerning the rise, displacement, and connection of land masses have left scarcely a spot which has not at some time been involved in a land bridge.[16] In spite of the repeated warning of conservative investigators, some zoögeographers continue to "make continents as easily as a cook makes pancakes" (Darwin).[11]

The opinion of geologists should carry the greatest weight in the reconstruction of former land connections. Unfortunately, however, geologists are not at all agreed on the fundamental question of the permanence or impermanence of the continental land masses. In view of the numerous changes in the shore line of present land areas in former times and of the widespread presence of marine deposits on the continents, there was at first no objection to the assumption that any desired part of the ocean might have been occupied by land, and land connections were invoked to explain similarity of geologic structure or faunal resemblance even when they involved broad oceanic areas. Dana [9] was the first to propose the theory that the continental and oceanic areas were essentially permanent. A. R. Wallace supported this position from the zoögeographic side, with the statement that the distribution of plants and animals could be explained without supposing radical changes in the extent of land and sea. The controversy over this question is by no means at an end. Jeffreys [22] and Matthew [27] defend the permanence of the continents (with the inclusion of the continental shelf) and of the oceans. Suess [55] and Haug [17] represent the opposing camp. Dacque,[7] after weighing the evidence on both sides, leaves the question undecided. Wallace [60] assumed a fixed oceanic depth of 100 fathoms as the maximum over which former land connections were possible, and this is plainly an inadequate view. The

whole geological structure of the area, the direction of submarine ridges, and the width of the intervening ocean must be taken into consideration, together with the faunal relations, in the reconstruction of former land connections.

The first step in the comparison of related faunae, whose components are "homologous," i.e., taxonomically comparable, is to determine the degree of relationship between the animals in question. This is not always an easy problem, and the views of specialists on the relations within the same group may be divergent. Every phylogenetic conclusion, unless supported by abundant palaeontological evidence, is dependent on assumptions, and these become less dependable the greater the degree of difference between the forms that are compared. The presence of large flightless birds in the southern hemisphere, ostriches in Africa, rheas in South America, emus and cassowaries in Australia, and the recently extinct moas in New Zealand, was regarded as important evidence of the connection of these regions by an antarctic continent by Hutton [20] and others. The assumption, however, that these forms belong to a natural group is highly dubious, and they are now placed in distinct orders. This evidence for an antarctic center of dispersal accordingly has reduced value.[5]

It was formerly believed that the shrew-like Centetidae of Madagascar were closely related to the *Solenodon* of Cuba and Hispaniola, and their wide separation in space was accordingly highly remarkable. More exact investigation has shown that there are numerous differences between the two groups, and they are now regarded as the "relicts" of a formerly widely distributed primitive type of insectivore.[2] The frogs formerly grouped together as the family Dendrobatidae were separated from the true frogs on account of their lack of teeth; they inhabit Madagascar and tropical America. The absence of teeth is now regarded as convergence; the neotropical *Dendrobates* is supposed to be derived from a neotropical genus such as *Prostherapis,* the Madagascan *Mantella* from an African ranid ancestor.[13, 33]

Different groups of animals are unequal in zoögeographic importance, especially with reference to the evidence they provide on land connections. Animals dispersed through the air, whether by active flight like birds, bats, and insects, or passively like spiders and small invertebrates with resting stages, are relatively unimportant in this respect. Relations between animals that are likely to survive an ocean journey in driftwood, such as snails and the pupae of longicorns and snout beetles, must be interpreted with discretion in zoögeography. The best evidence for former land connections is afforded by

groups such as the Amphibia and most earthworms, to which salt water is fatal, and by non-flying mammals, because the transportation, even by large rafts, of such large animals as ungulates is impossible; even small forms such as mice, shrews, and squirrels would be likely to starve on any rafting journey unless they were transported on sizeable rafts.

Mammals and birds have the great advantage for zoögeographic studies of relatively rapid and relatively recent evolution. Although the crustacean genus *Apus,* which is still living in fresh waters, was already in existence in the Triassic, and most living genera of fresh-water mollusks and insects are represented in the Eocene, and even the reptiles have numerous Eocene genera that still persist,* none of the living genera of mammals are present in the Eocene and very few indeed in the Miocene. The Pliocene genera of mammals are largely the same as the Recent, but nearly all the species are different, though 80 to 95% of the species of Pliocene snails are still extant. The reasons for this more rapid evolution of the warm-blooded animals are doubtless to be found in the general acceleration of their life processes, including the appearance of mutations, and in the greater probability of the survival of new forms on account of their adaptability to environments that are closed to other groups of animals. The degree of differentiation between related groups of mammals thus gives a clue to the amount of time since their origin, and consequently, in some cases, to the date of union of land areas now separated. Thus the presence of so many genera of mammals in Eurasia and North America represented by closely allied species or even subspecies in the two regions is the basis for the belief that these regions were connected in geologically recent times. Even a separation since the Pliocene, from the evidence of the extinct Pliocene forms, would have resulted in a greater differentiation than exists.

The rapid transformation undergone by the species of warm-blooded animals explains the fact that the faunae of Madagascar, South America, and Australia are so much more peculiar in these groups than in their insects or amphibians and reptiles. Celebes, as an example, has no endemic genera of land mollusks, 3 among the fresh-water mollusks, 1 for amphibians and reptiles, but it harbors 16 peculiar genera of birds and 6 of mammals.

Finally, the fossil remains of extinct forms are especially abundant among the mammals, more abundant at any rate than among other

* The lizards *Chamaeleo, Agama, Iguana,* and *Lacerta,* and the turtles *Emys, Testudo,* and *Chelonia.*

terrestrial animals. Study of this palaeontological evidence affords reliable information about former connections of land areas, and sometimes also of separations, as was illustrated above in the discussion of the relation between the North and South American faunae.

Other animals besides mammals furnish similar evidence of former changes in the distribution of land. Land connections between areas now separated but inhabited by related animals need not have been direct; they may involve other areas and may have been successive rather than continuous at any one time. The more ancient the groups of animals whose discontinuous distribution requires explanation, the greater are the possibilities for their emigration by roundabout routes. The occurrence of two genera of mantids, *Liturgousa* and *Stegmatoptera*,[14] in Madagascar and South America and nowhere else, and the similar example in the order Insectivora of the Centetidae and Solenodontidae in Madagascar and the West Indies, cannot be supposed to indicate direct connection between South America and Madagascar. Allied fossils have been found in the North American Eocene.

Numerous examples are known of modern discontinuous distributions that are connected by a wider distribution of fossil remains. The camel family is now represented in Asia by true camels, and in South America by the llamas and their relatives. This group had representatives in North America from the Eocene to the Pleistocene, and this affords a satisfactory explanation of the present discontinuity. The pleurodiran turtles are now confined to the southern hemisphere, where they are widely distributed, but fossils of this type are known in Europe from the Upper Triassic to the Miocene, in Egypt from the Eocene to Mid-Pliocene, in India in the Lower Eocene, in New Zealand and in the Americas in the Upper Cretaceous, and in the South American Eocene.[36] The North American Cretaceous representatives of the genus *Podocnemis* were clearly inhabitants of marine coastal waters.[47] Direct connections between the southern continents are accordingly not required to explain the present distribution of the side-necked turtles. Whenever good palaeontological evidence is available and when the relations have been adequately studied, a similar explanation seems to apply to the widely distributed families and genera of fishes, amphibians, and reptiles, whose present distribution is often a mere relict of a former world-wide range. Among reptiles, for example, the discovery in 1943 of the skull of an amphisbaenid lizard in Lower Oligocene deposits of Mongolia [15] throws new light on the disjunct distribution of these limbless forms whose principal representation is now in Africa and South America.

Although fossil remains of insects and spiders are relatively scarce, these groups also afford instructive examples of a more extensive distribution in the past, with a discontinuous or restricted distribution at the present time. The genus of ants, *Oecophylla,* now has a species in Africa, one in India, one in the East Indies, and a fourth in Australia and in the Aru Islands; but no less than four species are known from the European Tertiaries, and the genus was doubtless widely distributed in Eurasia. Another ant genus, *Ectatomma,* with numerous species in the tropics of America, Asia, and Australia, is represented by a species in the Oligocene Baltic amber and by another in the Miocene Sicilian amber. A third genus, *Macromischa,* now has two species in West Africa and many in Cuba and Mexico; five species are known from the European amber.[16] The related lucanid genera, *Lamprina* and *Neolamprina* in South America and *Sphenognathus* in Australia, are connected by an intermediate form, *Palaeognathus succini,* in the Baltic amber.

Termites, represented in the tropics and subtropics by about 2000 species, are now scarce in the temperate zones; two species reach southern Europe, although several live in the same latitude in North America. Fifty-six species of termites are known from the North American and European Tertiaries.* The primitive spiders with a segmented abdomen survive with three genera; the group is represented in the European and American Carboniferous.[48] There are numerous other examples of this tendency, and their number is likely to be greatly increased with the progress of palaeontological research. Although the incompleteness of the palaeontological record prevents the general application of this method to zoögeographic problems, the fact that gaps in distribution are frequently reduced by fossil forms indicates that a similar explanation of discontinuity of range is often to be invoked, even if the palaeontological evidence is negative.

With the exception of small volcanic coral islands, such as those of Micronesia and Bermuda, and volcanic islands, such as St. Paul and those of the Hawaiian and Polynesian archipelagoes, there are perhaps few land areas that have been continuously isolated from all others. This statement is undisputed for islands near the coasts like those of the Mediterranean, Ceylon, Formosa, Tasmania, New Guinea, and even Japan. The Indo-Australian Archipelago and the Melanesian islands extending from New Guinea to New Zealand were probably mutually connected and thus also joined with Australia and south-

* A. E. Emerson, personal communication.

east Asia, though these connections were by no means contemporaneous or of equal duration.

Zimmerman [66] reviewed this situation as follows: as a result of geological study, it is known that the Pacific Basin is underlaid by heavy basaltic rock; that in the continents generally lighter or metamorphosed rocks rest on heavier underlayers; and that continental shelves extend for various distances under shallow coastal waters and then terminate rather abruptly at the edge of the deep water, which is of remarkably uniform depth of about 12,000 to 15,000 feet and more in the true Pacific Basin; that the volcanoes now above sea level have risen from great depths and have been built of basic rock, and that in no islands in the central Pacific Basin have true continental rocks been found. So far as is known to geologists, the only pre-existing extensive land masses in the tropical Pacific since the rise of modern florae and faunae are those west and north of Australia and on the New Guinea-New Caledonia-New Zealand axis, possibly extending eastward to near the Tongan Trough in the neighborhood of Fiji. There is no geological evidence to indicate the existence of any large land masses east of Tonga and Fiji.

Africa was connected with Europe at times *via* the Strait of Gibraltar and probably *via* Sicily and Italy as well. Repeated connections between Eurasia and North America must certainly have existed, probably across the present Bering Strait and parts of the adjacent seas. This bridge must have been in existence during a warm period, when the Alaskan climate permitted the dispersal of numerous animals. These connections seem to provide for distribution to all the regions inhabited by animals whose distribution is rigidly dependent upon the existence of land. The West Indies, also, may have been anciently united with each other and with the mainland, and Madagascar was perhaps attached to Africa, though Matthew in 1915 [27] defended the opposite view, that Madagascar and the West Indies are strictly oceanic islands.

There is a growing tendency to place more and more reliance on aerial transport in furnishing an explanation of the arrival of the foundation stock of immigrants even on isolated oceanic islands. The bulk of the insect faunae of mid-Pacific islands appears to have developed from wind-borne individuals. Over-water transport by flying birds is also a contributing factor, and floating natural rafts or even driftwood provides another possible means of accidental dispersal. Zimmerman, after much collecting on diverse scattered archipelagoes of the Pacific, believes that, although evidence for the former exist-

ence of a land mass is lacking for that region, it is probable that high islands existed there in past ages in addition to those now present. Such islands could well provide steppingstones for the dispersal of biotic elements out even to the well-isolated Hawaiian Islands. Formerly the nearest high island was probably only some 500 miles from Hawaii in contrast to the 2000 miles by which they are separated today. This hypothesis breaks the need for postulating thousands of miles of above-water transport, if land bridges are rejected, and introduces the more probable hypothesis of a series of shorter over-water steps.[66]

If all the generally accepted connections are drawn upon a map regardless of their non-contemporaneity, the result is a connected land mass in the northern hemisphere with three great southward projections.

Theories about connections between the southern continents through the antarctic land mass must be regarded with suspicion, although such connections have repeatedly been proposed and defended with ability. Many authorities, however, have found no insuperable difficulty in the way of a derivation of the southern faunae from the general northern land mass, and as long as this is possible and in the absence of direct evidence to the contrary, the assumption of direct connections between the southern continents is certainly to be avoided.[27] There are theoretic considerations that favor a derivation of the southern faunae from the north, based on general phenomena of climatic change. Land bridges that extend right across the Atlantic or Pacific are so dubious even from biological viewpoints that they deserve no consideration. The ambitious attempt of Arldt [1] does not carry conviction to a critical reader on account of its failure to weigh the evidence for the permanence of continental outlines against the probability of transoceanic land bridges.

Wegener's hypothesis of continental drift is not in accord with many geological observations and not only is not needed to explain zoögeographical distribution but actually creates more difficulties than it adjusts.[61] The extensive literature on this subject cannot be summarized here. The interested reader should consult Wegener [63a] and Du Toit [11a] for the pro-drift argument. So far as the problems of animal geography are concerned, the weight of American opinion is strongly against any hypothesis of continental drift.[53]

The distributional relations of the terrestrial animals strongly support the assumption that centers in the northern hemisphere have been the places of origin of the principal advances in organization in the

more important groups of terrestrial forms. The vast land areas of the North Temperate Zone afforded a spacial basis for their development, and the successive periods of cooling and other climatic changes produced a periodic severity of selection and thus favored advances in organization. The groups whose adaptations or changes represented advances were enabled to enlarge their range and extend it to the south, at times driving more primitive forms before them. Successive impulses, following one upon the other, would push the earlier forms farther and farther to the south. Here and there, under the protection of specialized habits or on account of barriers, remains of the primitive forms would be left behind as "hanging relicts," but in the main they would be driven to the three southern land masses *via* present or geologically attested land connections. They would be preserved most effectively in these cul-de-sacs when the appearance of barriers prevented the later, more advanced, competitors from following them. This isolation is especially notable in Australia, which has been cut off since the Jurassic. It is not at all implied that advances in organization took place only in the north; favorable modifications may have arisen and adaptive radiation has occurred in various other areas, but the conditions for advance were most favorable in the north, as far as terrestrial animals were concerned.

Primitive southern forms

There is a great accumulation of evidently primitive and ancient vertebrate types in the southern hemisphere.[39] Australia leads in this respect, with its monotremes and marsupials and with the small rodents whose only relatives exist as relicts on the mountains of Celebes, Borneo, and the Philippines.[63] South America has its primitive marsupials, edentates, hystricomorph rodents; its tinamous among birds, and iguanid lizards. Africa south of Sahara has preserved primitive mammals such as the tragulid dwarf deer *Hyaemoschus,* the lemurs, the aardwolf *Proteles,* and the golden mole *Chrysochloris.* In Madagascar the lemurs and centetids are primitive forms; the civet genus *Eupleres* is intermediate between other genera and, as such, is primitive; the bird genus *Mesites* seems to be the most primitive member of the crane and rail group.[65] Primitive groups of invertebrates are also especially abundant in the southern hemisphere. Among insects, the most generalized type of termites occurs in Australia; the simplest Lepidoptera, resembling Trichoptera, are found in Australia and New Zealand; and about half the Australian bees belong to the

primitive genus *Prosopis*. Taylor [58] has shown that the most primitive land snails, Helicidae, are found in the southern continents and in New Zealand, and that progressively more advanced species are found in the north. The whole mollusk fauna of South Africa may be characterized as a primitive one. The distribution of earthworms is similar in its arrangement, with primitive forms in the southern hemisphere and advanced forms in the northern.

Discontinuous distributions, with the most varied arrangement of the respective isolated areas, are the rule in the southern land masses. The most primitive of the living odd-toed ungulates, the tapirs, are found in Malaya and in Central and South America. The dwarf deer (Tragulidae) are found in the East Indies, in southeast Asia, and in West Africa. The relatives of both of these groups are well represented among the North American and European Tertiary fossils. The iguanid lizards have their headquarters in South America and southwestern North America, with a single genus in the Fiji Islands and two in Madagascar. Their fossil remains are found in the European and North American Eocene.[67] The giant water bugs of the genus *Belostoma* are widely distributed in America, Africa, southern Asia, and Australia. An isolated species in Dalmatia testifies to the former continuity of this range, and fossil belostomas are known from the European Miocene and Jurassic.[16] Hanging relicts, like the group of spiders with segmented abdomens, now confined to southeastern Asia, present anomalous distributions that must be examined in this connection.[44]

The original continuity of the ranges of southern animals, now discontinuous, is made very probable by such fossil records. Other examples of discontinuity in groups in which no fossil evidence is available may be interpreted in the same way. Thus the worm-like amphibians, the caecilians, are confined to Africa, the Seychelles, southern Asia and the East Indies, and tropical America. The South American boid snakes of both *Constrictor* and *Boa* have representatives in Madagascar. Many genera of insects are restricted to the southern hemisphere, where their range is discontinuous. The Orthoptera *Liturgousa*, *Stegmatoptera*, and *Pauletica* occur in South America and in Madagascar. The carabid genera *Drimostoma* and *Homalosoma* are found in Madagascar, Australia, and New Zealand. Many genera of ants are confined to the southern continents. The Onychophora, *Peripatus* and its relatives, are found in Australia and New Zealand, East Indies and southeastern Asia, South Africa, and tropical America, including the West Indies.[4] The ancient earthworm

genus *Notiodrilus*, from which the widespread family Acanthodrilidae may be derived, has a genuine relict distribution. It is found in New Zealand and the Chatham and Snares islands; in New Caledonia; in the isolated oases of central and northwestern Australia, in southernmost Africa, with a species possibly in the Cameroons, in southern South America, and finally in the Central American Cordillera.[30] Many of these groups of soft-bodied animals are quite unsuitable for preservation as fossils and are scarcely to be expected in the palaeontological record.

Some of the regional fresh-water animals, as distinguished from universal forms, are also confined to the southern hemisphere with discontinuous distribution on the various land masses and islands. Their origin in the northern land mass or dispersal by this indirect route may explain some of these distributions. Difficulties in the way of this explanation exist in the fact that land bridges may not have their streams favorably directed for the spread of aquatic animals. In Africa and Syria, the long series of depressions from the Jordan Valley to the Central African lakes may once have been a highway for fish dispersal. The Central American connection between North and South America, however, does not appear to afford opportunity for the exchange of aquatic forms. The conditions governing dispersal of these forms are, to be sure, quite different from those of the terrestrial forms. The primary fresh-water animals, such as crustaceans and non-pulmonate snails, presumably came originally from the sea. Fresh-water groups now restricted to the southern continents may be derived from marine forms that had become restricted to the southern oceans, instead of from ancestral fresh-water forms now extinct in the northern hemisphere.

The three surviving genera of lungfishes are *Lepidosiren* in South America, *Protopterus* in Africa, and *Neoceratodus* in Australia. This is plainly a relict distribution, as the fossil genus *Ceratodus* had a wide distribution, throughout the Mesozoic, in Eurasia, Africa, and North America. The temporary and stagnant waters of the tropics and subtropics presented conditions in which a few forms were able to compete with more modern fishes by reason of their ability to breathe air. *Protopterus* and *Lepidosiren* burrow into the ground and aestivate for seven to nine months during the dry season. For the same reason *Neoceratodus* is able to live in the stagnant waters of pools left by the general drying up of the streams in which it lives. The cichlid and characinid fishes of tropical America and Africa (the cichlids in southern India as well) may have been marine and con-

fined to tropical and subtropical seas, whence they entered the fresh waters. Their disappearance in the sea may be laid to the rise of the spiny-rayed fishes, which were at first unable to follow into the fresh waters. Such an explanation of the distribution of *Galaxias*, confined mainly to the extreme south of South America, Africa, Australia, and New Zealand (Fig. 11), is highly probable, since this genus is not entirely restricted to fresh water. Members of the Gobiidae, Cottidae, Syngnathidae, Blenniidae, and Elopidae have entered fresh waters independently in different parts of the world. Thus the five

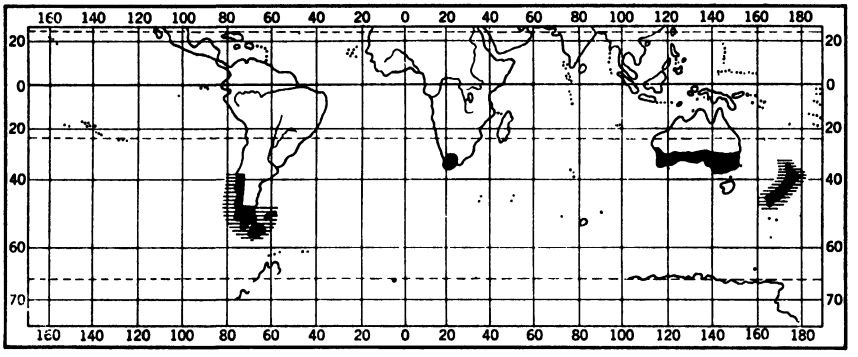


FIG. 11. Distribution of *Galaxias*. After Boulenger. A species of this genus is now known from New Caledonia.

species of the elopid genus *Megalops* are found on the coasts of India and Africa and on the east coast of South America; *M. thrissoides* occurs in the Magdalena system and in the rivers of West Africa.[36] Darlington [10] reviews the distribution of fresh-water fishes and of cold-blooded terrestrial vertebrates in a thoughtful paper in 1948. The gastropod genus *Potamides* has probably been independently developed from separate and distinct stocks of the marine *Cerithium* that have entered brackish water in different parts of the world (cf. Chapter 12).

The ancient crustaceans of the family Anaspididae, restricted to the fresh waters of Australia and Tasmania and to underground springs in Europe (*Bathynella*),[6] have a strikingly discontinuous distribution. Their Paleozoic relatives *Uronectes* and *Paleocaris* indicate a formerly much wider distribution.

It is by no means a mere assumption that the northern forms are more advanced. Their superiority has been shown by the practical experiment of introduction. Eurasian forms introduced into Australia

and New Zealand have frequently been able to displace the native forms of similar habits. Thus the two predatory marsupials, the Tasmanian wolf *Thylacinus* and the Tasmanian devil *Sarcophilus*, have survived only in Tasmania, and doubtless became extinct in Australia on account of the competition of the placental dingo (*Canis dingo*), an immigrant or introduction from the north, which has not reached Tasmania.

The native Australian songbirds are being crowded out by the forms introduced from Europe, such as the sparrow, starling, blackbird, goldfinch, and greenfinch. The skylark is rated the second worst bird pest in New Zealand.[58a] The goldfish (*Carassius auratus*), which was introduced in Madagascar, is displacing the native fishes wherever it comes into competition with them.[3] European ants and earthworms have spread in South Africa, South America, Australia, and New Zealand at the expense of the native species. In the reverse direction, of 490 exotic species of animals known to have been brought into Hamburg by shipping in the course of three years, only 5% could maintain themselves, and these only in greenhouses, in tanbark, and in warehouses, not a single species having spread so as to have come into competition with native European forms.[24] Another example of this phenomenon is found in the mammals that have crossed the Central American land bridge in recent times. The northern emigrants into South America have been better able to expand and survive in the new area than have the southern emigrants into North America.[49]

All these considerations support the theory that the forms now inhabiting the southern hemisphere, with a limited or discontinuous distribution, once inhabited the northern land masses, where they then enjoyed the same continuity of distribution as the more modern northern groups, which have driven their predecessors to the south.[27]

It has been suggested also that the Eurasian forms are similarly superior to the North American, and this appears to be true to a certain extent; witness the sparrow and starling, the house rats and house mouse, the carp, and the host of insect pests introduced from Europe. In the contrary direction, however, certain North American animals have proved themselves almost equally able to spread in competition with European forms, notably *Phylloxera* (the grape-root louse) and the muskrat, so that the superiority of Eurasian forms is certainly not without exception. In so far as such a superiority exists, it may be caused by the more stringent natural selection in the larger fields. Absence of parasites and of specially adapted predators

contributes to the success of introduced animals and may be difficult to distinguish from "innate superiority."

Faunal regions

The explanation of the principal features of the present distribution of animals is to be found in the changes in faunal barriers in the course of geologic time. The study of the actual data of distribution can thus become fruitful only if it is based on the phylogenetic relations of the animals in the various regions and takes into consideration the geologic and palaeontologic data. Faunal lists and statistics, unless subjected to phylogenetic and geologic analysis, are fruitless as a means of inquiry. Regions may thus be distinguished in which the fauna, at least with respect to certain classes, is more or less homogeneous. The earth was divided into such regions on the basis of its bird faunae by Sclater; and Wallace, principally considering the mammals, has adopted a quite similar division. Wallace believed that this division into "regions" would apply to all groups of animals, and under the weight of his prestige the delimitation and subdivision of the faunal regions have long constituted one of the principal branches of zoögeographic inquiry.

The belief that there is a division into faunal regions of general validity for all the classes of animals cannot be maintained in the light of modern knowledge. For the Mantidae, there is no sharp division between the Ethiopian and Oriental regions, which have numerous types in common. The few palaearctic forms are directly derived from these, so that in general, this family can be divided only into two regional groups, a palaeotropical and a neotropical.[64] Nor can the distribution of the non-European genera of mites be brought into harmony with the usual regional divisions.[54] With reference to the relations of its earthworms and termites, New Guinea would be grouped with southeastern Asia, whereas its other faunal affinities are primarily Australian. Ceylon, by contrast, agrees closely with Australia in its earthworm fauna.[41] Ceylon termites are clearly related to those of India proper but are usually specifically distinct.* Chile differs from the rest of South America in its mollusks, its freshwater fishes, and its earthworms, but its vertebrate fauna is typically South American.

An exact delimitation of the regions is also impossible, and opinions as to their proper limits have accordingly varied exceedingly. The

* A. E. Emerson, personal communication.

boundary between the Oriental and Australian regions has been a special bone of contention, and Celebes has been placed now with one and now with the other, according to the group of animals employed as a criterion. The creation of transition areas, equally allied to the regions between which they lie, shows that the supposed regions are not objectively defined areas. They are abstractions, combinations of more or less allied faunal elements, and they will be of varying extent and limits according to the animals emphasized.[28, 38, 50] Most important of all, the animal life of the major regions is composed of faunal elements of quite unequal age and of diverse origin. Thus we speak correctly of a holarctic element in the South American fauna, or of a neotropical element in that of North America. Mayr [29] remarks on the difficulty of defining the regions, and prefers the term fauna, defined in terms of its origin.

Nevertheless, the continuing usefulness of the terms neotropical, palaearctic, etc., indicates that there is some merit in the geographic partition of the earth as to the main features of the regional animal life of the present day. The classical major regions of Sclater, and of Wallace [60] were: Palaearctic, Nearctic, Oriental, Ethiopian, Neotropical, and Australian. It was pointed out by Heilprin [19] that these divisions are of very unequal value as to degrees of distinctness of their animal life, and that the Nearctic and Palaearctic, at least, should be combined as a single region, the Holarctic. The argument was carried to a logical conclusion by Huxley,[21] who, employing essentially the same reasoning as Mayr as to origin, proposes grouping the original six regions into the more nearly equivalent Arctogaea, Neogaea, and Notogaea:

Arctogaea	Palaearctic, Nearctic	Holarctic
	Oriental	
	Ethiopian (with Malagasy)	
Neogaea	Neotropical	
Notogaea	Australian	

This matter, with the questions of the limits of the major regions and their subdivision into major and minor faunal or biotic provinces should receive further discussion in an expanded treatise on descriptive and historical animal geography.

It is true that there are common features in the distribution of many different terrestrial animals. The conditions of dispersal and the barriers and highways available were the same for many groups.

The differences probably chiefly result from the relative ages of the different groups of animals. Classes that arose at the end of the Triassic could not spread by means of land connections that were available for the early Mesozoic scorpions, insects, and mollusks. The older a group of animals, the more manifold will have been its opportunities for dispersal. The differences in vagility must be taken into consideration. Flying animals, such as birds, bats, and some insects, have been able to spread by routes closed to other land animals, for, even though they do not fly across great stretches of ocean of their own free will, chains of islands and archipelagoes have facilitated their dispersal to islands that were permanently inaccessible to other forms. When a land connection is of short duration, rapidity of spread becomes an important factor. Of twenty-two species of amphibians and reptiles on the neighboring continent, thirteen reached the British Isles after the glacial period, but only five of these reached Ireland, which was cut off at an earlier date. Other factors have contributed to inequalities in dispersal. When a new land bridge is established, the emigration of animals from the connected regions will begin in both directions. Newcomers in each region come into competition with the resident forms, and some will be able to maintain themselves through adaptability and superiority of organization, while others will be unable to get a foothold. As a rule, a land connection will lead to a mutual exchange of forms rather than to a one-sided invasion of one region from the other. The emigrations of the South and North American faunae *via* the Panama bridge supply the classic example of this phenomenon.

The distribution of many groups will have the same limits, especially when there are effective barriers. New Zealand, Madagascar, and the Hawaiian Islands are well isolated. Even in such places, the different groups of animals are not differentiated from their relatives in other regions to an equal degree. Since their isolation, the groups in the separated regions may have evolved in different ways and at different rates. On the other hand, non-plastic groups, like many of the invertebrates, may have undergone little change. The mammals of Madagascar, for example, for the most part represent endemic families, whereas among amphibians, reptiles, and insects, numerous genera are the same as those of the African mainland. Australia is highly peculiar in its mammalian fauna, while its lizards, butterflies, and earthworms belong with those of the Oriental region.

The faunal regions are therefore divisions of the earth's surface in which the animal life bears a somewhat uniform aspect and differs

from that of the neighboring regions in consequence of independent evolution during longer or shorter periods of isolation. It is one of the problems of zoögeography to study the history of the colonization of the several regions and their subdivisions. In the course of this inquiry it will usually be found that the present fauna of an area is heterogeneous both as to the age and the origin of its various components. The course and direction of the dispersal of the various groups and their order in time must be discovered. These relations may be very different for different parts of the same region.

Celebes and Ceylon both belong to the so-called Oriental Region, according to the accepted scheme. But how totally different has been their history! Celebes is a geologically young island, which has received the bulk of its fauna over Pliocene and Pleistocene land bridges, and is therefore poor in endemic genera. Ceylon, on the contrary, is a land of vast age, neighboring an ancient continental area, and displays a geological history in its fauna and flora beside which that of Celebes seems like a single day···. In Ceylon the geologically older forms of animals, the planarians, mollusks, and reptiles, have followed different laws of dispersal from those which apply to the geologically younger mammals. Celebes, by contrast, received its fauna at a time when the mammals too had reached a high stage of development, so that in this island there is no difference in the history of the different groups of animals.[41]

Historical zoögeography is still at the beginning of its labors. Much detailed investigation remains to be made, and the insufficient scope of the preliminary work now available makes it difficult to attain a general view or a single interpretation (cf. Newbigin, 1948).[32] In the future, as more and more paleontological data become available, sounder and more illuminating conclusions may be drawn.

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8. *The Influence of Extent of Range*

THE AREA INHABITED BY A SPECIES (OR ANY PHYLETIC UNIT) IS TERMED its range. The range of an animal is delimited by the lines connecting the outermost localities at which it is found. A species need not occupy the whole extent of its range; for the most part it will be found only in special habitats that fulfill specific conditions. The extent of a range depends quite as much upon the presence of similar habitats and upon the arrangement of barriers as upon the history and character of the species. The ranges of animals of different groups are highly unlike. The extent or limitation of the range of a species may have an important effect upon the selection and constitution of its individuals. Such regularities as are discoverable in these factors are the subject of this chapter.

A subspecies, species, genus, family, etc., that inhabits a small range may be referred to as *stenotopic,* one with a wide range as *curytopic.* The extent of a range depends upon a number of factors, including especially the geologic age and variability, the vagility, and the ecological valence of the group concerned. The existing barriers, of course, prescribe a maximum to the range of any group. A species of frog on an oceanic island or a carabid beetle in a cave is usually limited in range to island or cave. The range, however, may be restricted to a special part of the island or cave by other factors.

The range of an individual species is not fixed but fluctuates with the passage of time, increases, diminishes, or may be shifted as a whole. The boarfish *Capros aper* of the Atlantic and Mediterranean was formerly rare on the coast of England but about 1888 became so abundant that its numbers were troublesome to fishermen. The noctuid moth *Plusia moneta* was unknown in England before 1890, but since then it has become one of the common English species. *Merops apiaster,* a bird belonging to the family of bee eaters, has

frequently entered south Germany and has failed to become established only because its conspicuous appearance invites persecution on the part of man. The cardinal *Cardinalis cardinalis* is at present actively extending its range in the Mississippi valley; and the prairie horned lark *Otocoris alpestris praticola,* a plains species, reached the Atlantic seaboard in the first decades of the nineteenth century. The great extension of the range of the Norway rat in the past century has had the effect of reducing the range of the black rat. The limiting factors, on different parts of the border of the geographic range, may be entirely different.

The capacity for active dispersal or passive transport (vagility) is an important factor in the range of a form. A great range is common among marine animals. Powerful swimmers, such as the tuna and other Scombridae among fishes or the toothed whales among marine mammals, frequently have a world-wide distribution. Among terrestrial animals it is usually the flying forms that are widely distributed. Of genera and families with a world-wide distribution, beetles and butterflies have the greatest number among arthropods, and birds and bats among vertebrates. Species with a world-wide range are confined to birds among land vertebrates, and principally to butterflies among invertebrates. The thistle butterfly *Vanessa cardui,* which has such a range, is often seen emigrating in swarms, and such emigrations often invade areas where the species is unable to maintain itself, as in the British Isles.[41] The milkweed butterfly is a wanderer of this type, and has spread from North America to the East Indies at a relatively recent date. It arrived in the Tonga Islands in 1863, in Australia in 1871, and in Celebes in 1873; it has reached the Azores in the opposite direction and is occasional in the British Isles.[30] The sphinx *Celerio lineata,* another powerful flier, has spread to all parts of the world. A small range is connected with lessened vagility, when related forms are compared. The Satyridae and Zygaenidae, with a weak flight, are usually very local in their distribution, often confined to special habitats or to specific localities. Such a distribution is unknown among the good fliers, such as the Pieridae or Nymphalidae.[38] Flightless birds and birds of weak flight have relatively small ranges, unless they are powerful runners, like the ostrich, or powerful swimmers, like the Adelie penguin.[28]

The facility with which some animals are transported may conduce to an equally wide range. The inhabitants of transitory bodies of water and of moss may be transported while in their resting stages by the feet of birds or by winds, and are frequently world-wide in

distribution. This is true, for example, of numerous rhizopods and other protozoans; of threadworms, one of which, *Bunonema richtersi,* occurs in the Black Forest, in Switzerland, in England, in the Canary Islands, and on Kerguelen and Possession Islands; of Entomostraca [13] and the salt-crustacean *Artemia salina;* and of tardigrades such as *Milnesium tardigradum.*[32] Conversely, only animals capable of active or passive dispersal can inhabit such bodies of water or masses of moss.

The animals that have been spread to all parts of the earth in the train of civilized man are further examples of more or less accidental transport. The Norway rat, house mouse, and domestic dog among mammals; the English sparrow among birds; the flea, various meal worms, various ants (e.g., *Camponotus rubripes*), and the house fly among insects; the slug *Limax flavus* and the edible snail *Helix aspersa* among mollusks; and *Eisenia foetida* and *Helodrilus caliginosus* among earthworms [26] may be cited as examples.

The geologic age of a group has an important bearing on the extent of its range. Highways for dispersal available for older forms may have disappeared before the rise of younger groups. The families of invertebrates, probably on this account, have wider ranges than those of vertebrates. The wide distribution of so many genera of scorpions, pedipalps, and centipedes is doubtless connected with their antiquity and their now diminished variability. Among fresh-water mollusks, the earliest known genera are likewise the most widely distributed, as is illustrated by the planorbids, physids, lymnaeids, ancylids, unionids, and sphaeriids, all of which are present in the Jurassic and some as early as the Carboniferous. *Anodonta,* which does not appear until the early Tertiary, has a much more restricted range. Greater geologic age seems to be as important a factor in wide distribution of the higher categories, such as genera and families, as vagility. The moths and butterflies are unquestionably more vagile than the beetles; some of them are pronounced wanderers as we have just seen; a few have a world-wide range. This is a rare phenomenon among the species of beetles, but it is a striking fact that nearly all the families of beetles have a world-wide distribution, whereas this is not true of the majority of the families of Lepidoptera. Coleoptera are an older group, abundantly represented in the earliest stages of the Mesozoic, whereas Lepidoptera are unknown until Mid-Jurassic. Willis [51] attempts to establish an invariable connection between extent of range and geologic age of *species,* but is forced to admit that this relation may be greatly veiled by the presence of physical and eco-

logical barriers, by the action of man, and by other factors, even among the slow-spreading plants. A restricted range may be characteristic of groups at their decline as well as at their inception, as is illustrated by *Sphenodon* of New Zealand and by horseshoe crabs now confined to the east coast of North America and to the Moluccas.

The extent of the range of a given group of animals is also dependent upon its "ecological valence." Adaptability of any sort favors the establishment of a species in new districts and hence favors the extension of its range. This relation is especially important for terrestrial animals on account of the wide variety of habitat conditions on land. The widely transported inhabitants of temporary ponds are eurythermal and frequently also euryhaline, like the salt-crustacean *Artemia salina.* The resistant nature of *Cyclops fimbriatus* is shown by the variety of situations that it inhabits. It is found in Greenland and Ceylon, on the plains as well as on Mount St. Bernard. It occurs in concentrated mineral waters, in iron-ochre deposits of brooks, and in caves and mines.[46]

Euryphagy is frequent in widely distributed forms. The food of carnivorous animals is least restricted, since mammals, birds, and fishes, and even insects, worms, and mollusks, are much more uniform in chemical composition than are leaves, fruits, seeds, or other parts of plants. Thus the most widely distributed mammals next to the bats and marine forms are the carnivores such as the Eurasian wolf, with the closely related North American wolf; the leopard, ranging through Africa and south Asia into China and Borneo; or the puma, whose range extends from Alaska to Patagonia. Both nocturnal and diurnal birds of prey may have a very wide range—so the sea eagle, the peregrine falcon, and the barn owl. The extraordinary euryphagy of the raven, which feeds on carrion and on living animals from roe fawn and birds to insects, worms, fishes, birds' eggs, plants, and seeds, must have had an important effect in giving it its wide distribution.

There is a relation, though sometimes obscure, between wide range of a species and position at the top of a food pyramid and between wide range of the individuals of a species and that of the species as a whole. A larger carnivore, in general, will have a wider range than will the smaller herbivores that constitute its food.

Euryphagy has plainly furthered the spread of herbivorous insects. The caterpillar of the nearly circumglobal cotton bollworm *Heliothis armigera* feeds mainly upon the tobacco plant at Delphi, on maize in

Java, and on the cotton plant in North America.[23] The caterpillar of the widespread *Utetheisa pulchella* is no less catholic in its food habits and also displays a high degree of tolerance toward climatic differences.[37] *Helix aspersa,* transported by man to all parts of the earth, has unquestionably been able to establish itself on account of its euryphagy.[45] Higher animals may show great latitude in foods eaten. The mourning dove takes 149 species of plant food,[33] the white-tailed deer 516 species.[3] This helps to account for the wide distribution of these animals and of related forms. On the other hand, animals limited to restricted environmental niches where food is scarce, as in mountain torrents, tend strongly toward euryphagy.

Restriction of range

Limited range, especially for species and genera, is, on the whole, a much more general phenomenon than wide distribution. Specialization, i.e., the exact inherited adaptation to given habitat conditions, affords so many immediate advantages that specialized species usually win in the struggle for existence. The advantage of flexibility of organization lies primarily in the capacity for wider distribution. The fatality in specialization lies in the corresponding loss of the capacity for adaptation. The disadvantages of adaptation to a special habitat appear only when the habitat conditions in the range of an animal undergo decided changes, which tend to kill off specialized forms unable to meet these particular changes.

The limitation of range of a species may be extreme. Small islands, high mountain ranges or peaks, mountain valleys, and other sharply defined areas may have species confined to them. Examples among Lepidoptera are to be seen in the *Attacus isabellae,* known only from a forest near Madrid; the notodontid *Rhymatophila alpina,* known only from the neighborhood of Digne in southern France; the hawk moth *Akbesia davidis,* from Akbes in Syria; and the genus *Zygaena,* with nearly 200 closely similar forms, most of them in the Mediterranean district and many with very small ranges. The flight area of *Z. seriziata* in Algeria is sometimes restricted to an area 8 to 10 m. broad.[39] Many flightless carabid beetles are restricted to particular mountain ranges or to parts of them; *Carabus adonis* is known only from the Parnassus and Taygetus, and *C. olympiae* only from the valleys of Aosta and Sesia in the Apennines.[4] Among snails *Radix involuta* is restricted to a small mountain lake in Ireland, and *Papilifera scalaris* is found only in a small calcareous area in Malta; one mollusk

genus *Lanzia* is confined to the moss of a mountain peak in Bourbon.[8] Among birds a restricted distribution is common among hummingbirds, as in *Oreotrochilus chimborazo chimborazo* from Chimborazo and *Eriocnemis glaucopoides* from Valle Grande in Bolivia. In Florida, the Cape Sable seaside sparrow is a full species. It inhabits a coastal grassland area about six miles long and no more than a half-mile wide. No other suitable habitat for this bird has been reported for a long distance on either coast of Florida.[19]

The combination of slight vagility with the presence of barriers to distribution usually produces stenotopy. It seems likely that stenotopic forms will be found to have in common other characteristics that influence the limitation of their range. Various reasons for limited distribution may be considered: slight power of expansion, high degree of specialization in adaptation to special conditions, youth of the species, or age and decline. Low vagility alone does not require consideration on account of the amount of time that has been available. The parts of Germany covered with ice during the glacial period have been completely repopulated by such slow-moving forms as snails and earthworms. The power of expansion possessed by a species must be associated with its fecundity, but no example of restricted range certainly assignable to a low degree of fecundity can be cited. New forms, in general, will arise in quite definitely circumscribed areas, as is to be seen in the melanistic forms of the Lepidoptera *Boarmia consonaria* and *B. consortaria* in the neighborhood of Maidstone in England.[17]

The melanic variety, *carbonaria,* of *Biston betularia,* the peppered moth, which appeared near Manchester, England, in 1850, has completely superseded the non-melanic parent species in parts of England and France.

This phenomenon, referred to as "industrial melanism," has successively attracted the attention of butterfly collectors, ecologists, and geneticists. It appears that the dark form is a recessive mutation that is so much favored by its protective resemblance on smoke-blackened walls, with a differential exposure to predation of the light-colored dominant form, that it rapidly increases in abundance wherever such backgrounds appear. The matter is reviewed by Ford.[15]

The fish *Atherina riqueti,*[34] which has been in existence only since the end of the seventeenth century, has appeared in the Canal du Midi between Garonne and the Mediterranean. It is a fresh-water derivative of the marine *A. boyeri.* The surviving relicts of ancient

forms frequently have a restricted distribution. Thus the Australian lungfish *Neoceratodus forsteri* is known only from the Burnett and Mary rivers in Queensland, whereas its extinct relatives were widely distributed; the ancient rhynchocephalian *Sphenodon* is confined to New Zealand; the duckbill *Ornithorhynchus* is found only in the streams of southern Australia and Tasmania; the genus of snails *Pleurotomaria* now occurs only in the Moluccas, Japan, South Africa, and the Antilles. Here the very barriers that limit the distribution of the forms in question have conditioned their survival by keeping out more efficient competitors. It must be added that a small range is not at all a necessary characteristic of a relict form. The singular cephalopod *Spirula,* the only one besides *Nautilus* with a chambered shell, ranges through the Atlantic, Pacific, and Indian oceans. The genus *Eukoenenia,* a small primitive arachnid of the order Palpigradi, has been found (represented by various species) in the Mediterranean region, in Texas, Siam, and Paraguay.

Local species arise among land birds on islands, in spite of their powers of flight. Such endemism may result on account of their very vagility, which, combined with a homing instinct, may condition the return of wandering individuals and thus increase the effectiveness of their insular isolation.[36]

In contrast with the relict forms, the wide distribution of a group combined with the appearance of numerous differentiations, such as numerous subspecies in a single species or of numerous species of the same genus, is an indication of vitality. Widely distributed genera tend to have numerous species. A world-wide (cosmopolitan) range is the maximum possible, and it stands in contrast with geographic limitation.

Extended ranges

An animal is said to be cosmopolitan when it occurs in all the places that afford it suitable habitat conditions; cosmopolitanism does not mean that it occurs alike in salt and fresh water and on land. An animal that is found to inhabit a wide variety of unlike habitats is said to be ubiquitous. The term cosmopolitan distribution is used in the geographic sense, and ubiquitous occurrence in the ecologic. Cosmopolitan species may accordingly be marine animals occurring in all oceans or air-breathers occurring in all the zoögeographic regions, although the polar regions are often omitted from consideration in this connection. The widest distribution in both the geographic

and ecologic sense is probably to be found among Protozoa, especially among the rhizopods. Thus *Cyphoderia ampulla* (Fig. 12) lives in the ocean, in salt-water marshes, in fresh water, in the sand of the seashore, in the springs and glacial lakes of mountains, and in the warm ponds of the lowlands. In addition to central Europe, this protozoan is recorded from the coast of the Arctic Ocean, from Russian Lapland, from the Rocky Mountains, and from Argentina and

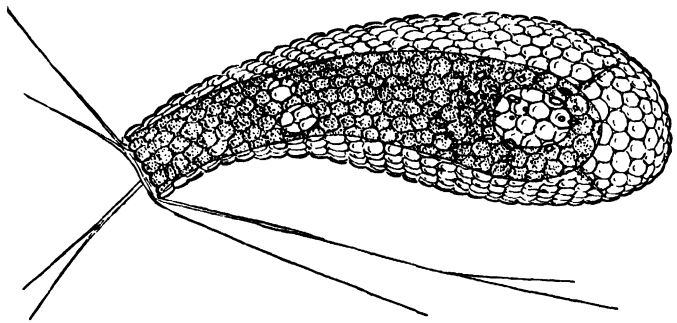


FIG. 12. *Cyphoderia ampulla.* After Schulze.

Paraguay. The thistle butterfly *Vanessa cardui* is an example of a widely distributed metazoan. It is known from all parts of the world with the exception of some small islands and South America, and ranges from the tropics to the arctic regions and from the plains to the snow line in the mountains. Animals found in all seas are the edible mussel *Mytilus edulis* and the thresher shark *Alopias vulpes.* World-wide distribution within the tropics has been referred to as circumtropical. Such a distribution is characteristic of many of the families and orders of animals. The geckoes among the lizard family Gekkonidae, and the order Crocodilia, the alligators and crocodiles, afford examples.

Wide distribution is more common for higher than for lower taxonomic categories. A wide range is much commoner for genera than for species; it is even more common for families and orders. The families of myriapods and scorpions, and very many families of insects, are cosmopolitan. Fresh-water fishes, amphibians, and reptiles have no cosmopolitan families, though Siluridae, Ranidae, and Colubridae are very widely distributed. Numerous world-wide genera of air-breathing vertebrates are to be found among the birds; witness *Turdus, Hirundo,* many birds of prey, owls, and numerous water birds. *Canis* and a few genera of bats are the only genera of mammals that

closely approach such a range. Species of such wide distribution are not uncommon among the marine invertebrates. Among terrestrial animals there are a few cosmopolitan species of arthropods,* but among vertebrates the only cosmopolitan species are a few birds, such as *Pandion haliaëtus* and *Asio accipitrinus.*

Species with a wide range usually belong to genera with a still wider distribution.[9] Thus the tiger, leopard, and lion belong to the more widespread genus *Panthera,* and the widely distributed wolves to the almost cosmopolitan genus *Canis.* The genera to which the raven *Corvus corax,* the peregrine falcon *Falco peregrinus,* and the ringdove *Columba oenas* belong are both widespread and rich in species. The same may be observed among reptile and amphibian genera (*Lacerta, Bufo, Rana*) and among invertebrates such as the land and fresh-water mollusks (Helicidae, Lymnaeidae). Species of monotypic or oligotypic genera, in contrast, usually have a narrow range. Among American moles the genera with the most restricted distribution are the least varied.[48] Other examples among mammals are the panda (*Aelurus*), the giant panda (*Aeluropus*), and the binturong (*Arctictis*), and among birds two Brazilian species of *Eurypyga, Mesites* with a single Madagascan species, and *Didunculus* with a single Samoan species.

Eigenmann [12] found in the course of his researches on South American fishes that in a given river system, even so vast as that of the Amazon, the widespread genera have several times as many species as the genera confined to the system in question. This indicates that a genus with a small range tends to have fewer species because there is less available space for them, with, of course, less possible variety of habitat niche. The examination of the conditions that make possible a wide range will cast some light on this problem. It is precisely the especially vital and adaptable genera that are differentiated into numerous species and have a wide range. Such genera are in the minority. Exact statistics show that among the most widely distinct families of plants and animals the monotypic genera are by far the most numerous, followed by those with two species, then by those with several or many.[51]

Many widely distributed species tend to develop numerous restricted varieties at the borders of their range while remaining con-

* A few arachnids (*Theridium tepidariorum, Th. rufipes, Tegenaria derhami*); a few insects (*Vanessa cardui, Celerio lineata, Heliothis armigera, Nomophila noctuella*) [30] among Lepidoptera; *Cercyon nigriceps* among Coleoptera; and the myriapods *Scolopendra morsitans* and *S. subspinipes.*

stant over wide areas in the center. This is true of the snail *Helix aspersa,* which shows unusual variation at its southern limit, in Algeria. The same is true of *Helix* (*Arianta*) *arbustorum,* which varies strongly at both the horizontal and vertical limits of its range (for example, in the Pyrenees) and of the "Formenkreis" *Levantina* in Palestine.[21] Albinism is reported by Paul Hesse (personal communication) to be especially common at the limits of the specific range, as in *H. arbustorum* in the Alps; and *Helix* (*Cepaea*) *nemoralis,* which is rarely albinistic in Germany, frequently has albinos in the southern part of its range, in Italy. The European newts sometimes have constant dwarf races in the south; males of *Triturus palmatus* from Porto, Portugal, measure 55 mm., compared with 70–80 mm. north of the Pyrenees.[52]

Another instance of this relation between distribution and variation is presented by the European birds of the genus *Parus,* called titmice. The least specialized form, *Parus pleskii,* occurs in central Russia, a form somewhat intermediate between the subspecies in the east, south, and west; toward the northeast and north it is replaced by *Parus cyanus,* in the southwest and west by *P. caeruleus* and its subspecies, and in the east it reaches the range of *P. flavipectus.*[47] The Eurasian deer have formed dwarf races at the western limits of their range in the Faeroe Islands, Scotland, Alsace, Corsica, Spain, and Algeria, as well as at the eastern limit in Japan. It is probable that the conditions of life at the limits of the range of a given species are less favorable and that these are responsible for the change and dwarfing of the species, especially in the somewhat isolated outposts whose inhabitants do not interbreed as freely with the central mass of the species. In a narrow range the habitat conditions will in general afford less variety, and the separation of the individual stations at which the species occur will be less.

There is a minimum value for the extent of the range, which depends upon the nature of the species and consequently varies with the species concerned. Each individual animal requires a minimum space in which it can satisfy its needs for food and movement. It is evident that an area that would seem large to a mouse would be small for an elephant, and that a flying insect or an antelope will demand a wider space in which to move than a snail or a sloth of similar respective size. Carnivores will require a larger area per individual than herbivores, being dependent upon them; carnivores must be much fewer than their prey, or they will die of starvation. Among many species of carnivorous animals an individual, or each pair of individuals, has a special area of its own within which the presence

of another animal of the same species is not tolerated. This is true of bears, foxes, moles, eagles, kingfishers (*Alcedo*), and dippers (*Cinclus*), and even the centipede *Lithobius* is usually found singly under a given stone, in contrast with the herbivorous milliped *Julus*. A minimum number of pairs, however, is essential to preserve the species from inbreeding and from "accidental" extermination by adverse conditions, and this number, multiplied by the area required by an individual pair, would express the minimum range of the species.

Territoriality

The concept of territoriality is related to the idea of home range. It may deal with the area or even with the spot to which an animal returns. In a more narrow sense, territory has been defined as "any defended area." Different kinds of vertebrates, including particularly fishes, lizards, birds, and mammals, actively defend a part of their total range especially during the breeding season. Territorial defense is also known among certain invertebrates including, among others, *Uca*, the fiddler crab, and ants.

The territorial habit usually has one or more of the following probable values: (1) produces a more uniform occupancy of local fragments of the habitats; (2) limits the breeding population and hence helps control the population size within the limits of carrying capacity; (3) furnishes partial protection of helpless young; (4) when well developed in territorial birds, provides a reserve of unmated males and females, allowing more prompt replacement of a mated animal that dies; (5) with larger territories, tends to ensure an adequate supply of near-by food; (6) parasites and disease spread less rapidly; (7) predators are more easily avoided on account of the close acquaintance of the territory holder with the given locality; (8) apparently for psychological reasons, there is increased vigor of defense by the occupant and decreased vigor of attack by an intruder of the same species.[2] The territorial habit is widely developed among birds.[18] The St. Kilda wren defends from trespass a far larger area than is required for its food. The limitation of the number of pairs able to breed in a given area may on occasion be controlled by the pugnacity of the male birds, but this limit is seldom reached in populations of land birds.[29] The size of suitable territory apparently required by different species of birds that do not nest in colonies may vary from 0.2 of an acre for the wood thrush [49] to about 60 square miles for the golden eagle.[10] The territory held in the breeding season is smaller in years when the population is more dense.

Effects of space limitation

It is very likely that other factors affect the problem of minimum range. The smallest bodies of water, springs, ditches, and puddles, harbor only small mollusks such as the spring snail *Bithynella,* the small clam *Pisidium,* etc. Some small mollusks, *Galba truncatula, Gyrorbis leucostoma,* and *Pisidium* certainly are more frequently found in small bodies of water than in large. Perhaps the small ponds provide a refuge from larger enemies or competitors for which the area in question would be too small. Thus the Panamanian caiman is driven from the larger bodies of water by the crocodile. Also we may be dealing again with a direct effect of size of habitat upon growth size. On the other hand, the larger fresh-water fishes occur only in the larger bodies of water, such as the North American "sheepshead" *Aplodinotus grunniens,* about 25 kg., the arapaima *Arapaima gigas* in the Amazon, and the giant catfish *Silurus glanis* in the larger rivers and lakes of Europe. It thus appears obvious that the species of larger animals in general require a wider range than do smaller related animals, although the widest known ranges are those of the protozoans.

Large animals, in consequence, are not to be expected on small islands, though if introduced they may be able to maintain themselves for a time, like the cattle that were landed on New Amsterdam (66 sq. km.).[7] No exact definition of the size of islands that can maintain a given species is possible. The tiger is absent from Ceylon, though present on the mainland opposite and present on the much smaller island of Bali (about 5000 sq. km.). The size of Ceylon cannot therefore be the determining factor; the tiger may have been exterminated in Ceylon by man. The absence of coastal species of sharks from inshore waters of the small Pacific islands, the Hawaiian Islands for example, may be explainable on the ground that the available space is not sufficient to maintain them.[14] The introduction and self-extermination of rabbits on Laysan and Lisiansky Islands, described by Wetmore,[50] is an instructive phenomenon in this connection. Only small animals have been able to maintain themselves as relicts of the ice age or of the steppe period in central Europe, since available areas are too small to support larger forms, such as the musk ox or reindeer. The relicts usually range from the size of the hamster down, and are for the most part much smaller. Thus trout, the turbellarians *Planaria alpina* and *Polycelis cornuta,* and the spring snail *Bithynella* are relicts of the ice age, and some xeric snails and grasshoppers are relicts of the steppes.

The extent of the space available has a direct effect upon the constitution of its inhabitants. Experiments have shown that the individuals of a species reach different sizes varying with the amount of space given them. In the original experiments of Semper,[40] made with *Limnaea stagnalis,* the specimens grown in 100, 200, 600, and 2000 cc. of water attained a shell length of respectively 5, 9, 12, and 18 mm., in the same length of time, and if larger numbers of specimens were kept in the same container, their size remained smaller than when there were fewer. The results of numerous recent researches in this field which confirm and extend those of Semper have been comprehensively reviewed by Allee,[1] who discusses at length the different causal factors involved.

Although the causes at the bottom of this relation between size of animal and range are not yet clear, a large number of facts may be brought together from this standpoint. Thus the size of the pelagic copepods of the genus *Diaptomus* depends on the size of the bodies of water they inhabit.[35] Fresh-water mussels *Unio* and *Anodonta* have smaller individuals in brooks than the same species in rivers.[20] Trout from the Aar averaged 240 gm., those from its affluents, 132 gm.[44] The whitefish *Coregonus* from the small lakes in Switzerland are dwarfs compared with those from the Lake of Zürich.[16] The smaller size of most of the animals of the Baltic and Mediterranean seas compared with those of the Atlantic probably does not fall into this category; the physical conditions in these basins may be the determining factors. It is probably true, however, that the frequent presence of dwarfed forms of animals on small islands depends on space relations. Dwarfing in consequence of reduced range may also be seen in the numerous Alpine animals whose ancestors had a much wider range in the glacial times and were much larger. Their formerly continuous range has been reduced and split up by the encroachment of the forest into the mountains from the plains.[43] A conspicuous exception to this relation appears to be the Komodo Island monitor *Varanus komodoensis,* which is much larger than the *Varanus salvator* of the larger neighboring inlands and the mainland.

Small well-defined situations like islands or oases have fewer species than uncircumscribed areas of similar size. The vast multiplicity of animals that characterizes a continent may not be expected on an island.[9] Iceland has fewer species of birds than Norway. Tasmania, according to Gould's figures, has only 181 species of birds, whereas New South Wales has 385. Sikkim, whose bird fauna is one of the richest in the world, has 500 to 600 species of birds in 4015 sq. km.,

while Celebes, about 45 times as large, has only 337. The Azores (2388 sq. km.) have fewer than 30 breeding species, and the Cape Verde Islands (3851 sq. km.) only 38.[27] A palace garden in Bonn, of about 22 acres, has 43 species of birds nesting within its confines. This difference is necessarily conditioned by the fact that the least range of a species in an interbreeding community is larger than the area required by a single pair of the species within the range. The lessened possibility of chance and increased difficulties in the way of the immigration of new forms, on islands, are factors that do not apply to parts of a mainland.

On the other hand, broader areas, with other conditions equal, in general have the richer fauna. A principal reason may be that they afford a wider range of habitat conditions, and thereby increased possibilities for the formation of species by adaptation. This is evident when the amphibian and reptile faunae of various large islands with similar climatic conditions are compared.

Island	Area, sq. km.	Number of Species	
		Amphibians	Reptiles
Borneo	715,100	85	243
Madagascar	591,563	88	181
Sumatra	443,234	61	199
Celebes	200,132	22	106
Java	131,733	38	157
Ceylon	65,690	37	97
New Zealand	268,461	2	15
Cuba	118,833	23	56
Hispaniola	77,253	29	66
Jamaica	10,859	16	28
Puerto Rico	9,314	13	30

The comparison of the New Zealand fauna with that of the East Indies shows that the extent of the area concerned is the deciding factor only when other factors are similar or comparable. The West Indian islands, likewise, are comparable only with one another.

A somewhat similar result though with equally necessary exceptions is exhibited by the numbers of species of fishes in the faunae of the larger river basins.* In similar climatic zones the larger stream tends to have the larger fish fauna. The greater extent of the oceans in the southern hemisphere similarly reacts favorably on the evolution of genuinely pelagic animals. These seas have larger numbers of whales. The same relation appears among the plankton.[25] Chun [6] characterizes

* For details, see the original German edition of the present work.

the Antarctic pelagic fauna as in general richer in comparison with that of the Arctic; even among the bottom-dwelling forms the Antarctic fauna is the richer, as among echinoderms [22] or among pycnogonids, which have 82 Antarctic species as compared with 62 in the Arctic.[5]

Large areas with uniform conditions like great stretches of forest, prairies, steppes, and extended mountain ranges are especially favorable to the development of specifically adapted forms, since they afford residence and perpetuation to large numbers of individuals, and the prosperity of a species, its further development and progressive adaptation, are in general more favored by wealth of individuals. Regions with a wide variation in habitat conditions contrast with such uniform areas, and these favor the existence of numerous species and subspecies, since they afford conditions adapted to needs of varied animals. The subdivision into varied situations of the sea bottom of the Sagami Bay near Tokyo has its share in conditioning the surprising wealth of species in this area.[11] The Norwegian coastal herrings show much more variation and division into races than the herrings of the open Atlantic and of the North Sea,[42] on account of the great variation of physical conditions on the coast. The variety of conditions in the littoral affords habitats for a greater number of gorgonians than the deep sea, but the littoral species have much more circumscribed ranges than the deep-sea forms.[24] The broken and varied east coast of the Adriatic affords a greater variety of habitat than the more uniform west coast; of 143 species of decapods in the Adriatic, 116 are found on the east coast and only 65 on the west, while on the east coast itself the maximum wealth of species is reached in the broken Dalmatian coast with its islands.[31]

It has been supposed, on this account, that a richly differentiated fauna in a relatively small area would warrant the supposition of its former greater extent. This has been postulated for the Seychelles, with their giant land turtles, their giant birds, and otherwise rich animal life; Wallace applies the same reasoning to Australia. There is unquestionably a certain relation between the size of a region and the variety of its fauna, but it cannot be expressed in figures or otherwise sharply enough defined to afford a sufficient basis for conclusions of this nature.

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9. *Biotopes and Biocoenoses*

ANIMAL AND PLANT LIFE OCCUPIES THE WHOLE SURFACE OF THE EARTH, including both land and sea. Life extends into the depths of the ocean, but it penetrates only a few meters deep in the solid earth. It rises higher into the air, but not for long periods. The whole space occupied by living organisms has been called the "biosphere." [13]

The biosphere presents extremely varied aspects in its various parts, both according to the habitat conditions and the forms of life represented. A study of the biosphere thus requires a subdivision into the component parts corresponding to these differences. Little has been done in this direction by zoölogists, whereas plant geographers have long given serious attention to biogeographic studies upon an ecologic background. From the botanical viewpoint we already have a completely worked-out classification and nomenclature for the major parts of the biosphere, although unfortunately no unanimity has been attained in this respect.[2, 5]

Zoölogy cannot take over a phytogeographic system without revision. Other principles of subdivision must frequently be applied for animals on account of their vagility, with their consequently completely different mode of distribution, and on account of the relatively greater importance of marine and fresh-water animal life. Furthermore, what are primary divisions for the botanist, such as forest and grassland, are themselves in turn the habitats in which animal life is found. It is true that the zoölogical subdivisions will frequently be based upon the botanical, but they must not slavishly follow the botanical scheme and must find new principles of their own as the occasion demands.

The primary topographic unit is the niche or biotope. Such a unit is an area showing uniformity in the principal habitat conditions. The biotope is as basic for the ecologic subdivision of the biosphere as the species is in the systematic classification of living beings, though

neither can be defined with exactness. The biotope is directly conditioned by the similarity of regional factors, such as the medium, climate, and soil, and these factors condition an analogous development of the fauna and flora of a given biotope. Particular modifications of a biotope, differing from the typical conditions in recurrent minor respects, may be characterized as "facies" (originally a geological term with a similar application). These bear the same relation to the typical biotope as do subspecies and varieties to a species.

As species are combined into genera and these into families and orders, so may biotopes be grouped according to their resemblances into "biochores." Thus the biotope rock resert combines with sandy desert and stony desert into the biochore "desert." This in turn may be united with the biochore ice desert under the superbiochore wasteland. The marine biotopes mud beach, sand beach, gravel beach and shingle beach (boulder beach) belong together as the subbiochore "depositing shore," which with the subbiochore eroding shore makes the biochore seacoast. This together with the sea bottom from deeper water makes the superbiochore benthal.

The biochores and superbiochores are finally combined into still higher groupings, which may be called "biocycles." The biosphere may be divided into three such biocycles: ocean, fresh water, and land. Each of these represents special exclusive habitat conditions to the animals inhabiting it, and they are thereby fundamentally distinct. This is reflected in the nearly complete difference in their animal populations. Certain animals enter more than one biocycle, like salmon or eel in the ocean and in fresh water, amphibia in fresh water and on land, and some birds occur in all three, but these are so obviously exceptions that they "prove the rule."

Among the biochores differences in general aspect, the so-called "habitus," appear in varying vertical or horizontal position. Vertically arranged provinces are called strata or layers; horizontally distinguished ones, zones. Thus, independently of other subdivisions of the biosphere, we have depth and altitude strata and climatic zones. The depth strata of the sea are those of different degrees of pressure, motion, and light (see Chapter 12), and on land the altitude strata are of two sorts, those based primarily on stratification of plants as in a forest and those based on physiographic features such as lowland, hills, mountains, and high mountains, with their subdivisions. The customary climatic zones are the polar, the temperate, the subtropical, and the tropical, and since these are represented in mountains in the altitude strata it is customary to call these zones also.

All these divisions are independent of the historically based faunal regions. The biotopes and biochores include analogous provinces whose faunae are similar on account of the influence of similar habitat conditions, and though they may be of joint origin are not necessarily so. The faunal regions and their subdivisions are based on common origin, on relationships among the inhabitants, and their populations are homologous.

The ecological divisions of the biosphere are accordingly (to summarize) the three biocycles, ocean, fresh water, and land; in these, subdivisions with a general similarity of habitus are recognized as biochores, which may be united as superbiochores or subdivided into subbiochores; areas within the biochores that have uniform external habitat conditions are biotopes, and their variations are called facies. This logical classification of habitats originated by Hesse [7] deserves wider use.

The concept of the "biome," for the largest recognizable ecological formations, cuts across Hesse's classification, since it takes account of ecological succession and of the interrelations of land and fresh-water communities.[1] Thus the "spruce-moose biome," extending across northern North America from Alaska to Labrador, is defined as *including* the innumerable lakes of the glaciated region. By continuity of vegetation type and operational overlap of successive communities it includes peninsular extensions in the mountains of western North America and in the Appalachians even where neither spruce nor moose is represented.

Biotic communities

The sum total of living things, plant and animal, corresponds with the biosphere, while the biocycles have their respective faunae and florae, called the biota when both plants and animals are included in one category. The plants considered with regard to their ecological relations rather than their taxonomic affinities may be spoken of as vegetation [2] or as the phytome, while the animal life similarly considered is called the zoöme. The clearest correspondence between an area and its population is found in the biotopes, whose inhabitants constitute a well-characterized unit often called a biotic community. Such assemblages may be split into "plant communities" and "animal communities" only by arbitrarily disregarding the essential ecological unity of the whole.[1] Such assemblages of organisms have also been called biocoenoses.[11,17] A biocoenosis is the association of living things inhabiting a uniform division of the biosphere and correspond-

ing in the selection and number of species with the average external habitat conditions. The members of a biocoenosis are dependent upon each other and are thus forced into biological balance, which is self-regulating and fluctuates about a mean. Biocoenoses form characteristic ecological communities, with interlocking interrelationships, without necessarily including a single species limited to an individual biocoenosis.*

Not every biocoenosis is to be considered as representing a biotope in a biogeographical sense. The life of an oak forest, including the forest itself, forms a biocoenosis, but so does an anthill in the forest, or a hazel thicket on the edge of the woods, with their respective inhabitants. The oak woods is a biotope; the two others are not. Biogeography cannot carry subdivision to the extent that is possible for ecology in its consideration of animal communities.

The biotope as a biogeographical unit presents a characteristic bit of the face of the earth, includes an area of determinate physiognomic value, useful in a description of the earth's surface, for example of a landscape, more or less sharply distinguished from its surroundings. A lower limit is set for the size of biotopes in their relation to geography; and this limit is not necessarily valid for the biocoenosis or for the habitat niches of ecology.

Since a biotic community forms a unit whose members are mutually dependent, it is accordingly not logical to separate the study of plant and animal elements. But it is sometimes helpful, for the sake of simplification, to carry out such a division and to place consideration of the animals near the foreground. The dependence of the animal element on the plants is well known; plants are the producers, animals the consumers.

If these mutual relations were present in every community and if the amounts of foodstuffs supplied were equivalent in both directions, the biocoenoses would form closed systems, would be "autarchic";[9,1] but it is very rare that a biocoenosis does not require food supplies from without, and usually food is contributed to other communities. The nearest approaches to such closed systems are perhaps furnished by lakes without outlets or by oases in deserts. Some biocoenoses are wholly dependent on the outer world for their food supply and may

* The tendency to regard a *biotic community* as an assemblage of species primarily controlled by the biotope, in contrast to a *biocoenosis* in which the interrelations between constituent organisms make the primary binding unity, introduces aspects of ecology not particularly pertinent to the present geographical approach.[3]

then consist entirely of animals, as in caves or in the communities of the lightless depths of the sea.

Within the biocoenosis, the plants are most directly dependent upon the conditions within the biotope. Land and shore plants are confined to the earth, whose chemical constitution regulates their food supply. They are unable to withdraw from periodic climatic influences. The plant cover of the given biotope to a large extent determines the nature of the animal population. Vegetation affords the animals not only food but also shelter; it determines their mode of motion, and sometimes hinders orientation. In water, plant metabolism supplies an abundance of oxygen. Carnivores are dependent on plants also, though secondarily. The protective devices of plants against browsing may exclude certain animals completely from a biocoenosis; the presence of the unpalatable ferns must have an important influence on the composition of a community in which they predominate. Reciprocal effects occur; animals are an influential part of the plant environment, particularly when they are permanently present in sizeable populations. By grazing, animals hold grasses in a preclimax stage and by overgrazing may cause a retrograde replacement of the vegetation. Much of the tall prairie grass in Kansas gave way to short grass under pressure of grazing by bison, and part of the area was invaded by the cactus *Opuntia,* as a result of overgrazing by cattle. Deer may enable the red spruce to become locally dominant by selective browsing on its competitors. On English chalk, the succession leads to chalk grassland only if grazing operates; otherwise scrub develops.

Animals may actually destroy the plant association upon which they subsist, with subsequent profound edaphic changes. In West Africa the desert is encroaching upon the savannas because of grazing; [16] in the arid pastoral belt of Australia between the 10-inch isohyet and desert, the desert is spreading because of destruction of *Atriplex* and *Kochia* by rabbits and stock.[12] Similar changes can be seen in various parts of the grassland-desert ecotone in the southwestern part of the North American continent.

The whole composition of a biotic community, its plant foundation, and the cooperation and competition among the animals that enter it help to determine both the species and the number of individuals in a given biotope. There is a general balance, so that the changes by death or increase cause only relatively slight fluctuations about a mean. This equilibrium, however, is unstable. It is disturbed through the variations in the habitat conditions themselves, which undergo fluctuations. When the numbers of a single species change, the in-

timate nature of the internal relations within a community causes the other members to change. Thus an excessive multiplication of the processionary caterpillar of the oak (*Cnethocampa processionea*) directly affects the oaks, which are eaten bare, and the other forms dependent on them, such as the oak tortricid *Tortrix viridana* and gall wasps, whose breeding places and food are reduced. Fertilization of the forest bottom by the caterpillar dung has an effect in a richer

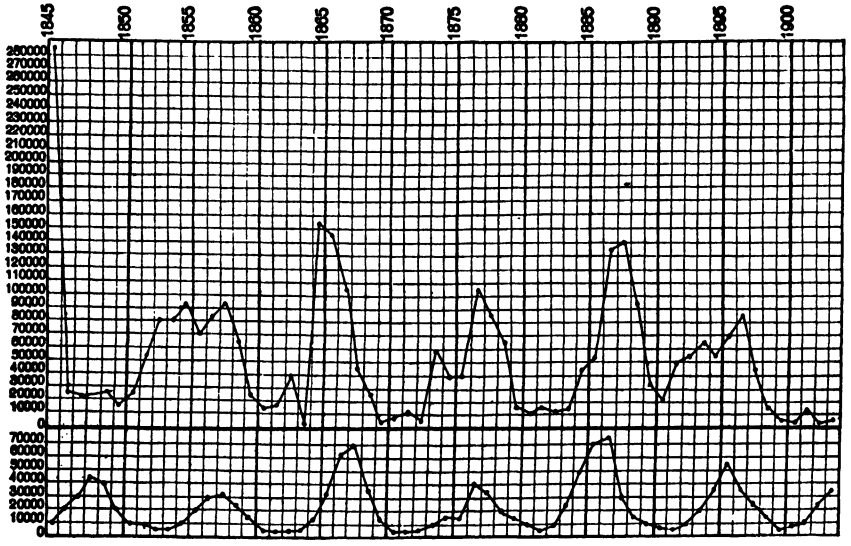


FIG. 13. Receipts of skins of *Lepus americanus* (above) and *Lynx canadensis* (below) by the Hudson Bay Company from 1845 to 1905. After Seton.

growth of the ground cover. Wild animals that take up with their food the widely disseminated poisonous and irritating hairs of the caterpillars may leave such forests. Cuckoos, on the other hand, flourish, since the hairs are not objectionable to them. As the increase in the caterpillars comes in May and June, the concentration of cuckoos must have an important effect on the breeding of the smaller perching birds, in whose nests the parasitic European cuckoo lays its eggs. Additional pertinent examples may easily be found. A notable increase in the plankton of a given part of the sea has an important influence on the numbers of fishes in the following years, as the food supply favors the growth of the fry. The number of predaceous animals is dependent on the number of food animals; the abundance of lynxes in Canada, for example, seems to depend directly on the abundance of snowshoe rabbits (Fig. 13).

Such fluctuations in general are rapidly equalized on account of the superabundant fecundity of all members of the community. Permanent changes in the faunal composition and the numeric relations of the species result when one of the members of an association disappears or when a new one is added. The caribou has been almost exterminated in Labrador by ruthless hunting; two other species that were dependent upon it disappeared with the caribou—wolves and Indians.[4] The introduction of numerous palaearctic species, such as passerine birds and earthworms, in New Zealand, Australia, and other countries, has operated to destroy and drive out the native forms.

In addition to being conditioned by their biotic interrelations, the members of an ecological community are dependent on the physical conditions of their biotope. These habitat conditions demand a higher degree of adaptation on the part of plants and animals the more they depart from the optimum, and thus have progressively more rigorous selective action. Forms that cannot survive extremes must perish (cf. Chapter 11). In regions of optimum physical environment, such as tropical seas and the tropical rain-forest, the communities are characterized by numerous negative features, in correlation with the absence of the adverse conditions found in less favored regions. Any permanent change in the physical environment (as in the biotic) conditions a change in the biocoenosis. Some members will drop out, others will thrive better, and still others will be enabled to enter. The lakes of Finland and south Sweden were once part of the Littorian Sea; their separation was followed by freshening, and the entire marine fauna was reduced to a single fish (*Cottus quadricornis*) and a number of crustaceans (*Mysis relicta, Idothea entomon, Pontoporeia affinis,* and *Limnocalanus macrurus*). Similarly, climatic changes since the last glacial period have completely changed the mid-European and North American biomes.

On account of this selective influence of the environment upon animal life, the ecologic communities in widely separated parts of the world may be similar, if similar processes and conditions are concerned. Thus corresponding biotopes with similar biocoenoses arise in different parts of the biosphere, quite independent of each other. They are, however, analogous formations. The members of the regional communities, the families, genera, and species, are often entirely different. The most different grassland areas—the North American prairies, the pampas of the Argentine, the steppes of Africa, Eurasia, and Australia—are independently populated by members of each faunal area; in spite of the similar general impression the in-

habitants are taxonomically usually more nearly allied to those of other biocoenoses in their region than to those of the similar habitats in distant regions. The grassy steppe of Australia is populated by marsupials, the South American by histricomorph rodents, the North American and Eurasian by other families of rodents and by rabbits and hares. They agree in having strong chewing apparatus, a large number of jumping types equipped with long hind limbs, and a variety of burrowing forms. In addition, numerous necessary differences between the faunae of similar habitats result from the different degrees of adaptation to the similar conditions.

One important set of animals for the characterization of a biotope are those that are limited to the corresponding biocoenoses, the index species, which may be characterized as autochthonous. These are so exactly adapted to the ruling conditions of their habitat that they are unable to live in another environment. They are usually herbivores, since the carnivorous and omnivorous animals tend to have a wider distribution. Such animals may be distinguished as eucene, and correspondingly, in the individual biotopes and biochores: eupolar, in the ice-dominated tundra; eunival, in the snow zone of mountains; eucaval, in caves; euhaline, in the saline inland waters; euvastal, in steppes; eudesertal, in deserts; etc. The number of these most closely adapted index forms is small for most communities; it increases with the severity of selection as the conditions depart from the optimum and is very large, for example, in the biocoenosis of moss, where resistance to long-continued cold, heat, and drought are required, and only such animals can persist as are able periodically to suspend their living functions, awaking to renewed life when favorable conditions reappear. In smaller biocoenoses such autochthonous forms are frequently lacking.

A much more numerous biotic element occurs also in other biotopes, whether only in similar adjacent ones or in widely scattered very different habitats, as ubiquitists (forms with high ecological valence, i.e., eurytopic forms). Such members of a biocoenosis may be distinguished as tychocene. These are frequently adaptable forms that flourish equally well under very different habitat conditions. Tychocenous animals fall behind the eucene element in numbers only when the selection by unfavorable conditions is especially severe. Examples of tychocene forms are the raven, in the Arctic; the ground beetle *Carabus silvestris,* in the snowy zone of the Alps; the wolf, in the tundra; and all migratory birds. Tychocene animals may be of greater importance in the animal community than are the autoch-

thonous eucene forms. On the basis of relative importance in the community, animals are classified as dominants, influents, and subinfluents. Dominant animals are those of outstanding abundance or conspicuous influence that are present at least throughout the entire active or open season. Influents are common animals of less importance, and the subinfluents are regular members of the community with but relatively slight influence.[15]

In addition to these regular elements of a biocoenosis, a few more or less accidental forms may be present. These are guests, tramps, heterotopic animals, which live for a time in a biotope into which they have wandered, but inevitably perish if they do not find their way in time to more favorable environment. A fish in a spray pool on a rocky coast, a bird of the high seas blown inland, and a butterfly on a glacier are examples of such accidental occurence.

The biocoensis of a given biotope is accordingly the more uniform, the more severe the selection by the physical habitat conditions, and in general it will be the more distinct the poorer it is in species. The most distinct biocoenoses are those of deserts and ice waters, caves, moss, and temporary pools. This is not a uniform rule, however, for the sparse fauna of hot springs consists in the main of ubiquitous forms that are sufficiently resistant to withstand the unfavorable conditions.

Both the biotopes and their accompanying biocoenoses are constantly changing. Changes of biotopes, such as the filling of lakes or increased aridity as in the Arabian peninsula, have already been discussed. Such changes are accompanied by obvious changes in the biota. Even when the climate and other physical conditions remain constant, the biocoenosis may still undergo ecological succession from pioneer to mature, so-called climatic climax communities. Such succession is effectively illustrated in dunes where, with the passage of time, largely as a result of the activity of plants, the communities of the bare dunes evolve through various stages until the climax community of the region is reached. The biotic communities in the dunes along Lake Michigan evolve towards the beech and maple forest community as a climax. Such a climax is insensitive to its own effects and, other things being equal, will remain as long as the present climate persists. This is the climax community for much of eastern United States; in it the gray fox and the bobcat are index mammals, or were before man's influence became too important.

Population density

The amount of animal life present in an area, which may be termed the bio-mass, is different in each biotope. It depends primarily upon the amount of food available in the biotope in question. If the association is a closed one (autarchic), the amount of animal life will depend on the amount of the plant element in the association, which in turn depends directly on the biotope. Such a relation does not apply when the greater part or all of the food comes from without, as in the associations on the sea bottom or in bird rookeries.

The amount of animal life in a given biotope may be considered from different viewpoints. The population density must be distinguished from the species density. The former is measured directly by the mass of animal substance present. If it were to be estimated from the numbers of individuals, no comparable values would result, since small animals such as hydroid polyps, midges, or even mice are generally present in much larger numbers than larger ones, and associations between larger and smaller animals should be richer than those between small forms alone, the numbers of individuals being equal. It must be admitted than an exact estimate of the amount of animal life in the terrestrial biocoenoses is excessively difficult to make. This factor, however, is well established for marine and freshwater plankton. Species density, on the other hand, is well known in many regions. This is the number of species that are encountered in an area of considerable size, whether they are abundant or scarce. The knowledge of this factor, from a species list, does not give a direct insight into the composition of a biocoenosis. A picture of the butterfly life of the palaearctic fauna gained from a species catalogue would be quite wrong. An illustration written in 1890 makes the point: "One would find *Pyrameis* with 4 species, *Vanessa* with 12, *Pieris, Epinephele,* and *Pararge* with 20, and *Coenonympha* with 25; the genera *Satyrus* with 56 species, *Sesia* with 78, and *Erebia* with 80, would be much better represented. He would accordingly expect on an excursion, to catch principally *Sesia, Erebia,* and *Satyrus* species; with good fortune he might catch a *Pieris,* a *Coenonympha,* or an *Epinephele,* but it would be too much to expect that he would meet with a *Vanessa* or *Pyrameis.* The reality stands in complete contrast. *Pieris, Coenonympha,* and *Epinephele* are present in great numbers; he might encounter the species *semele* of the genus *Satyrus,* but of the 78 species of *Sesia* he could not expect to find one!" [14]

Whereas the population density represents an absolute value, the

species density is a relative one. Species density depends on one hand upon the selective action of the environment but on the other upon historic relations. Thus the species density upon an oceanic island will in general be less than that upon an island of equal size near a continent, other conditions being equal. Under optimum conditions, the species density is very great but decreases as the environment becomes less favorable. Two biotypes with equal population density may be very unequal in species density.

"Each biocoenotic area has the greatest mass of life in every generation that it is capable of producing and supporting. All of the usable food-materials present in it will be claimed by the life produced there," says Möbius.[11] This applies, however, especially for animals, only to the extent to which the members of the biocoenosis are able to make use of these organizable substances. The full use of the food materials prepared by the higher plants of a region may be prevented by the absence of animals, conditioned by historic factors. The utilization of vegetable food requires certain adaptations and is not possible for all animals. The principal herbivorous groups of the land are the land snails, insects, birds, and mammals. In all the remaining groups of animals, herbivores are only sparingly represented. The colonization of several regions, especially islands, such as New Zealand, the Falklands, and others, with hoofed mammals has shown how much more animal life they were able to support than was actually present on them; animals able to utilize the available food supplies were absent.

In equal areas with similar conditions of food supply the total mass of life produced, i.e., the animal population density, will not be very different. From this results the peculiar inverse proportion between number of species and number of individuals in the species. Thus the polar seas have a smaller number of species of most groups of animals than the tropical waters, but not a smaller population density. Plankton catches are mostly quantitatively larger in summer in the arctic seas than in the tropics, but single species of Radiolaria, Copepoda, and fishes appear there in enormous numbers of individuals, while in the tropics, with a greater wealth of species, the number of individuals of any one is smaller. This is a rather direct corollary of Möbius' proposition. The oligochaetes of the seacoast, which are necessarily euryhaline on account of the varying salt content of the water, are present in very great numbers when food conditions are favorable, though in small variety of species.[10] Only a very few adaptable animals inhabit the ooze banks of the shallow North Sea, but,

as these banks are rich in food matter, the few animals are present in enormous numbers.[6] The slimeworms *Tubifex*, which feed on the rich deposits of food materials, share this biotope with only a few other forms; as the unfavorable conditions of this habitat prevent pursuit, they may be present in such numbers as to color to a deep red broad areas in shallow water.

The available food accordingly determines the population density, but whether the fauna will be uniform or varied depends upon other factors. Newly developed forms are more likely to be preserved under optimum conditions than where the selection is more severe. Variety in the plant world also favors variety of animal life.

In the temperate and colder regions active life is concentrated into a certain season, which may be short. The development of organisms is slow, and often, as in insects, may extend over several years. The resting stages, necessitated by the winter, interrupt the active life of the great majority of animals and probably increase the longevity of the individual. The European may beetle *Melolontha vulgaris* has a three-year generation south of the Main, a four-year period in north Germany, and in east Prussia its development takes five years.[8] It is quite otherwise in the tropics. In favorable regions development is scarcely or not at all interrupted. Generation follows generation; the high temperatures hasten the development of the poikilothermal forms, and in birds and mammals as well as in other vertebrates the breeding period is often not restricted to any season of the year. Here life pulsates with much more rapid beats, and even if death comes earlier, as in an insect whose life is closed with the conclusion of egg laying, those that die only make room for the new generation that follows.

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Part 2

The Distribution of Marine Animals

INTRODUCTION *

THE OCEAN PRESENTS THE MOST EXTENSIVE HABITAT FOR LIVING ORGANisms. If the total surface of the earth is reckoned at about 510,000,000 sq. km., more than two-thirds, or 361,000,000, are occupied by the oceans and only 149,000,000 by land. If the level of the sea bottom were equalized so that the oceans, including adjacent seas, would be everywhere of the same depth, that depth would be 3795 m., from which the volume of water contained in the ocean basins may be reckoned at 1,370,000,000 cu. km. In contrast the mean elevation of the land is only about 700 m. If all the land were submerged in the sea, only a relatively small amount of water would be displaced. At present about 3,000,000,000 metric tons of material from the land are being washed into the sea annually.

In many ways it is convenient to discuss hydrobiology as a unit instead of dividing it into its oceanographic and limnological aspects. From the zoögeographic point of view, however, inland waters, whose physical and biotic characteristics constitute the subject matter of limnology, are more easily dealt with separately. Such waters occupy only a small fraction of the land surface. North America is rich in lakes and has at least an average river and stream surface, yet Welch estimates [37] that only about 2% of the land surface of this continent is covered by inland waters (see Chapter 16).

The oceanic mass of water forms a single continuous domain. It falls into two main divisions, the Atlantic with the Arctic on one hand,

* The general problems of oceanography are discussed cogently by Coker in his 1947 book, whose title, *This Great and Wide Sea*, suggests its readability but conceals its accuracy. Sverdrup, Johnson, and Fleming (1942), in *The Oceans*, present a more detailed summary.[6, 34] (Citations are given at end of Chapter 10.)

and the Pacific and Indian oceans on the other. The separation of these is incomplete, and their waters are united by wide stretches at the south, and at the north by the narrow opening of Bering Strait. While a number of smaller divisions are essentially independent seas, such as the Mediterranean or the Baltic, they are connected with the principal oceans by straits. Completely separated salt-water basins, like the Aral and Caspian, are few and vanishingly small compared with the oceanic area. A division like that of the land into continents is thus entirely wanting for the oceans.

This vast space is everywhere inhabited by living organisms. It contrasts with the atmosphere, whose inhabitants are constantly, or for the greater part of their life, confined to the ground. The atmosphere is not a true habitat—it is, rather, one of the ecological factors in the life of land animals. Its low density makes it impossible for living organisms or their developmental stages to float in it continuously, and air-breathing animals are therefore superficially distributed and in principle confined to the earth's surface. In the ocean, living organisms are permanently suspended, and may be represented in all their stages at all depths. It is true that the strata are not equally dense in population; the upper ones have in general the larger number of inhabitants. Very few animals are found in the deeper regions, but living animals have been brought to the surface from even the greatest depths.

Terrestrial life occupies but a thin stratum, which, even in forests, does not ordinarily exceed some 30 m. in thickness. When this is contrasted with the mean depth of the oceans of almost 4000 m., and when we remember that the ocean occupies more than twice the surface area of the land, it is readily seen that there is more than 300 times as much space available for marine as for terrestrial organisms.

In spite of the much greater extent of their domain, the number of species of the inhabitants of the sea is much smaller than that of the air-breathers. On the basis of Pratt's figures of 1935, out of 822,000 species something like one-fifth are aquatic animals, including the fresh-water forms. From this it may be concluded that the evolution of species is less favored in the sea. This has its reason in the great uniformity of habitat conditions and the much smaller development of barriers to distribution. The isolation of a group of animals, which contributes so much to its evolution into new forms, is made difficult by the confluence of all parts of the ocean, whereas such isolation is favored on land.

Despite the smaller number of species in so much greater a space,

the animal life of the sea exhibits a greater diversity of form than does that of land and fresh water; the variety of structure among marine animals is much greater. Disregarding parasitic types, only 4 classes out of the total of 59 recognized by the 1943 text of Storer,[33] the Onychophora, Chilopoda, Diplopoda, and Amphibia, are wholly wanting in the sea. On the other hand, 25 classes, including the entire phylum Echinodermata, are purely marine. When a phylum has representatives in fresh water and on land as well as in the sea, the former tend to be less varied in form than their marine relatives: thus, for example, the Mollusca, with only the Pulmonata and a few Prosobranchiata on land as compared with the varied marine classes; or the Chordata with the exclusively marine subphyla Acrania, Enteropneusta, and Tunicata, and the predominantly marine Cyclostomata, Selachia, and several other classes [2a] referred to under the general heading of fishes, as compared with the 4 air-breathing classes. Among the Arthropoda, by way of exception, the air-breathing classes are more numerous than the marine.

The explanation of this fundamental diversification of marine life lies in its much greater age. Marine representatives of all the invertebrate phyla are already present in the earliest fossil-bearing strata of the Palaeozoic. The air-breathing forms appeared later and one by one, although it is possible that the remains of terrestrial animals of the same age have not been found or have not been preserved, on account of the different conditions of fossilization on land and sea. Among the vertebrates, the fishes appear first, in the late Cambrian, and the first air-breathing vertebrates, the Amphibia, in the Devonian, thus still in the Palaeozoic.

This set of relationships is most simply explained by the assumption that the ocean is the original home of life, and a weighty argument in its favor lies in the fact that the body fluids of the marine animals (with the sole exception of the highest and most recent forms, the bony fishes) are isotonic with the sea water, so that no osmotic exchange takes place between their body fluids and the surrounding medium. Fresh-water animals, on the contrary, require special modifications to prevent the dilution of their body fluids by the water in which they live, and terrestrial forms require protection against the too great concentration of their body fluids in consequence of the loss of water (cf. Chapter 4). It appears certain that this relation in the marine forms is the original one, and that in the other two we are dealing with new acquirements or "adaptations." The waters of the ocean approach the ideal medium for living substance.

The rôle of bacteria in the general economy of the ocean is still a matter requiring further investigation. Apart from their food value, of which we know practically nothing for the ocean in general, bacteria in the sea are chiefly concerned with the decomposition of biotic residues and with the transformation of certain simple compounds or elements.

There are three centers of bacterial life in the sea: the marine plankton, the sea bottom, and, least important, the sea water itself. In fact, ordinary uncontaminated sea water in nature appears to be a relatively poor medium for bacterial growth. Earlier investigators plated out their samples in order to estimate numbers present; modern direct counting methods show that the bacteria are from 200 to 1000 times as abundant as was indicated by plating.[36]

Waksman has found that in the Gulf of Maine in water from 200 to 350 m., and on George's Bank in 60–75 m. of water, the numbers of bacteria per cubic centimeter of plankton tow ranged from 202,000,000 to 347,000,000; [35] the ratio between numbers in the tow and numbers in the sea water alone was from 225:1 to 2270:1. The differences depend on the type of plankton rather than on depth or other factors, when contaminated areas are avoided. Off Andros Island as many as 160,000,000 bacteria were found per cubic centimeter of mud.[8] They live both at the upper surface and in decreasing numbers deeper in the mud. Bacteria are present in fewer numbers on or in sand, but they are more abundant in the water immediately above sandy as compared with muddy bottoms.

The number of bacteria on the continental shelf decreases with distance from land except in the deeper layers of mud, where they remain constant. Still fewer bacteria are contained in bottom materials from oceanic depths, and they have been reported as being entirely absent in some of the samples, at least by the methods used.

The long dispute concerning the presence or absence of nitrifying bacteria in the sea continues despite conclusive evidence—produced, among others, by Waksman and associates using the facilities of the *Atlantis* of Woods Hole—that abundant populations of the aerobic *Azotobacter* and the anaerobic *Closteridium* occur in the sea. Both are nitrogen-fixing organisms. ZoBell in 1946 [39] (p. 153 of ref.) records his belief that "besides the soil-like nitrifier which has been commonly found in bottom deposits and near land, there are other marine nitrifying organisms which have escaped detection." Waksman suggests the following hypothesis concerning the nitrogen cycle in the sea: [35]

Decomposition of the organic nitrogenous compounds takes place in the sea water but largely on the sea bottom, with the result that the ammonia is then liberated. This ammonia is rapidly oxidized by specific bacteria living in the bottom to nitrite and later to nitrate. This nitrate remains in the sea bottom and is not reduced, due to a lack of available energy for the nitrate-reducing bacteria and not to a lack of such bacteria. The small amounts of ammonia found in the sea water originate from the plant and animal residues in the plankton and in the water. The nitrate formed in the bottom gradually diffuses into the water where it remains as such. On reaching the zone of photosynthetic activities, this nitrate is consumed by the phytoplankton or is reduced by the nitrate-reducing bacteria to nitrite, which may also be gradually consumed by the plants. Very little nitrate reduction to gaseous nitrogen or complete denitrification is possible under normal sea conditions. Reduction of nitrate to nitrite does not mean necessarily any loss of nitrogen from the cycle of life in the sea.

By such relations there are seen to be good reasons, in addition to those to be given later, for the greater richness of life in the shallower waters of the continental shelf, on oceanic banks, and in polar regions where the circulation tends to bring the nitrites and nitrates up to the lighted zone.

10. *Physical Conditions in the Ocean in Relation to Animal Life*

MARINE ANIMALS ARE INFLUENCED IN MANY WAYS, IN BOTH STRUCTURE and activity, by the physical and chemical properties of the surrounding medium. Partly under the direct phenotypic effects of these influences, partly by adaptation to them by means of selection, similar changes not infrequently appear in animals of similar habitats, which may afford a means of characterization of certain communities. These influences of the medium concern us here only in so far as they influence the evolution and distribution of animal life. The importance of single characteristics in this respect is very unequal, and their treatment will be more or less detailed accordingly.

Light

The amount of light in the different strata of sea water determines primarily the development of plant life and thus influences animal life secondarily. It has also a primary influence on the coloration of animals and upon their organs of vision. The amount of reflected light that falls on the surface of the sea and is reflected back reaches a minimum of 3 to 4% in Buzzards Bay near noon on clear calm days. It increases a few units when there are waves and a few more on cloudy days. As the sea's surface becomes more disturbed, the "surface loss" of light becomes greater although the reflection is increased but little. Apparently, under these conditions the amount of light absorbed in the upper meter or so of depth becomes larger. The surface loss is usually about 15%, although it has often been reported as being much greater.[5, 30]

The amount reflected from the surface is greater with greater slant of the rays. To this must be added the fact that the absorption occurs in the direction of incidence. Slanting rays do not reach as great a

depth as those that strike more nearly perpendicularly. Thus the amount of light reaching a given depth at a given place varies with the time of day and year, and, at a given time, differs according to the latitude of the place. Monaco observed that the "day" in the water at the harbor of Funchal (March, 1889) had a length of 11 hours at a depth of 20 m., 5 hours at 30 m., and only about a quarter of an hour at 40 m. Toward the poles the light falls at a lower angle with the surface of the water and thus in general reaches a lesser depth. The vision depth, i.e., the depth at which a Secchi disk disappears, is about 50 m. at 33° N. latitude, 40 m. at 50°, and 25 m. at 67°. With the same position of the sun (i.e., at the same moment of time) the light at 800-m. depth at 33° N. is about equal to that at 500 m. at 50° and to that at 200 m. at 67°.[25]

Traces of light can be detected at a depth of 1000 m. in the open ocean in the subtropical zone by means of photographic plates. The amount of light at this depth is one three-millionth of the amount at a depth of 1 m. At 1700 m. the photographic plates are unchanged after two hours' exposure. Beebe,[2] diving in a bathysphere near the Bermudas, found light visible to the human eye at 579 m.; at 610 m. all evidence of sunlight had vanished. The composition of light in the water is quite different from that in air, and the deeper the water, the greater is the amount of this difference. The different wave lengths composing ordinary light are differentially absorbed by the water. In clear water the long wave lengths are absorbed much more rapidly than the short. At 100 m. all the colors are still present, but the red rays are most sparingly represented, the green more abundantly, while blue and violet predominate. At 500 m. the blue to ultra-violet rays are still abundant, while even 40 minutes' exposure of suitably prepared plates fails to discover a trace of red or green. Animals at intermediate depths are frequently red in color and presumably appear black in the absence of red rays. Beebe in his bathysphere dives detected no violet with his eye, but only a strange blue that appeared brilliant even after losing power to illuminate objects.

Transparency of sea water also depends on the amount of material in suspension, whether organic or inorganic, and thus varies with location, according to the presence of large amounts of plankton or of finely divided silt, as at river mouths. Yellow or orange rays penetrate such water most readily. In fact, little light with wave lengths less than 6000 Ångström units (Å; orange) penetrates more than a meter into strongly colored water. The depth at which light is reduced to 1% of its surface value is found at 8 m. in the Woods Hole Harbor,

at 32 m. in the Gulf of Maine, and at 149 m. in the transparent waters of the Sargasso Sea. The transparency of the Sargasso Sea is the greatest yet measured, with the possible exception of the Mediterranean. Transparency decreases greatly on the continental shelf. The relative opacity of fresh waters is better realized when it is known that the clearest yet measured, Crystal Lake, Wisconsin, is approximately equal in transparency to the water of Vineyard Sound, which in turn approaches that of Woods Hole Harbor.[1a,5]

The differential absorption of light exerts an important effect on the distribution of plant life and its dependent animal life. It is precisely the red, orange, and yellow rays that are most important in photosynthesis, and these are present in sufficient amounts only in the uppermost levels. Plant distribution is accordingly very unequal at different depths. The maximum development of plant plankton comes between depths of 20 and 50 m., and the maximum is approached at the depth of 10 m.; at 75 m. there is only one-half the amount at 50 m., and at 100 m., only one-fifth. The reduction of the amount of plant life with depth occurs still more rapidly in polar waters, where the light extends to a lesser depth. The same effect, in a still higher degree, is notable in coastal waters, where light is excluded by turbidity. Seaweeds and algae scarcely extend below 40 to 50 m. on the Danish coast. Even before being much reduced by mycetozoan attack, the eelgrass Zostera grew * only to a depth of 14 m. in most transparent coastal waters, whereas in the fiords of Jutland, rich in plankton, it was even more limited, reaching depths of 4–5 m. It reached depths of as much as 40 m. in the North Atlantic.

The waters of the ocean have been divided into three strata with reference to the amounts of light present. The terms introduced by Chun are:

1. The euphotic stratum, rich in light, rich in phytoplankton and in herbivorous animals, extending from 0 to 80 m. according to Chun; from 0 to 30 m. according to Lo Bianco; [19] from 0 to 100 m. according to Murray and Hjort.

2. The dysphotic stratum, weakly lighted; 80–200 m. according to Chun; 30–500 m. according to Lo Bianco; down to 500 m., Murray and Hjort. Above 200 m. this corresponds to the "shadow flora" of Schimper.

* By 1949, eelgrass had been greatly reduced on both sides of the Atlantic, apparently as the result of the attack of a protozoan parasite. Despite some signs of recovery there is no certainty whether eelgrass reduction is temporary or permanent.

3. The aphotic stratum, below 200 m. according to Chun; below 500 m. according to Lo Bianco; below 1700 m., Murray and Hjort; it is lightless and without herbivores; only detritus-eaters and predaceous forms are present.

The more nearly the poles are approached, the shallower is the euphotic stratum and the closer to the surface is the main mass of marine life. This perhaps explains why the sea birds, dependent on marine life for their food, are so abundant in both individuals and species in the polar seas, where their food is both accessible and concentrated.

Density

The density of the oceanic waters has an important influence on the statics of marine organisms. The density of living protoplasm is slightly greater than that of sea water, so that it sinks slowly to the bottom. Many marine animals, however, are enabled by various arrangements to equalize this difference and to swim or float in the water. As the special adaptations for motion in open water lead to various convergent transformations, which characterize pelagic life, these will be examined in more detail in the discussion of that fauna (Chapter 13). The density of the sea water acts essentially as a support to the animal body, so that only minor supporting structures are required. Thus the strengthening of the body for support and protection, which is required by terrestrial animals, is not an invariable condition for marine life, and the removal of this limitation helps make possible the variety of structure in the sea.

Pressure

The pressure of water in great depths of the sea reaches an enormous figure, and departure from the pressure at sea level is much greater than can occur in the atmosphere. A column of sea water 10.07 m. in height, of average density, exerts a pressure of one atmosphere. In one of the greatest oceanic depths yet known, 9750 m., north of the Tonga Islands, the pressure at the bottom is 962 atmospheres, or 731 *meters* of mercury. It was formerly believed that such an enormous pressure must crush all living beings and that the greater depths of the ocean must be lifeless, an assumption that seemed to be confirmed by the investigations of Edward Forbes in the Aegean Sea in 1843. Finds of living animals, however, from more than 2000 m. gradually became more frequent, and though none have yet been taken in the greatest known depths, perhaps on ac-

count of the difficulty of dredging operations, the presence of life at depths between 6000 and 7000 m. has been fully confirmed. Any impoverishment of animal life at such depths results from the scarcity of nourishment and not from the pressure. These animals live under a pressure of 600 atmospheres, but as the same pressures exist in their body fluids, there is no possibility of their being crushed.

In deep-sea dredging it is the general experience that almost all the animals from great depths are dead, or at least greatly injured, when they reach the surface. The rapid reduction of pressure seems to have less to do with this than the difference in temperature between the depths and the surface. At any rate, in dredging from 1650 m. in the Mediterranean, where in contrast with the ocean a uniform temperature of 12.9° rules from a depth of about 160 m. down to the bottom, the animals of the depths reach the surface in good condition.[27] Great variations of pressure in short periods are the daily experience of many animals of the open sea. Many plankton animals and pelagic fishes live by day at depths of 400 m. and more rise vertically at night, often to the surface, to return at daybreak to the greater depths. They are not affected by a 30- or 40-fold variation of pressure, quite in contrast with the air-breathing animals, for which a reduction of the atmospheric pressure by one-half produces extreme injury.

The assumption that greater amounts of gas are dissolved in the water at great depths, in correlation with the increased pressure, and that this creates changed conditions for animal life, is not borne out. Steel cylinders filled with water from the greater depths did not burst by the expansion of the contained gas with the reduction of the outward pressure, as was expected. It is true that, in the bony fishes without an opening to the swim bladder, the gas in the bladder expands to a great degree when the fish is brought up from the depths, and may project from the fish's mouth or even explode and burst its body. Such fishes are probably capable only of gradual changes from the level they habitually maintain.

With the exception of these fishes, the pressure factor apparently does not play an important rôle in the life of marine animals, and at any rate it does not prevent the existence of life at great depths. The many species of animals that have a great vertical range in the sea may be referred to as eurybathic. Among 20 annelids that reach depths greater than 1800 m., 12 are to be found also within the 200-m. line.[9] A considerable number of pelecypods and some snails range from the surface to 2000 and even 4000 m. Thus, among the former,

Modiolaria discors is found from 0 to 3250 m., and *Scrobicularia longicallus* from 35 to 4400 m.; among snails, *Natica groenlandica* ranges from 35 to 2350 m.[7] Examples of the contrastingly stenobathic forms of shallow waters are the mollusks *Patella, Purpura, Haliotis,* and *Mytilus,* the annelid *Arenicola,* and the reef corals (Madreporaria). Stenobathic forms of deep water are represented by the snail *Turris,* the mussel *Limopsis,* and the selachian *Chimaera.* It is likely that pressure relations have little to do with this limitation. Temperature probably is of greatest importance; then there is the struggle for existence and perhaps other causes as yet unknown.

The internal friction or viscosity of sea water, with its variations from temperature changes and salt content and its influence on the suspension of organisms in the water, will be discussed in connection with the pelagic fauna (Chapter 13).

Waves, tides, and currents

The distribution and nature of the marine faunae are influenced in the highest degree by the varied movements of the sea water, alike by the waves that break as surf on the beach, tides, which result from cosmic causes, and the more or less constant oceanic currents, caused primarily by constant winds, augmented by differences in density in different latitudes. The effects of these movements of the water upon its animal life are in part direct and in part secondary.

The pounding force of the surf may reach high values. Engineers reckon the average force for the North Sea at 15,000 kg. per sq. m., or 1.5 kg. per sq. cm. Animals exposed to moving water on rocky coasts are thus in danger of being crushed by the water or torn from their places and hurled against the rocks. The inhabitants of rocky coasts within the surf line must therefore have strong protective covering and must be able to attach themselves tightly in at least one of a number of ways. They may be grown fast to the rocks, like the barnacles, or hold themselves by means of a powerful suction apparatus like the foot of the chitons and many snails (*Patella, Haliotis*), or they may anchor themselves by means of glandular secretions like the byssus of certain mussels (*Mytilus,* for example). The shells of the limpet (*Patella*) are lower, smaller, thicker, and more irregular in outline in exposed places than in sheltered ones.[29]

A *Mytilus* shell from the wave-beaten west coast of England may weigh 58 gm. as compared with 26.5 in one of the same size from the protected Bay of Kiel.[24] Many species of sea urchins on exposed coasts bore holes into the rocks, while the same species in the quieter

seas (*Strongylocentrotus* in the Mediterranean, for example) does not make use of this means of protection.[20] Corals in moving water tend toward a rounded or flattened and thick mass, with the single polyps closely attached to the upper side. In quiet waters the stalks are lightly calcified and finely branched.[12] The delicate Alcyonaria (*Spongodes*), on the contrary, in lesser depths where the wave action becomes effective at low tide, are elastic and wave back and forth like grain fields in the wind; in greater depths, where the water is quiet, they have stiff skeletons.[16] The hydroid polyp *Bougainvillia ramosa,* in deeper water, is delicate, slender, and branching. In moving water the stalks become stouter and were thought to represent a distinct species until the supposed *B. fruticosa* was experimentally transformed into *ramosa.*[10] Similar transformations have been demonstrated in *Campanularia integra* and *Sertularella tricuspidata.*[3]

Continuous currents contrast with the oscillating motion of the waves and tides and are of the greatest importance for the distribution of marine animals. Currents carry characteristic forms of the cold-water plankton, such as the appendiculates *Oikopleura labradoriensis* and *Frittilaria borealis,* from the Arctic Ocean into the North Sea in the spring, and in summer they carry warm-water species like the siphonophore *Physophora hydrostatica* as far north as the Lofoten Islands. The free-swimming stages in the life history of many fixed or slow-moving animals, like hydroids, corals, and echinoderms, are carried great distances by currents.[9a] Thus the gorgonid-fauna of the Bermudas is almost completely West Indian, the larvae being brought to the Bermudas by the Gulf Stream.[17] Occasional surface currents, caused by continued winds, may also carry animals away in definite directions. Thus in the Bay of Naples, where the surface fauna after the sirocco is especially rich, it is much impoverished after continued north winds, which drive the surface water out of the bay. The jellyfish *Aurelia aurita* sometimes is blown into enormous masses in the river mouths of the south shores of the Baltic by the summer winds.

Ocean currents are indirectly of extreme importance for the marine fauna. In the first place, they produce the general mixing of the water and maintain the average chemical composition of the sea water at a uniform level, with relatively small local variations. Wave motion favors the solution of oxygen from the air, by increase of the surface area, especially in the crests of waves and in surf and spray. The motions of the water are not merely superficial, but extend to considerable depths. Wave motion in the open sea extends to depths

of several hundred meters; it reaches a lesser depth near the coast, not below 40 m. on the Algerian coast; and 200 m., the "mud line," is usually given as marking the extreme lower extent of wave action near land. This coincides with the usual lower limit of the continental shelf. The tidal currents in many places appear to extend to great depths; whereas in 10 years at least 25 mm. of globigerina ooze is deposited in the open ocean, a cable near the Canary Islands in depths of 1800 to 2000 m. was found to be entirely free. The same was true of rocks on the sea bottom off the south coast of Ireland, at a depth of 1800 m.

A compensatory movement of the deep water must equalize the effect of the surface currents. On the lee coasts within the influence of the trades, the warm surface water is continually blown away and driven against the windward coasts, where it accumulates. It is replaced by the upward flow of cold water on the lee coasts, especially in bays. The warmth-limited reef corals accordingly thrive, especially in the tropical east coasts of the continents, and are less abundant on the west coasts, with their colder water from the depths, which reaches the surface at 15° or even 14°. In the Bay of Kiel, which is open to the east, continued west winds blow the surface water away, and the rise of the water from the depths is noticeable on account of the higher salt content, which is characteristic of the deeper water of the Baltic (cf. Chapter 15). The colder and hence denser waters of the polar seas sink and flow slowly along the ocean bottom toward the equator. The rate of flow at great depths has been estimated at about 1.5 miles per day.

The vertical currents, both up and down, are of especial importance in the mixing of the sea water; they will be discussed at greater length in a subsequent chapter. They have been observed with certainty in some places; in parts of the Bay of Naples a heavy dredge may be lifted and supported for some distance by such currents.[18] The currents, both up and down, and the whirlpools of the Straits of Messina are famous; 43 species of deep-sea fishes have been collected on the beach at the lighthouse,[22] and other deep-sea forms are found at the surface there. These currents appear to be caused by the difference in tidal phases in the Ionian and Tyrrhenian seas, so that counter currents meet in the Straits of Messina. The rate of upwelling near southern California is apparently about 20 m. per month.[23] The so-called "tongue of cold" in the south equatorial current north of Ascension Island is supposed to be produced by the rise of sea water

from the bottom. Descending currents seem to be present in the Sargasso Sea and perhaps in similar centers of oceanic drift.

The rate and direction of all these currents are subject to continual fluctuation, in part with a kind of periodic pulsation, whose nature and origin are as yet obscure. The combination of all these motions produces a phenomenon of extraordinary complexity.[25]

Heat and temperature

The oceans are a great storehouse of the heat that comes ultimately from the sun as a part of the radiation falling on the earth. The majority of this insolation strikes directly on the seas, since they occupy much more than half the earth's surface. In addition, some heat from the land is carried to the oceans, particularly to their bays and gulfs by the inflowing waters of rivers and smaller streams.[26] The vast oceanic reservoir of heat does much to regulate the temperature of the world. Approximately nine-tenths of the heat surplus of the oceans is used in evaporation and is stored or transported in water vapor until released by precipitation, perhaps over the sea or, perhaps after considerable delay, far back over the land. This is one of the principal means of heat transport.[6] Temperature relations of the water are of maximum importance to marine zoögeography. The temperature of the sea water varies not only with location but also with the seasons, in different degrees. The extremes range from about $-3°$ to 42°, although even in the tropics the surface water of the open ocean does not exceed 30°;[34] in the Red Sea the temperature reaches 34° in summer. The amplitude of seasonal variation in temperature depends on the location. Temperatures of the tropical and polar seas are relatively uniform, whereas seasonal variation is high in the temperate zones. The annual variation in temperature is less than 5° on almost three-quarters of the oceanic surface, and on one-third of this (especially in the tropics) less than 2°. The greatest variations appear in localities where warm and cold currents meet and predominate by turns. Variation is also high in arms of the sea in the higher latitudes. The annual temperature range in the northern Mediterranean reaches 14°, in the Baltic 17°, in the inner parts of the Yellow Sea 27°. Such seasonal variations apply only to the surface layers, ceasing at depths of about 200 m. Regional temperature differences are of importance as barriers and as impetus for variation (Fig. 14).

A stratification of temperatures is a result of the property of water whereby it increases in density as the temperature drops. The heavy

cold polar water sinks and gradually spreads out on the bottom toward the equator, and the lighter warmer water of the tropics flows toward the poles. The radiant heat of the sun does not reach deep into the water, and the effective distribution of heat in the depths is accom-

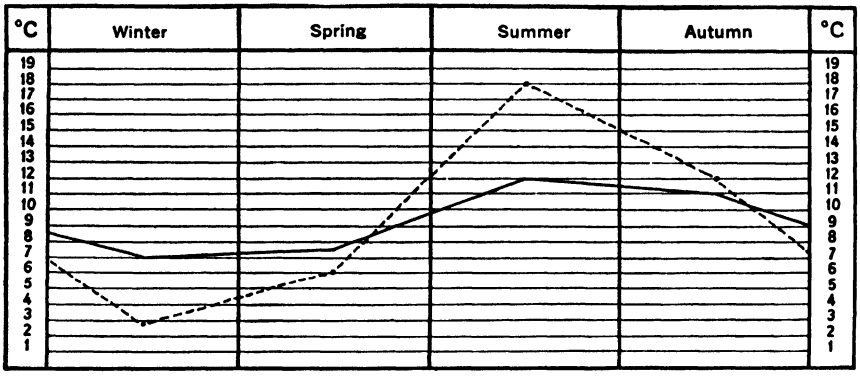


FIG. 14. Variation of the surface temperature in the open ocean off the west coast of Scotland (——) and in the stagnant Baltic Sea (----). After Meyer and Möbius.

plished by currents. The average temperatures at different depths for the oceans as a whole, according to Murray and Hjort,[25] are:

Meters *	Degrees Centigrade	Meters	Degrees Centigrade
183	15.95	1097	3.89
366	10.05	2012	2.28
549	7.05	2743	1.83
732	5.44	4023	1.78

* Over 80% of the ocean floor is a mile or more below the surface and has a temperature of 3° or less.[38]

Unlike fresh water, sea water with a salinity of 24.7 per mille (‰) * or more continues to become heavier until its freezing point is reached. Fresh water becomes lighter below 4°, a property limiting the minimum temperature at the bottoms of lakes to 4°. In the sea, bottom temperatures of −1° may occur in regions with polar currents; temperatures of the abyssal waters are usually slightly above zero. On account of the presence of salt, the freezing point is depressed; for water with a salinity of 35‰, it is approximately −1.9°. Tempera-

* *Per mille* (‰) has obvious advantages over per cent (%) when discussing salinity of the ocean.

ture differences between bottom and surface at the equator, a distance of six miles or less, are much greater than those between two points on the bottom 10,000 miles apart.

Special conditions are found in seas connected with the adjacent ocean by more or less shallow straits, such as the Red Sea, the Sulu Sea (west of the Philippines), the Caribbean Sea, the Gulf of Mexico, and the Mediterranean. The Straits of Gibraltar have a greatest depth of about 400 m. As the Mediterranean waters have a higher salt

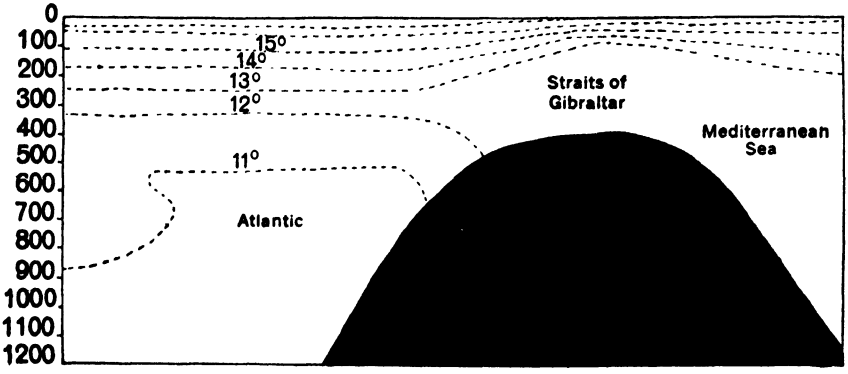


FIG. 15. Diagrammatic vertical section from west to east in the sea at the Straits of Gibraltar, with the isotherms of the sea water; depths in meters at the left. After Murray and Hjort.

content than those of the Atlantic, on account of more rapid evaporation and smaller influx of fresh waters, their greater density causes a sinking of the surface waters, which are replaced by an inflow of the less dense Atlantic water. The countercurrents in the straits consist of the broader superficial inflow and a deeper outflow. The deeper waters of the Mediterranean accordingly have a temperature of about 12.9°, corresponding with that of the lowest level of the inflow; colder water does not enter; the temperature from about 160 m. to the deepest part of the sea (3968 m.) is uniform at 12.89° (Fig. 15).[22] In the Sulu Sea the temperature of the water is 10.5° from about 750 m. to the bottom. A. Agassiz [1] found the water in the depths below 1100–1200 m. in the Caribbean Sea and the Gulf of Mexico to have a uniform temperature of 4.17°. Here the strait between Cuba and Santo Domingo, which keeps out the colder waters of the Atlantic, has a depth of 1300 m.

The gradation of temperature in the sea is not uniform with increase in the depth. At a certain depth the drop in temperatures is

notably greater than in the strata above and below, sometimes more than 2° in 25 m., in fact. This level is called the "thermocline." It is found in all warm seas and usually lies between a depth of 50 and 150 m. The origin of the thermocline [15] is explained by the evaporation from the surface, which makes the surface water slightly more dense, so that it sinks to a level where its density is equaled by that of the colder water below. The thermocline often is the border between two different animal communities.

The temperature relations of the oceans have played an important part in the whole history of the evolution of the marine faunae and of land animals as well. Contrary to the older point of view, these temperature relations have not consisted of a simple cooling process that allowed life to originate in the first-cooled waters of the polar seas and to spread gradually south as world temperatures fell; rather it now appears that temperatures in the polar regions have fluctuated widely; that there have been successive ice ages and successive periods when mild temperatures were world wide and even the polar seas were free from ice the year around. In fact, the present temperature zones appear to be a relatively unusual world condition. Under the more usual temperature relations, tropical or subtropical vegetation would grow in Greenland and coral reefs could flourish in high latitudes as they are known to have done from fossil remains.

The response of marine animals to temperature is naturally varied. Examples of stenothermal, warmth-limited forms are the reef corals, ranging only between the 20° isotherms of the surface waters, and in general the Salpae and Heteropoda. Among individual species, the crustacean *Copilia mirabilis* is confined to temperatures between 23° and 29°. Amphipods tend to be cold-tolerant stenothermal animals, and find their principal development in the polar seas; the tunicate *Salpa magalhanica,* and many other animals belong in this category. The oyster *Ostrea edulis,* which endures temperatures from −2° to +20° on the Holstein Bank without harm, is eurythermal, and even more so the barnacles like *Balanus balanoides,* which, if attached to rocks near the tide limit, may be exposed to temperatures below freezing at one time and to the direct rays of the summer sun at another. The bivalve *Cardium edule* and the lugworm *Arenicola* are others. Eurythermy and stenothermy, of course, intergrade. Nothing is thus far known as to what may be the physical basis of adjustments to such variations.

The greater temperature differences in the sea obviously form effective barriers to distribution. Thus the faunae of the west and east

coasts of Florida have a very different composition.[32] The Gulf Stream, which washes the west coast, gives the fauna a tropical character, while on the east coast, at least as far as Cape Canaveral, there is a cold countercurrent that brings the Carolinian fauna southward. Fewer than half the species of mollusks are common to the two sides of the peninsula; about a third are confined to the west coast, and about a fifth to the east. Similar differences exist between the west and east sides of Spitzbergen; the west coast is reached by outlying parts of the Gulf Stream, and the character of its fish fauna, for example, is Atlantic; the much lower temperatures of the eastern coasts bring with them an arctic faunal character.[21] The Dogger Bank in the North Sea forms an important temperature barrier; north of it the difference between surface and bottom temperatures is 7.7°, while to the south, where the cold northern water is kept out, the difference is only 0.8°. The fauna of the northern side of the bank is thus markedly boreal, while to the south it is Atlantic; out of 167 crustaceans on the north side, 85 are absent on the south, and of 97 on the south side, 15 fail to reach the northeastern part of the North Sea.[4] Finally, we may mention the abrupt temperature barrier formed by the submarine Wyville-Thomson Ridge, between the Shetland and Faeroe Islands.[25] Northeast of this ridge the temperature at 1100-m. depth is −0.41°, while at the same depth, scarcely a degree further to the south, on the other side of the ridge, the temperature is about 6° (Fig. 16). Accordingly two entirely distinct faunae are brought into immediate contact, the arctic to the northeast of the ridge and southern forms to the southwest. Out of 385 species of animals in this area only 48, or 12.5%, are common to the two sides of the ridge.

Marine animals present a number of correlations of structure with temperature. Notable among these is the increased number of vertebrae in teleostean fishes from the tropics north, or from warm waters to cold.[13] Among acanthopterygian fishes the vertebrae number uniformly 24 in all the tropical species of a whole series of families, whereas the cool-water species belonging to these same families have an increased number. Among flounders of the subfamily Hippoglossinae, the number of vertebrae increases from 35 in the more southern species on the American coasts to 50 in the Arctic.[14] Increase in length in arctic fishes is produced by increase in the number of vertebrae, while many elongate fishes of the tropics have acquired the same body form by increase in the length of the individual vertebrae, without increase in their number.

The larger size of northern and cold water marine forms is a fre-

quent phenomenon, both as applying to the individuals of a wide-ranging species and to the northern or cold-water species that replace tropical forms within a given genus. Delayed sexual maturity, which favors growth in size, appears to be directly dependent on retardation of growth at lower temperatures, and this is a common characteristic of northern marine creatures.[11] Large-yolked eggs, with more complete development of the embryo within the egg, and the brood care

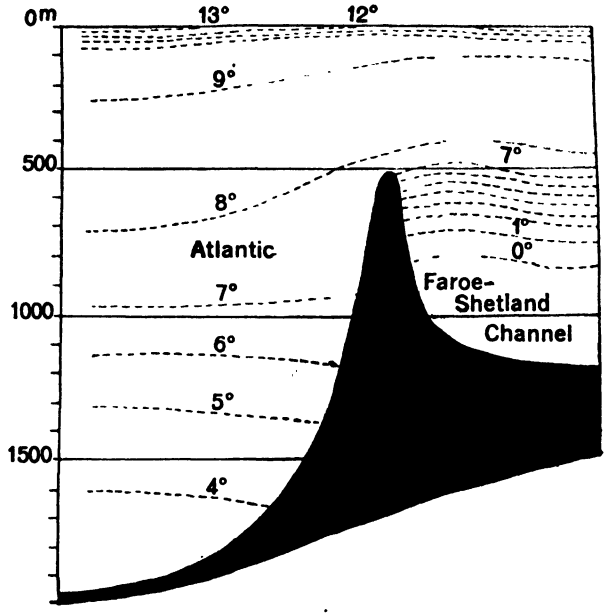


FIG. 16. Diagrammatic vertical section across the Wyville-Thomson Ridge with the temperature stratification shown.

or ovoviviparity associated with such eggs, are by no means confined to cold waters; but the frequency with which these phenomena appear among the most diverse groups in arctic and antarctic seas indicates a convergent association with low temperatures.[11]

Water masses

The oceans consist of distinct water masses each separated from its neighbors by transition zones rather than by sharp boundaries. The different masses are identifiable by their temperature-salinity characteristics. Their consideration forms a fitting connecting link between discussion of the physical conditions in the oceans in the present chapter and the chemistry of the sea in the one to follow.

Typically the oceans have a relatively thin surface layer about 100 to 200 m. thick. Temperature-salinity values vary greatly within this layer, and great seasonal variations occur, particularly in middle latitudes.

The Antarctic Ocean extends around the world, with the Pacific, Indian, and Atlantic oceans somewhat resembling great annectant bays. The Pacific and Indian oceans are practically closed to the north, and so is the Atlantic, if its arctic extension is considered as the North Polar Sea comparable to an enlarged Mediterranean or Caribbean sea. Each of the larger bodies of water has its own set of water masses that despite their basic similarities are organized into fairly distinctive geographic patterns.

No attempt will be made here to catalog all the water masses. The subject is discussed in much detail and with the aid of maps, tables, and diagrams, by Sverdrup, Johnson, and Fleming,[34] with particular attention to the relation between water masses and ocean currents. Selected examples will be given to convey a general idea of the masses occurring in the oceans and their mode of origin.

Antarctic Circumpolar Water surrounds Antarctica. It comes up to the Surface Water about a hundred meters below the surface of the sea and overlies Antarctic Bottom Water. To the north, in the antiboreal or subantarctic region, five vertical water masses can usually be distinguished, arranged in the following order: (1) Subantarctic Upper Water, (2) Antarctic Intermediate Water, (3) Upper Deeper Water, (4) Lower Deeper Water, and (5) Bottom Water.

The subantarctic water mass extends northward in each ocean as Intermediate Water sandwiched according to density between the appropriately named Central Water and the Deep Water below. The intermediate water mass of subantarctic origin extends as much as 20° north of the equator in the Atlantic but does not cross the equator in the other oceans.

Unlike the Pacific and Indian oceans, the Atlantic lacks an equatorial water mass. South Atlantic Central Water passes by a broad transition into North Atlantic Central Water that overlies Arctic Intermediate and the transequatorial extension of Antarctic Intermediate Water. Both intermediate waters extend over a considerable expanse of more dense Mediterranean Water fanning out from the Strait of Gibraltar. This whole North Atlantic system of water masses overlies the southward-flowing North Atlantic Deep and Bottom Waters. Coastal, continental slope, oceanic current, and large-scale transition masses also exist.

Most subsurface water masses are formed when in contact with the atmosphere; they sink and spread as a result of the relation between their own density and the general distribution of density in the oceans. The general rule that all oceanic water masses originate at the surface has two exceptions in that the equatorial masses of the Indian and Pacific oceans are formed by subsurface mixing. Again with two exceptions, provided by the intermediate masses originating in the Mediterranean and Red seas respectively, no subsurface water mass is formed at the sea surface in low latitudes; rather, such water masses have their origin in polar, subpolar, or cold temperate regions. The place of origin is indicated by the area in which, at some season of the year, the horizontal temperature-salinity relations are similar to the vertical ones of the given mass.

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11. *The Chemistry of the Sea and Its Influence on Animal Life*

Salt content

SEA WATER IS A SOLUTION THE COMPOSITION OF WHICH IS NOT EVERYwhere exactly the same. In the open ocean the salt content at 300-m. depth approximates 35‰, but there are differences in the composition of the surface water. In the tropics the evaporation exceeds the inflow, and the salt solution becomes more concentrated. In the polar regions the melting ice causes a dilution of the solution in summer. The most marked deviations from the average composition occur in the seas and gulfs. The intermixture of their waters with the open ocean is limited by their degree of separation, and differences in one direction or the other arise accordingly. Thus the Mediterranean, with its relatively low influx of fresh water, has a salt content of more than 37‰ in its western part, 39.5‰ at Crete, and even 40‰ on the Syrian coast. The Red Sea, with no regular supply of fresh water, has as much as 45.4‰ to 46.5‰ salt. By contrast, in the western Baltic the salt content is 12‰, 7.4‰ at Bornholm, and in the Gulf of Finland only 0.6‰. The fresh water from melting glaciers and icebergs dilutes the surface water of the polar seas so that the salt content may fall below 15‰. As the more concentrated solution is denser, the salt content may increase with depth. This is especially evident in the Baltic, where a bottom current of more concentrated salt water flows in while the more dilute surface water flows out; thus in the western Baltic the salinity at the surface may amount to 8–12‰ and in the depths may reach 27‰.

"Chlorinity" is often used in determining salinity or even as a working substitute for it. "Halinity" would be a preferable term. The halogen ions—chlorine, bromine, and iodine—make up about 55% of the dissolved solids. Their quantitative analysis is readily

made by titration with silver nitrate. Combined, they are usually referred to as "chlorine," and the chlorinity of so-called normal sea water is slightly less than 19.4%.

The greater part of the salts in sea water consists of the chlorides of sodium, magnesium, and potassium, of which common salt (NaCl), with 27.37 gm. per liter, preponderates. To these must be added the sulphates of magnesium and calcium. Other elements are present in much smaller amounts; some, like silver, copper, and vanadium, only in traces. The question as to whether the salts of the sea water have been derived from the earth by the solvent action of the rains and streams touches us in this connection only in so far as it bears on the biologically not unimportant problem as to whether the sea was formerly less saline than at present. The assumption that the sea salt is derived from the land is not necessarily true. Seas without outlet whose salinity is exclusively derived from river water do not have the composition of the sea water, and, for example, may contain Epsom salts or borax. Rivers, furthermore, contain only very small amounts of chlorides, which predominate in the sea water. Salt masses from the sea bottom itself may have conditioned the composition of the sea water.

The salts of the sea are important in the life of its animals. Indirectly, animals profit by the substances taken up directly by the plants; in addition to potassium, sodium, calcium, magnesium, sulphur, and chlorine, which are present in excess, plants use among others phosphoric acid, nitrates, nitrites, and ammonia. Animals are able to draw directly upon a number of the inorganic materials of the sea water to build up their bodies, especially sodium, magnesium, and calcium, and also silicic acid. Occasional animals may use rarer elements, as, for example, the radiolarians of the suborder Acantharia, which use strontium sulphate; horn corals store bromine and iodine in their skeletons; and ascidians contain vanadium as a coloring material in their blood. The differential withdrawal of NaCl is fatal to most marine animals, even when it is accomplished gradually; but this is a condition that does not concern such animals in nature.

The osmotic properties of sea water are of high importance to marine life. Osmotic pressure rises with increasing concentration and falls with decreasing concentration. It amounts to no less than 26.7 atmospheres in the water of the Red Sea, of 40‰ salinity, at 30°. In the waters of the Baltic at Bornholm, of 7.5‰ salinity, at 18°, it is only 4.9 atmospheres. Marine animals, with the exception of the bony fishes, are adapted to the medium in which they live in having their

body fluids isotonic with sea water, so that these are not altered by diffusion. It is probably for this reason that some marine animals are very sensitive to variations in the salinity of the surrounding water. Others, on the contrary, are able to live in waters of widely different salinities, and some can even withstand relatively rapid change from weak to strong concentration, and *vice versa*. The former animals are characterized as stenohaline, the latter as euryhaline. There are all possible degrees of the sensibility to variation of salt content.

Stenohaline animals are subject to certain restrictions in their distribution. They are found primarily in the open ocean, where they are little exposed to this variation. Even the surface forms, for which rains may dilute the sea water, can escape this variation at the depth of a few meters. Stenohaline animals may live on the coasts away from river mouths and below the level of tidal variation. Great depths are also suitable for them. Colonial radiolarians, reef corals, juvenile stages of the fish *Fundulus*, and many others afford examples of stenohaline animals.

Euryhaline animals are, of course, able to live side by side with stenohaline forms, in habitats in which they make no use of their ability to withstand variation of salt content. Other situations, however, are accessible only to them, and more exclusively so with greater limits of variation in this respect. Such situations afford euryhaline organisms the advantage of freedom from competition, above all from pursuit by stenohaline enemies. Euryhaline forms include the coastal fauna that lives between the tide levels and is thus exposed to rain water at low tide; the animals near the mouths of rivers, where the extent of the influence of the fresh water varies with the variable volume of flow of the river and the state of the tide; the inhabitants of the salt marshes, whose waters are concentrated by the summer sun and freshened by fall rains and melting snow in the spring; and the fauna of spray-pools on rock coasts. Examples of euryhaline animals are such jellyfish as *Aurelia aurita* and *Crambessa tagi*, which are driven into river mouths without harm; the edible mussel *Mytilus;* the lugworm *Arenicola;* the green crab *Carcinides maenas;* the appendiculate *Oikopleura dioica;* some sharks that range into fresh water; and numerous others. Closely related animals behave differently in this respect. Among the chaetognathous worms, *Sagitta hexaptera* is very sensitive to fresh water, whereas *Sagitta bipunctata* has an unquestionable adaptibility to brackish water.[24]

The composition of the faunae of waters with varying salinity is regulated by selection, as in saline lakes and in the Baltic, and in fact

in all brackish waters. This is also plainly shown in the impoverished fauna of the Caspian Sea; important groups of animals, widespread in the ocean, are entirely absent, such as Anthozoa, scyphozoan medusae, Ctenophora, Echinodermata, Tunicata, Brachiopoda, Pycnogonida, Scaphopoda, as well as Cephalopoda and Selachia; and yet there can be no doubt of the marine origin of the fauna.

Adaptation to lowered salinity is frequently connected with reduced size. Sea urchins wander into the mouth of the Rhone as larvae and become mature, but do not reach more than a third of the normal size.[17] Marine bivalves exhibit strikingly reduced size in marine basins with reduced salt content of the water.[10] Heincke compares two flounders (*Pleuronectes platessa*) 21 cm. in length from the North Sea and the Baltic; the former was three years old, the latter six.

Among the most persistent of the inhabitants of the brackish waters of the Baltic and of the Mediterranean lagoons is the annelid *Nereis diversicolor,* which is also able to resist highly concentrated saline waters. The small number of stenohaline brackish-water animals confined to brackish waters includes the hydroid polyp *Cordylophora lacustris* and crustaceans such as *Eurytemora hirundo* and *Temora longicornis* of the Baltic. Among fishes the Syngnathidae are inclined to take to brackish water. No group of animals has produced as many brackish-water forms as the mollusks. Whole genera of lamellibranchs and snails have gone over to this habitat. The greater number of brackish-water forms occur at present in the tropics, where the immigration from the sea into this habitat and into fresh water appears to be much easier than in higher latitudes; the reasons for this are still unknown. The production of special brackish-water forms may occur in two ways: by mutation, so that the direct relation with their marine ancestor is no longer evident; or by the extinction of the ancestral form in the marine habitat, so that the brackish-water derivative remains as a relict. The latter seems to be plainly the case with the clam *Tagelus gibbus,* now confined to brackish waters in America; its marine ancestors have been found fossil in the Miocene of North America and the Argentine.[13]

Calcium compounds

Calcium is the only one among the more important constituents of the sea salts whose proportionate amount fluctuates to a significant degree. It varies from 1.59 to 1.82% of the total salts, averaging 1.6%. Since sea water is in general alkaline, it does not retain calcium carbonate in solution, and the calcium occurs principally as sulphate,

in contrast with the condition in fresh water, which is able to dissolve the carbonate, thanks to the presence of free carbon dioxide. Calcium is utilized by innumerable animals in building up spicules, shells, armor, and skeletons. $CaSO_4$ is usually precipitated for this purpose by $(NH_4)_2CO_3$. Experiments show that this reaction proceeds very rapidly at 26–29°, but very slowly at lower temperatures (4–7°).[21] The free use of calcium salts by marine animals is thus conditioned to a considerable extent by temperature. It has been shown by direct observation that crabs change their shells and grow new ones more

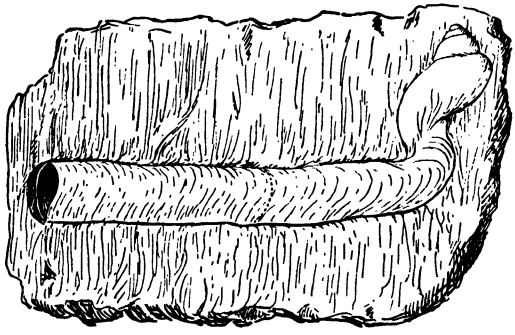


FIG. 17. *Magilus antiquus* with the coral limestone cut away to show the shell, which is filled with calcium carbonate to the dotted line.

rapidly at high temperatures than at low. Calcium deposits by animal life reach their maximum in the tropics, where the reef corals build gigantic masses of rock. Tropical mollusks often have shells of great thickness; the snail *Magilus,* living among coral reefs (Fig. 17), as its shell lengthens with increasing age, fills a large part of it with lime. The shells of the giant clam *Tridacna gigas* may reach a weight of more than 250 kg. In very cold waters, the calcium in the sea water is inaccessible to the marine animals, and the tropical forms with strong shells or skeletons of this material are accordingly often replaced in polar seas by naked or soft forms, without shell or with a delicate chitinous armor, as among Coccolithophoridae, Foraminifera, and Pteropoda. The serpulid worms, which build lime tubes, also reach their highest development in tropical seas and have few representatives in polar waters. Animals that deposit large amounts of lime are also absent in deep seas; serpulids, for example, are wanting, and the deep-sea sea urchins are forms with a soft shell (Echinothuridae). This constitutes an important factor in the distribution of marine animals.[22] Murray [19] has pointed out that the calcium,

which the rivers bring into the ocean and which comes from the decomposition of continental rocks, is thus deposited more and more in the tropics at the present time.

The presence of the inorganic substances of primary importance to plant life, especially those not present in excess, such as carbon dioxide, phosphoric acid, and the nitrogen compounds, determines the quantitative distribution of plant life in the sea and thus secondarily influences the distribution of animal life.

Sea water contains 40 to 50 mg. carbon dioxide per liter, of which only a few tenths of a cubic centimeter per liter is present in simple solution; [20] it is combined as carbonate or bicarbonate, on account of the excess of basic compounds. Experiments have made it certain that plants are able to use the carbon dioxide contained in bicarbonates. The expended carbon dioxide is replaced in the sea partly from the air, partly by that produced by the marine animals, and partly by the large amounts constantly brought in by the rivers. Carbon dioxide is used by plants only in the euphotic and dysphotic strata of water. The animals inhabiting the aphotic depths give off carbon dioxide, and the decomposition of the sinking bodies of plants and animals adds to this, so that carbon dioxide is stored in the depths. This store becomes available to marine plants only where vertical currents bring the bottom water to the surface. The observations of Atkins [2] show that the carbon dioxide in the upper layers may be rapidly used up. He found that the reaction of the surface water on the English coast varied with the season from *p*H 8.14 in December to *p*H 8.27 in May at the time of the highest amount of sunshine. This seemingly small variation really amounts to a fall of 25% in the hydrogen-ion concentration and results from the accumulation of the carbon dioxide produced by the excess of animals in winter and its use by plants in their flourishing summer growth. Marine plants accordingly flourish most where there is a constant inflow of water with available carbon dioxide.

Nitrogen compounds

The situation is similar with the nitrogen compounds,[4] which are unconditionally necessary to plant life, together with carbon dioxide and phosphoric acid. Nitrogen in combination as nitrates, nitrites, or ammonia, and thus available to plants, is present in the North Sea to the amount of about 300 mg. per cu. m., and rather less in the waters of the open ocean. The amount in milligrams varies with the temperature, about as follows:

Average temperature	3.4°	12.6°	17.8°	23.2°	27.7°
N as N_2O_3 and N_2O_5	216	144	142	91	78
N as NH_3	68	75	46	36	45

In view of the great requirements of plants for nitrogen, it seems likely that the smallness of the amounts present in sea water limits the amount of plant life and thus also the animal life of a given part of the sea.

The sources of nitrogenous compounds in the sea are various. They originate in the seas themselves by the metabolism of animals and by the decay of dead organisms. The supply from without is brought in by rivers in the form of nitrites, nitrates, and ammonia, and perhaps also in organic compounds, and by rains, which contain a little nitric acid, especially in the zones of frequent electric storms. The question whether nitrifying bacteria normally occur in sea water has not been settled with finality. The conclusions of Waksman and of ZoBell, cited in the introduction to this section, are worth rereading. Nitrate-fixing bacteria may well be present on the ocean bottom. The supplies are diminished by loss of ammonia, which is freed from the ammonium compounds by the considerable "ammonia pressure," passing into the atmosphere and blowing over the land, where it is absorbed by rain drops and transmitted to the soil.

In any case, as for carbon dioxide, the nitrogen is available for green plants only in the lighted upper levels. The nitrogen content consequently also increases with depth; on the average, nitrogen as nitrate and nitrite occurs in the oceanic surface water to the amount of 101 mg. per cu. m., 313 mg. at 400 m., and 485 mg. at 800 m. (Brandt). The loss of nitrogen in the upper layers is increased by the fact that the bodies of many dead organisms sink far below the plant-inhabited levels before they decompose. Thus in moderate depths, water near the bottom of the sea is thought to be richer in nitrogen. Where such bottom waters are brought to the surface, plant life will flourish. At greater depths (5400 m.) Krogh found that the total nitrogen present was approximately constant from surface to bottom at the time tested.[16] There is conflicting evidence on this matter.

The fertilization of the lighted upper levels of the ocean by nitrogenous compounds thus occurs in a variety of ways, principally through the thorough mixing of the waters, the upwelling of deep water, and the inflow of fresh water. The different amounts of these fertilizers in different areas explains the difference in the abundance of marine life.

A general mixture of marine water to the bottom occurs only in

shallow seas. It is produced in shallow coastal waters by the tides, and to greater depths by storms. There is a periodical mixing of the waters, in consequence of the cooling of the surface water in the winter season, in the temperate and cold zones, and this is sufficient to bring up the nitrogenous water from the bottom in shallow seas. The mixing extends to a depth of 140 m. in the Atlantic and to greater depths in cold seas; to 800 or 900 m. south of Iceland. This is one of the reasons why coastal waters in general are richer in animal life than the near-by deeper seas with similar physical conditions (light and heat), and why shallow seas, like the North Sea and the western Baltic, and shallow banks, such as the Dogger and Newfoundland banks, have such a rich flora and in consequence a rich fauna, and thus become favored fishing grounds. It also explains, in part, the greater concentration of organisms in the milder part of the Arctic and Antarctic seas. Coloring of the sea by thick masses of plankton appears only in shallow seas, as in the Baltic, the Gulf of Guinea, the Gulf of California ("Purple Sea"), and the "red tide" of the Japanese coasts. The deeper the ocean the more difficult such mixing of the sea water from the surface to bottom becomes.

On coasts where continued offshore winds carry away the surface water, a compensating current rises from the depths. Such currents stir up the bottom strata, which are rich in nitrogenous compounds, and carry them to the surface, where they become available as foodstuffs. Their origin is betrayed by the coldness of the water. No oceanic waters swarm with so much life as the upward streams of deep water in tropical and subtropical latitudes. Such regions are consequently adapted to extensive sea fisheries. Such localities include the Algerian coast, with its renowned sardine fisheries, some places on the Portuguese coast, the west coast of Morocco and the African coast opposite the Canary and Cape Verde Islands, and the coast of southwest Africa. The astonishing richness of the fish fauna in the cold-water areas of the Arabian Sea near Oman and at Cape Hafun on the Somali Coast is even more striking. The coasts of Chile and Peru, with their cold upward currents, are especially notable for wealth of marine life;[3] the guano deposits of the outlying Peruvian islands are the indirect result; and the luxuriance of the submarine forests of algae (*Macrocystis pyrifera*) with their rich fauna, on the coast of Chile, doubtless also depends primarily on this kind of fertilization.[7]

The Kiel Fiord exhibits an occasional upward current of cold water. A southwest or west wind drives the surface water out of this bay so that the bottom waters rise; when the westerly wind prevails

for a considerable time, as in early spring, the water of the fiord become grass green from the multitude of diatoms.[5] The development of diatoms is slight with northerly and easterly winds. Deep-sea currents may be diverted into an upward direction by submarine banks and ridges, as by the Wyville-Thomson Ridge, south of the Faeroes, where the surface water is also rich in life.

Vertical mixing also appears in places where a warm current passes a cold one, in consequence of the differing densities of the adjacent masses of water, and in the polar seas the deepest waters are involved in the movement. Examples are presented by the Newfoundland Banks, where the Labrador Current and the Gulf Stream adjoin, and the west coast of Japan where the warm Kuroshio and the cold Ojashio pass each other. Both localities are the sites of important fisheries. Deep water is drawn to the surface even when two neighboring currents have a similar temperature if the currents are diverted in opposite directions. The existence of the so-called "tongue of cold" of the South Equatorial Current, north of Ascension Island, with its richness in plankton, may be ascribed to this cause. The Straits of Messina between Italy and Sicily also have a rich plankton; the waters are mixed in consequence of the different tidal phases of the Tyrrhenian and Ionian seas to the north. Downward currents attract surface water whose nitrogen and carbon dioxide have been exhausted, and areas where they occur, like the Sargasso Sea, are poor in life. The small importance of thermal currents in the Mediterranean, whose waters are no colder than 12.9° at the bottom, results in general poverty in plankton despite local exceptions. Many of the relations of phosphorus and silicon are similar to those that have been discussed for nitrogen. In the higher latitudes there are distinct seasonal fluctuations of the amounts of these essential mineral nutrients, accompanied by seasonal variations in the quantity of plankton organisms.

Phosphates

Phosphates in the sea resemble nitrogen compounds in their importance as limiting factors in the development of plant plankton. Phosphates may be the more important, in part because they are present in smaller concentration. The ratio of marine nitrate-nitrogen to phosphate-phosphorus in the seas roughly approaches 15:1 in milligram-atoms, or 7:1 in weight. The two sets of chemicals are similarly distributed both regionally and in depth. Both have seasonal variations with lower concentrations during the summer growing season. The "regeneration" of phosphates takes less time and is

apparently less complicated than is the similar release of nitrates.[11] Phosphates, like nitrates, are brought to the sea in large amounts by river drainage from fertile areas, but even with ready regeneration and inflow, about three-quarters of the observed phosphorus near the surface of the Bay of Maine comes from the depths by vertical transport.[14] Compounds of silicon, carbon, and other chemical elements, many present in trace concentrations only, are also important in the economy of the sea.[25]

Influence of rivers

The distribution of rich faunae in the ocean is influenced also by the amount of materials received from the land, principally from the rivers. This is probably an additional factor in the wealth of marine life in coastal waters. Such materials are very unequally distributed in the oceans. The Atlantic and Arctic receive the largest amounts of river water. They receive the waters of all the European rivers and of the most important African rivers; the major part of North America and almost the whole of South America drain into the Atlantic; and the waters of the mighty Siberian rivers, draining into the Arctic, are carried toward the coast of Greenland by a westward current. The Atlantic-Arctic is thus surrounded by tributary land masses, and with a surface of 103,000,000 sq. km., receives the drainage from over half the land surface of the earth. The Atlantic has in addition wide shallow areas, especially at the north, with 13% of its extent within the 200-m. line and only 47% deeper than 400 m., and so is well equipped to produce maximum returns from its enriched waters.[25] The Indo-Pacific-Antarctic, on the contrary, receives its land waters almost entirely from Asia; with 265,000,000 sq. km., it receives the drainage of only 27% of the land surface. The southeastern Pacific is least supplied with land waters, and this source of fertility is almost negligible. The result is that the Atlantic differs from the Pacific Ocean biologically as well as geographically.

These facts help explain the poverty in life of the open southeastern Pacific, though it must be added that almost three-fourths of the extent of the entire Pacific Ocean is more than 3600 m. deep and that the absence of a continental shelf on the west coast of the Americas, with the lack of coastal habitat differentiation, contributes to the same results. The waters of the Pacific have the lowest content in nitrogen compounds. The surface water contains, per cubic meter (the figures in parentheses refer to the tropical belt between 24° S. and 25° N.):

Ocean	Nitrogen in Nitrates	Nitrogen in Ammonia
Atlantic	102 mg. (88 mg.)	47 mg. (46 mg.)
Indian	119 mg. (77 mg.)	52 mg. (43 mg.)
Pacific	69 mg. (66 mg.)	46 mg. (50 mg.)

The tropical parts of the oceans are probably poorest in life, the only exceptions being places where there is extensive upwelling of the bottom waters. Alexander Agassiz [1] refers to the middle Pacific as "barren grounds," in sharp contrast with the abundance of life in the Gulf of Mexico or in the main current of the Gulf Stream along the Florida Reef. The western Pacific, into which the great Asiatic rivers flow, with its wide shallow areas and good development of coastal formations, is much richer in life. Mitsukuri [18] speaks of the plankton of the Japanese sea between Honshu and Shikoku as quantitatively the richest known to him. The fisheries of the Japanese coast and of part of the Chinese coast are among the most productive in the world.

The rivers of southern Asia and the great extent of the coast lines in the East Indies are favorable to a rich marine life. In contrast, Chun [6] finds the crystal-clear surface waters between the Seychelles and the east African coast poor in animal life.

The general conclusion that the tropical seas are poor and the cooler and cold seas rich in plankton, although relatively true, requires some modification. The distribution of life in the sea depends on the fertility of the water, and this depends in turn on a number of factors varying from place to place and sometimes from season to season.

Even at its best, sea water is a very dilute solution of many of the mineral nutrients essential for plant growth; the concentration, even of essential substances, may be many times less than in good soil. This means that planktonic plants must secure many of their essential salts from an extremely dilute solution, and this necessitates that they be of small size in order to have a high ratio between area of surface and bulk. In contrast to the trees, shrubs, and grasses of the land, the marine plants that form the base of the food chain consist of minute diatoms and other, even smaller, algae, together with bacteria.

Oxygen

Of the substances dissolved in sea water, oxygen is one of the most important for marine life. The amount of gas absorbed by water is larger at low than at high temperatures, and the amount dissolved in sea water is accordingly greater at the poles than at the equator. A liter of sea water of 35‰ salinity may contain 8.03 cc. of oxygen at 0° and only 4.93 cc. at 25°; on account of the presence of salts, oxygen

is about 20% less soluble in sea than in fresh water. The most superficial layers replace used oxygen from the air, and it is distributed to moderate depths by wave action. Within the lighted zone the metabolism of plants is an important source of oxygen. In the lower reaches of the lighted zone, plants consume as much oxygen as they liberate, or more; the level at which consumption balances production is called the "compensation point." In the Gulf of Maine this compensation point is mostly around a depth of 25 m.[9] In depths of about 500 m. there is frequently greater oxygen deficiency than at lower depths. Thus in the Atlantic at 500 m. in latitude 10° N. there may be a deficiency of almost 100%; deeper waters of the Atlantic have a deficiency of only 25%.

In the great oceanic depths, which receive their waters from high latitudes, the oxygen content is only a little below normal. When there is no such bottom drift of cold water, carbon dioxide accumulates at the bottom and there is a lack of oxygen. This occurs in some places in the Mediterranean; Natterer found the bottom waters at 3700 m. with only 2.64 cc. of oxygen per liter, at another place at 1005 m., 3.85 cc., and at a third at 1210 m., 4.60 cc.; but even 2.64 cc. of oxygen per liter will support much life. There are, however, descending currents of surface water in the Mediterranean at isolated places (Aegean Sea, southern Adriatic, northern Balearic Sea) which extend to great depths, thus affording a limited oxygen supply.[8] In the deep troughs of the Baltic the water stagnates, with a resultant lack of oxygen in the bottom waters and with attendant reduction in the number of species at these places. Bornholm deeps, Bay of Danzig, and the Gotland deeps [23] are such localities.

In many places where there is stagnation of the water at the bottom but a rich surface fauna, the want of oxygen becomes so great that hydrogen sulphide produced by the decomposition of animal bodies is no longer oxidized and accumulates in the deeper water. The bottoms of isolated bays, lagoons, and harbors accumulate a black ooze filled with hydrogen sulphide. The Bay of Naples and the Gulf of Guinea on the west African coast are examples. Bottom life becomes scarce in such places, and only the most resistant forms persist, like the tubicolous worm *Spio fuliginosus* in the Bay of Naples. Where the accumulation of hydrogen sulphide continues, all life is absent, with the exception of anaerobic forms. The depths of the Black Sea contain increasing amounts of this poisonous gas below 180 m., up to 9.58 cc. in a liter. In the Mogilnoje Sea (Murman coast) the hydrogen sulphide extends to within 13 m. of the surface.[15] Hydrogen sulphide also accumu-

lates in summer at the bottom of certain of the Norwegian fiords, salt-water basins of moderate depth (up to 30 m.) connected with the sea by shallow channels, but in these it is removed by the winter overturn of the waters. When storms or occasional advances of currents carry the poisonous gas into the upper levels, the animals there may be killed. In the summer of 1911 the entire *Mytilus* culture at Ganzini near Messina died out because the ooze was stirred up by a current.[26] A number of reports of great mortality in the fishes of the Gulf of Guinea are on record. In the Norwegian "Polls," when the cover of ice prevents the oxygenation of the water, the hydrogen sulphide may reach the uppermost levels and spoil oysters kept there in baskets.[12]

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12. *The Biotic Divisions of the Ocean: the Benthal*

THE VARIETY IN THE ENVIRONMENTAL CONDITIONS IN DIFFERENT PARTS OF the ocean produces corresponding differences in adaptation of the inhabitants. In consequence, the animal communities exposed to a given set of conditions, in spite of being composed of animals from groups separated in zoölogical classification, bear the stamp of a similarity produced by adaptive resemblances in structure and habit. Such common characters appear more plainly the more numerous the adaptations required by the environment. At the hypothetical original site of the development of life, in the coastal areas of warm seas, where all conditions approach the optimum, the possibilities for variety of organization are greatest. Every change in the environment in the direction of the unfavorable brings limitations with it, and these become more sharply defined the more extreme the conditions, as in the littoral area in polar seas, in the deep sea, and in brackish seas. At such places the number of species is diminished and the variety of structural types is reduced.

In the ocean as a whole, two main divisions may be contrasted, the sea bottom and the open sea, the "benthal" and the "pelagial" (Fig. 18). Each falls vertically into two parts, a lighted zone and a lightless one. The lighted zone of the benthal is designated as littoral, the lightless as abyssal. The boundary between the two zones may be set at the border of the continental shelf, which on the average lies at a depth of 200 m. At many places there is no sloping littoral shelf, and the coast drops steeply off to great depths. The lighted zone in such places must still be called the littoral. Two subdivisions of the littoral are to be recognized, according to the steepness of the coast and the

nature of the shore: depositing shore, usually with more or less loose shore material, and eroding shore, more or less steep and rocky. Each of these groups divides into a number of biotopes according to the nature of the shore; for example, pebble beach, sand beach, mud beach, rock coast, coral coast, etc.

In the pelagial, the lighted zone, which lies above the littoral, is designated as the neritic region, and contrasts with the oceanic, which

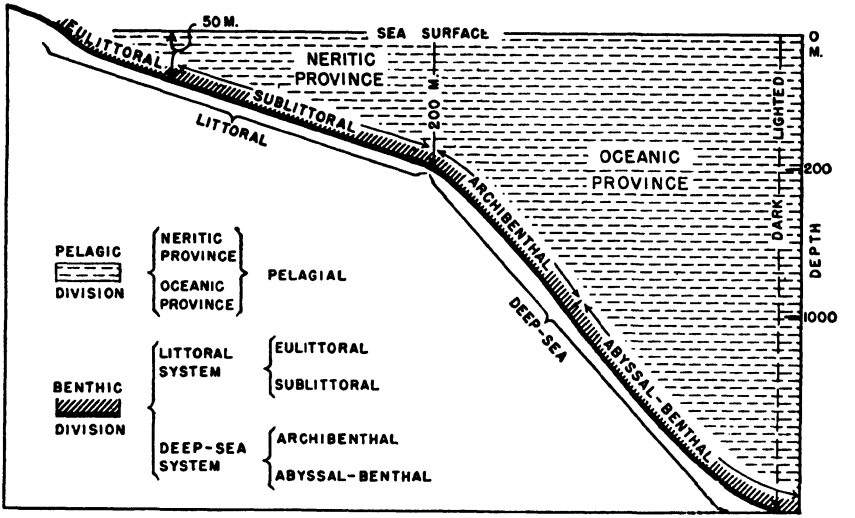


FIG. 18. Primary subdivisions of the marine biocycle. Modified from Sverdrup, Johnson, and Fleming.

lies over the greater depths and includes them. Special biotopes in the pelagial are conditioned by the movements of the water, e.g., regions of upwelling or sinking waters, currents, and quiet water.

The benthal

The primary difference between the life of the benthal and that of the pelagial lies in the necessity for animals in the latter to be independent of any support except that of the water. To be sure, an animal that is capable of remaining suspended in the open water may also move or rest on the bottom. The bottom-dwelling forms, however, are not able to float continuously, even though they may be able to swim about for a longer or shorter time, like the scallops among bivalves or like the flounders among fishes. The borderline between the animals of the pelagial and benthal is thus not very sharp. If one emphasizes the characteristic of free swimming too

much, even fishes like the mackerel could be regarded as only partially pelagic, since it is highly probable that they rest from December to February on the sea bottom after the strain of continued swimming. Even though the same species of animal may at some times be pelagic and at others benthic, the distinction between the bottom fauna and that of the open water is none the less a natural one.

The "benthos," as the animal life of the bottom may be called, is composed of animals wholly or for the most part dependent on the bottom for support. Thus the squid *Sepia* belongs to the benthos, although it can swim for a long time; the mullet *Mullus barbatus* belongs to it because it depends on this section for its food. One might hesitate about the classification of the skillfully swimming labrid fishes, which frequently rest on the bottom to sleep,* or *Labrus* males, which watch over the eggs that are placed on the bottom, although their food is taken from the open water.

Within the benthal the different kinds of shore material produce important differences in the environmental factors influencing its life. The substratum may be loose or solid, with every sort of transition. Loose bottom may be coarse or fine gravel, sand, or mud. In water subject to motion, such a bottom moves with the water above it. Solid shore material is found only on steep slopes and in actively moving water, consequently mostly near the surface, occasionally at depths up to 1000 m. In quieter water, sediments accumulate and maintain themselves even in the face of slow movement of the water.

Other differences in the life of the benthal depend largely on the motion of the water and on lighting. Both light and motion diminish with depth, but the decrease in light in clear water is uniform, while that of motion is subject to various irregularities and special conditions imposed by cosmic and terrestrial influences.

Subdivision of the benthal

The sea bottom is accordingly divided vertically into two main zones: the lighted sea bottom, littoral benthal, or, more briefly, the littoral; and the lightless archibenthal and abyssal benthal. The littoral zone may be divided into two subdivisions, the littoral proper, or eulittoral, extending to the limit of more abundant vegetation at 40 to 60 m., and the sublittoral, from this point to the edge of the continental shelf, which drops off toward the abyssal depths at about the 100-fathom (200-m.) line. We follow *The Oceans* [82] in recogniz-

* *Coris, Julis, Crenilabrus.*

ing an upper archibenthic zone (200 m. to 1000 m.) above the abyssal benthal. Thermal differences appear to offer the best basis for such a division. The littoral is divided into three vertical zones according to motion of the water. The first is that of the tides, bounded above and below by high- and low-tide marks. The second zone is that of wave motion, and below that is the third zone of quiet water. The depth of these zones varies with locality. On the west coast of Europe the difference between tide marks amounts to about 2 m. In the Mediterranean it is only 35 cm. on the average. Where funnel-shaped bays confine the tide wave, the tidal differences are much greater; thus at Chepstow in the Bristol Channel, and in the Strait of Magellan, the difference amounts to 11.6 m.; at Granville on the west coast of Normandy, 12.4 m.; in the Bay of Fundy, Nova Scotia, up to 15.4 m. The upper limit of the quiet water is also variable with local conditions.

A supratidal spray zone may be distinguished above high tide mark; its inhabitants are a mixture of terrestrial and marine animals, and are exposed to a special set of conditions. In many regions, animals from just below the low tide mark differ significantly from those of the deeper, but still wave-affected, waters. Such a region is spoken of as adtidal.[2,3]

The littoral benthos

The littoral bottom fauna is the common mother of gill-breathing marine animals. The faunae of the deep sea as well as the life of the open ocean are nothing more than specializations derived from the littoral bottom faunae by special adaptations. Bottom life at moderate depths in coastal waters requires the fewest adaptations to physical conditions, so that all groups of marine animals are represented, while many groups are wholly wanting in the pelagial and others are represented only by a few aberrant forms, as in echinoderms and mollusks. Pelagic animals may always be traced to an origin from bottom-dwelling forms, and differ from them regularly by their swimming organs and arrangements to secure suspension. This is especially evident in the pelagic medusae, with their fixed ancestral stage; only highly specialized forms of worms occur in the open water, and the pelagic mollusks, heteropods and pteropods, are plainly derived forms. Bottom animals, on the other hand, could not enter the abyssal depths until the pelagic animals and plants had established a food supply for them.

Marine animal life is most richly developed both in number of

species and individuals in the littoral. The dredge nets of the *Challenger* rarely produced more than 10 to 15 individuals of a species from depths over 1800 m.; in about 900 m., hundreds of specimens of single species, holothurians and pycnogonids for example, were taken; and at about 180 m. on the continental coast vast numbers of single species were dredged.[58] The lists of species show almost equally as great differences according to depth as the numbers of specimens. The striking differentiation into numerous species in the littoral fauna is favored by the great local variation in conditions and by the frequent opportunities for isolation. Island regions, with their extreme elaboration of coast line, afford the richest development of the littoral fauna. Thus the littoral selachians are nowhere so richly differentiated as in the island archipelagoes of the Oriental region, with 33 species each in the Indian and Malayan provinces. Marine mollusks are much the most richly developed in the Indo-Pacific region; those of the Philippines are estimated at 6000 species. The West Indies also have a great number of species. Although only 7% of the total ocean surface lies within the 180-m. line, the great majority of benthic animals are found within this narrow coastal strip, and their numbers are much greater than those of the pelagic forms.

A comprehensive characterization of the coastal area, either with reference to its environmental conditions or to the animal life dependent on them, is extremely difficult. Its extension in depth to about 200 m. produces great differences in lighting, temperature, motion of the water, and oxygen supply, and the various combinations of the conditioning factors produce a surprising multiformity in the whole. The only natural division appears to be that based on the nature of the substratum. Movable, more or less loose beach material and solid rocky coast differ in many important respects in their influence on animal life.

Below the low tide mark a rich plant life appears in coastal marine waters. This is strongly influenced by the substratum, like the animal life. Where the bottom is argillaceous or sandy, flowering plants can establish their roots and so take up the salts required by them. Where the bottom is hard such root functions are impossible, and the plant growth is confined to algae and kelp. The distinction of loose bottom from rocky coast is thus equally justified with reference to plants.

Littoral shores with loose substratum, the depositing shores

Coastal areas with sandy or muddy bottom are grown over below the low tide mark, in sheltered places, with "seaweed," i.e., plants of

the family Potamogetonaceae. These are represented by various genera, the eelgrass *Zostera* in the North Atlantic, *Posidonia* and *Cymodocea* in the Mediterranean, and these with the addition of *Halodule* and *Halophila* in the Red Sea. Such plants are wanting where there is too much wave action, which stirs up and redeposits the sand. As has been mentioned for *Zostera* these meadows of seaweed extend to various depths, depending in general on the entrance of sufficient amounts of light.

A very rich animal population develops in these thickets of seaweed. Animals find in them hiding places, support, and abundant oxygen. The seaweed supplies food for many forms, but less frequently from its living tissue than from the organisms borne on its surfaces and the detritus originating from it, which is distributed by the movements of the water through the neighboring area.[32,66,70] The inhabitants of the seaweed masses not only attach themselves to the living and dead leaves and stems, but also dig down among its roots, swim among the plants, or creep upon the bottom.

Common forms in this biotope are the small snails of the genera *Rissoa, Bittium,* and *Columbella,* with other snails, which feed primarily on the algal growth and slime that cover the living and dead leaves of the weed. On this algal growth there is a microfauna of protozoans, nematodes, and copepods. The delicate branches of the hydroid polyps attach themselves to leaves and stems, as do small sea anemones and the curious sessile medusa *Lucernaria.* Here also are to be found the polyps of the sessile generation of the medusae *Aurelia* and *Cyanea,* and both individual and colonial tunicates, such as *Ciona* and *Botryllus.* Crustaceans—amphipods, isopods, schizopods, and macrurans—live in great numbers in the seasweed beds. Various types of worms maintain themselves on and in the bottom among the seaweed roots. A few lamellibranchs join this community, feeding directly on the seaweed débris. With so many herbivores; the predators naturally are attracted in numbers. The starfish *Asterias* feeds on various mollusks, and the crab *Carcinides* takes a variety of prey. The larger carnivorous snails, such as *Murex* and *Tritonium,* appear in the *Posidonia* beds in the Mediterranean. Numerous fishes depend on this fauna for their food. Constant components of this biocoenosis are the pipefishes (such as *Nerophis* and *Syngnathus*), which resemble the eelgrass leaves in both coloration and form, and are difficult to find. In the Mediterranean, in the same situations, the related sea horses appear. *Gobius, Blennius,* and the common stickleback are regular members. Lobsters and certain crabs dig themselves burrows

and live in them, as does the conger eel. The seaweed forms a breeding place for many fishes and for squids, as well as feeding ground and refuge for juvenile fishes.

Where no plants are available as protection and hiding place for animal life in the eulittoral, a surprising number of animals of loose bottom areas secure their positions by boring more or less deeply into the sand, for the most part remaining fixed in position, though some

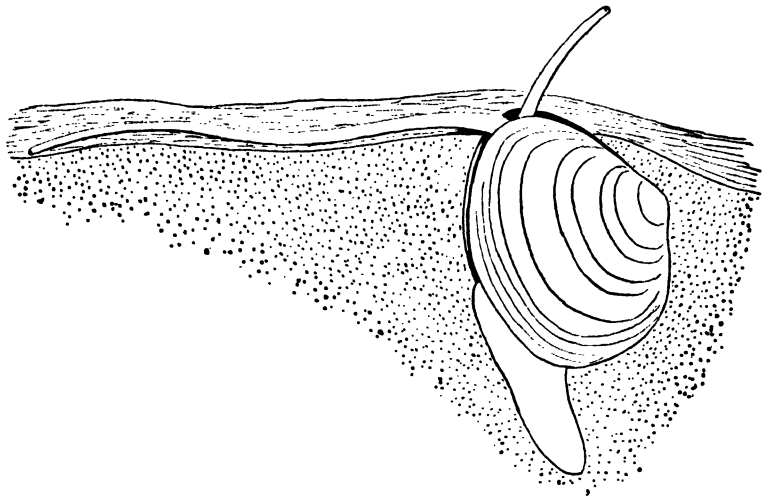


FIG. 19. *Scrobicularia piperata,* in the sand; the afferent siphon to the left, the efferent or anal siphon to the right. After Meyer and Möbius.

wander slowly about. Animals of very different organization have become adapted to this mode of life and have acquired certain common characteristics. The great majority of these sand-dwellers feed on the decomposing remains of the seaweeds and of other animals. This material is ingested together with the admixed sand by many forms; just as earthworms take in their organic food with the earth in which they live, so do the lugworm *Arenicola,* the hemichordate *Balanoglossus,* the holothurian *Synapta,* and various sea urchins. Others secure food with less admixture of sand by creating a current of water that brings them the finely divided particles of débris floating in the sea water. Amphioxus and many mollusks feed in this manner. Other mollusks, such as *Scrobicularia* (Fig. 19), draw in the fine deposit of food material on the surface of the sand by means of their long intake siphon, with which they search the surface about them.

Breathing is a matter of special importance to these sand-dwelling

creatures. The lamellibranchs and amphioxus receive their oxygen with the water current that carries in their food particles. The sea urchin *Echinocardium* (Fig. 20), by movement of its spines, pro-

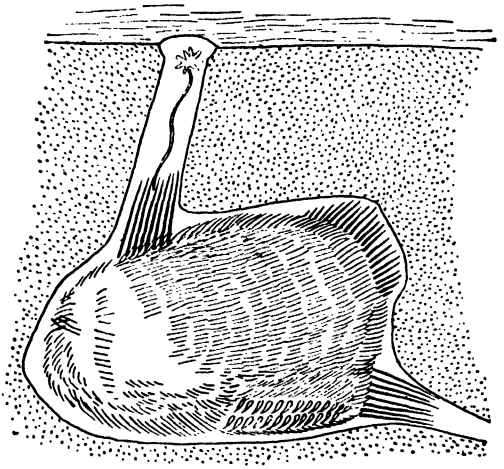


FIG. 20. The heart urchin *Echinocardium cordatum* in the sand; the breathing and feeding chimney is reinforced by a secretion; the tubular arrangement of the spines and one of the prehensile tube feet are shown. After v. Uexküll.

duces a current of water that reaches it through a chimney-like tube, kept open by means of specially developed tube feet. The starfish *Astropecten* bears a series of small spines along its arms, whose vibrat-

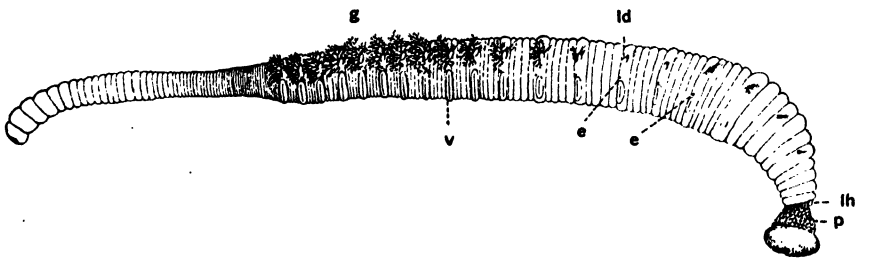


FIG. 21. *Arenicola*, from the right: *g*, gills; *ld*, dorsal setae; *v*, ventral setae; *e*, excretory openings; *lh*, head folds; *p*, papillae on the protruded pharynx. After Ashworth.

ing motion forces the water along its surface. The lugworm (Fig. 21) has a series of much branched gills on both sides of the middle portion of its body, through whose extensive surface the haemoglobin of the blood efficiently takes up the scanty oxygen supply of its sur-

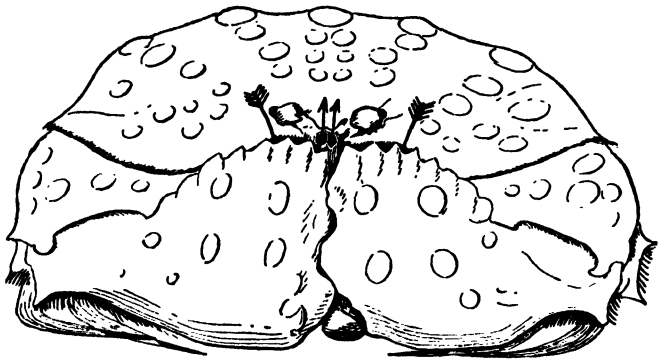


FIG. 22. Burrowing crab *Calappa granulata* from the Mediterranean, front view. The arrows indicate the afferent and efferent openings to the gill chambers; the eyes may be seen on each side of the arrow points, and the claws just below the arrows. After Garstang.

roundings. Singular breathing arrangements are developed in the box crabs, which burrow in the sand. In them the water intake is situated in front, where the crab projects out of the sand, and the water is conducted to the gill cavity by variously arranged channels. This occurs in *Calappa* (Fig. 22), *Matula,* and *Ilia.*[21] In most crabs the water enters at the posterior border of the cephalothorax and is discharged forward. In the anomurous decapod *Albunea* (Fig. 23) the two large antennae together form a long tube for the intake of the water for breathing, so that the crab can bury itself in the sand without being cut off from its oxygen supply.

The number of forms concealed in the sand is astonishingly great. Many sea anemones build tubes in the sand in which they can withdraw completely. Turbellarian and nemertine worms conceal themselves in the sand, from which they may be lured to the surface by means of bait, such as a dead fish. Among the annelids, *Arenicola* is important; its burrows, often closely crowded, are recognizable by the spiral heaps of excrement pushed out of them. In the same habitat occur various other annelids, both larger and smaller, among which may be named the primitive *Polygordius* and

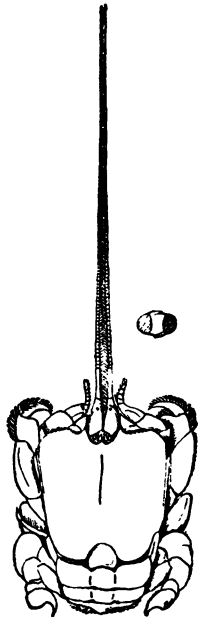


FIG. 23. *Albunea symnista* from Madras, from the dorsal side. An enlarged cross section of the breathing tube formed by the antennae is shown to the right. After Garstang.

Protodrilus, without bristles, and the numerous nearly sessile forms, the terebellids, clymenids, chloraemids, ophelids, maldanids, etc. The latter agree in having relatively poorly developed bristle bundles, in connection with their sand-boring habits, and were formerly united into the group Sedentaria. A curious companion of the worms is *Balanoglossus* (Fig. 24), a worm-shaped relative of the chordates which lives

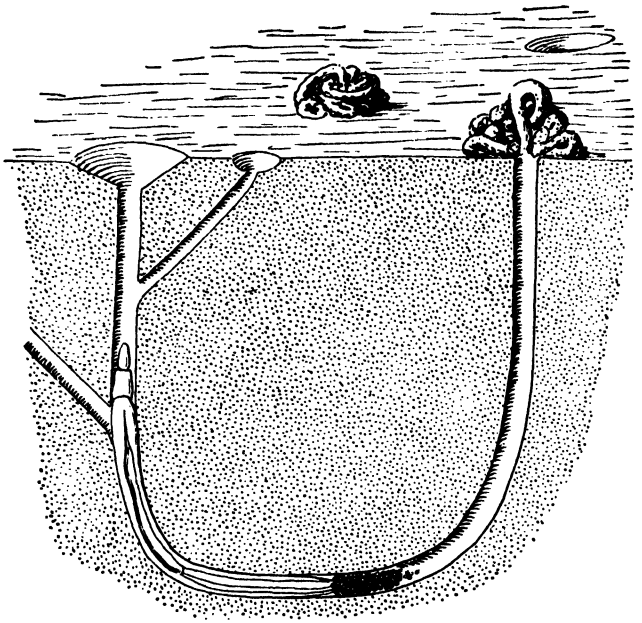


FIG. 24. *Balanoglossus clavigerus* in its tube in the sand (30–60 cm. in depth); the height of the heaps of excrement is 3–6 cm. After Stiasny.

in a U-shaped tube open at both ends and puts out piles of excrement like those of *Arenicola.*

The mollusks of this habitat have much in common. They are uniformly thin-shelled, flat, smooth-surfaced, have a well-developed foot without a byssus gland, and have siphons formed by the union of the posterior edges of the mantle into more or less elongate tubes, occasionally united, which establish the connection with the surface. The ventral siphon is the intake, bringing in the food and oxygen in the water, while the dorsal cares for the outgoing current with the excrement (Figs. 19 and 25). These siphons are convergent adaptations that have developed in phyletically distinct groups of mollusks,

in adaptation to life in sand and mud. Siphons appear to be unknown in mollusks before the Cretaceous.

The lamellibranch genera, *Venus* and *Tellina* * among others, are sand-inhabiting forms. The razor clam *Solen* (Fig. 25), is notable for

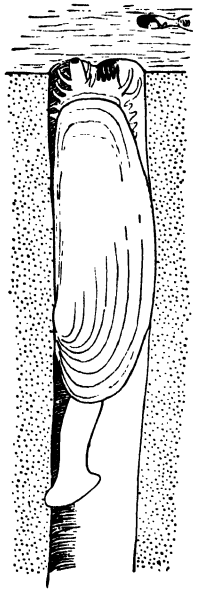


FIG. 25

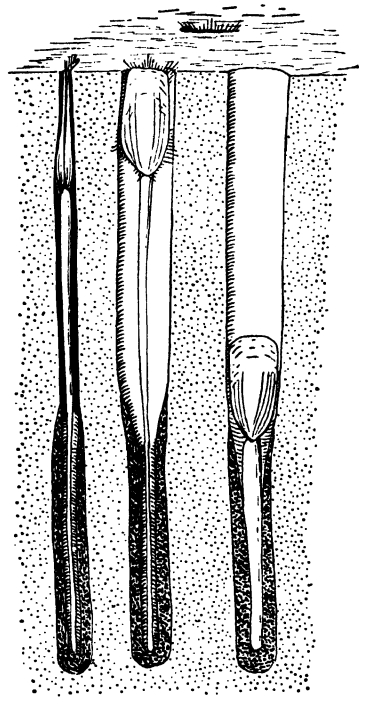


FIG. 26.

FIG. 25. Razor clam *Cultellus pellucidus* (=*Solen pellucidus*) of European seas, in the sand. Enlarged one and one-half times. After Meyer and Möbius.

FIG. 26. *Lingula anatina* in sand, seen from the edge, from the side, and withdrawn into its burrow. The opening of a burrow to the rear. After François.

its habit of digging tubes as much as 50 cm. deep, in which the animal retires from its surface position at any disturbance of the water. The pismo clam of California burrows deeply into sand otherwise devoid of large forms. *Cardium*, which bores shallowly in the sand and which can jump by means of its angular foot, has, in contrast, a shell strengthened by its rounded form and strong ribbing.

A few echinoderms are sand dwellers. The irregular forms *Brissop-*

* Also *Donax*, *Cytherea*, *Mactra*, *Tapes*, *Psammobia*, and *Scrobicularia*.

sis and *Echinocardium* (Fig. 20) regularly live in sand, which they ingest with their food supply as does the sand dollar *Echinarachnius*. The sea cucumbers of the genus *Synapta* are also sand diggers and swallowers. Many brittle stars of the genus *Amphiura* live buried in the sand. The brachiopods of the ancient genus *Lingula* (Fig. 26) are sand dwellers in the eulittoral zone of the Indian and West Pacific oceans. They live in holes into which they can withdraw by means of their contractile stalks.

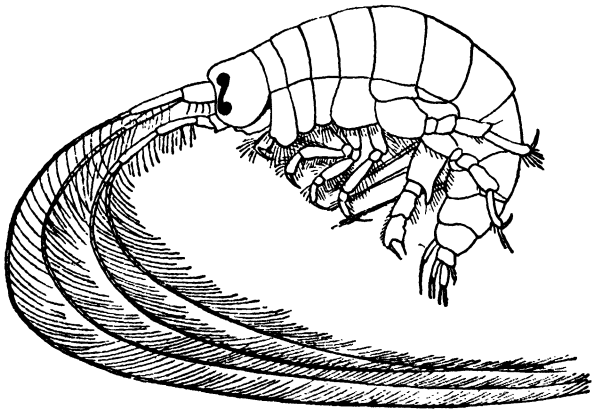


FIG. 27. *Haploops tubicola*. Enlarged five times. After Della Valle.

A great number of crabs and small crustaceans dig burrows in the sand—for example, *Haploops tubicola* (Fig. 27), and, among decapods, the thalassinids, *Gebia* in the North Sea, *Callianassa* in the Mediterranean, and the shrimp *Crangon* in the Baltic; the last three are represented along the New England coast. By excavation of a space 1 m. square and 30 cm. deep at the mouth of the Elbe, between tide marks, Dahl secured more than 800 individuals of an amphipod (*Bathyporeia*). Where they occur, the horseshoe crabs bury themselves in the sand during the day, coming out at night to feed. Amphioxus must be included in this list of sand dwellers, lying in the sand with only the oral opening exposed (Fig. 28).

As everywhere, the carnivores pursue their prey in this habitat also. A number of predators search actively through the sand for their prey. The starfish *Astropecten* eats small worms, echinoderms, and mollusks. The snail *Natica* (Fig. 29) moves about 2 to 5 cm. below the surface of the sand and attacks mollusks, boring through their shells and sucking out their contents by means of its proboscis.

Some fishes also hide themselves by burying wholly or partly in the sand, and thus lie in wait for their prey. All these have a flattened, light-colored ventral side, eyes usually directed upward, and the mouth also often turned up. Whereas in free-swimming carnivorous

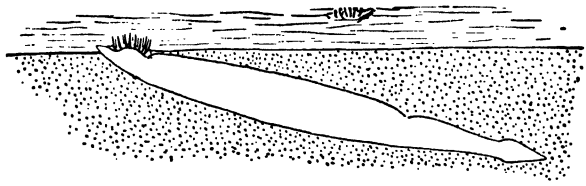


FIG. 28. Amphioxus *Branchiostoma lanceolatum* burrowed into the sand. Slightly enlarged.

fishes the eyes are only slightly movable, with their fields of vision overlapping only a little (10–30°), the eyes of the flatfishes and of other bottom dwellers are very mobile and their fields of view overlap to the extent of 35–80°, according to the species. This binocular vision probably makes possible an estimation of distance, which is of the greatest importance in securing their prey.[73] The air bladder is absent or reduced in the fishes of this habitat. *Trachinus* and *Uranoscopus* bury themselves deeply. The great majority of the flatfishes lie upon the bottom, adapting their coloration to that of their background by means of their power of color change. They stir up the sand with a few undulating motions, and when this settles it hides the outlines of their bodies. Among rays, the tropical Trygonidae bury themselves in sand; otherwise sharks and rays for the most part lie on the surface, protected by their spiny coat and rendered indistinct by their coloration.

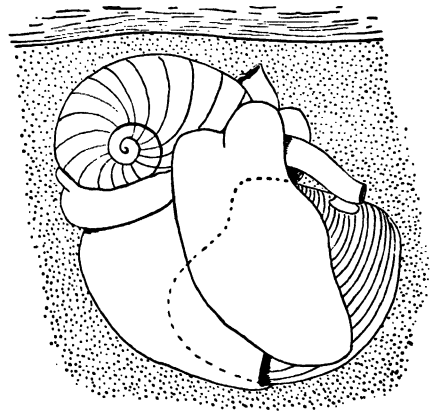


FIG. 29. *Natica josephina* attacking a bivalve in sand, holding its prey with the divisions of its foot while boring through the shell. After Schiemenz.

Among the squids, *Sepia* tends to keep itself slightly embedded in sand or mud, adjusting its coloration to that of the bottom material.

The number of forms living on the surface of the sand is small in contrast to the hidden inhabitants of sand bottom. Numerous brittle

stars and some starfishes have this habit, and in them the tube feet are rounded instead of ending in a sucking disk. A number of carnivorous snails, such as *Buccinum* and *Nassa,* creep over the surface of the sand. Such snails, on account of the looseness of the bottom, require a broad foot, a contrast with snails in rocky habitats, especially in quiet water, where only a small foot is required (Fig. 30). A number

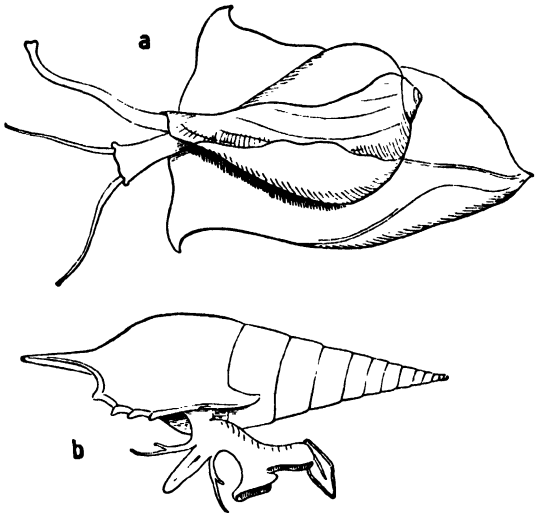


FIG. 30. *Pyrula* sp. (*a*), with broad flattened foot, living on loose bottom, contrasted with *Rostellaria curta,* (*b*), with narrow foot, from solid bottom at 45-m. depth. After Hornell.

of crabs, such as *Portunus, Hyas,* and *Inachus,* live on the sand surface, and this is the typical habitat of hermit crabs, which often occur in great numbers.

Fishes of varied origin are provided with a rostrum with which they can plow the sand in search of prey. *Belone,*[11] with its elongate lower jaw extending beyond the upper, roots out the *Ammodytes* and annelids, and the halfbeaks (Hemiramphidae) [63] and Pegasidae feed in the same way. The sawfishes *Pristis* and *Pristiophorus,* with transverse teeth on their "saws," are said to dig up the bottom to secure their food.

The smaller fishes of this littoral formation lead a precarious life. They are attacked from the air by terns and gulls and from the deeper water by larger fishes. *Fundulus,* one of the most common genera to be found along the Atlantic coast, commonly lives in shallow water; there, as the tide comes in, e.g., along the coast of the Carolinas, it follows its advance in over the sand, rooting in the newly covered

sandy bottom for food. It continues with the advancing tide and often enters pools that retain the water for some time without holding it until the next tide. In such places, when the tide begins to ebb, the minnows apparently test their line of retreat from time to time and return to feed along the bottom with their fellows. In a long series of observations, Mast failed to find any *Fundulus* stranded in these sandy tide pools. When he dammed the outlet to such a pool, the fishes collected in aggregations near the old outlet and, individually or in groups, passed out of the pool over the damp sand to the retreating sea water. He found that they could climb a ridge 10 cm. high and travel over land for 3 m.[51]

The size of the particles composing the bottom has an important effect on its inhabitants. Gravel and pebble beach is found only in strongly moving water, close to the water's edge; this biotope is quite azoic, since the movement of the stones on each other destroys all life. Coarse sand is poorer in animal life than fine. Muddy bottom is rich in life, but mud mixed with sand is still more so.

This region of the sandy depositing shore is a climax formation comparable with the beech and maple community on land. The ecological processes here are in approximate equilibrium, and neither organisms nor physical forces are changing the environment with rapidity. Of course, there may be deposits of sand that tend gradually to raise the shore line and so cause the whole complex to move further out to sea; but the community conditions are relatively stable in their instability, and so is the animal life to be found there.[77]

Muddy deposits

The large amounts of organic materials constantly brought into the sea by the rivers, and in the main also the detritus from the rich littoral vegetation, are only slightly heavier than sea water and sink very slowly to the bottom, being stirred up by any movement, so that they come to rest only where waves and currents are absent. The deposition of mud occurs at various depths according to local conditions. It accumulates in shallow waters on coasts protected by strings of islands, in quiet bays, and at river mouths, where the water stagnates twice daily on account of the opposing tidal current. Mud flats in the Bay of Naples occur at 20 to 40 m., and at much less depth in the Mergellina Harbor at Naples. In the open ocean, these deposits do not come to rest until much greater depths are reached. The "mud line," which marks the approximate limit of deposition of muds from the land, lies on the average about 200 m. below the surface.

The mud affords a rich food supply. Vast numbers of minute forms, protozoans, nematodes and other worms, and swarms of small crustaceans, ostracods, amphipods, and isopods, develop at the expense of the organic food materials and create a new source of food in their turn. Mollusks bury themselves in the mud, and nudibranchs and crabs wander over its surface.*

The mud dwellers are on the whole more delicate than the sand inhabitants: more fragile, thinner shelled, more weakly muscled. A yellowish gray or white coloration is frequent among them. Degeneration and loss of the eyes is common. These differences are excellently illustrated by comparison of two sipunculid worms, *Sipunculus nudus* from sand and *Phascolosoma vulgare* from the mud. In the mud dweller, the skin is softer, the musculature weaker, motility less, nervous system less well developed, and the proboscis longer and more slender.[29]

The mud dwellers have a mode of life in the main like that of the sand-bottom animals, but on account of the want of oxygen in their habitat there are fewer of them. The process of decay uses up the oxygen supply, mainly by the oxidation of the hydrogen sulphide produced. Where the supply of fresh water is too small, the population decreases with the decrease in oxygen and the increase in hydrogen sulphide; and deep black, homogeneous mud, without admixture of sand, is for the most part without microscopic life. Certain lamellibranchs and the tube worm *Spio fuliginosus* are the most persistent survivors.

Mixture of mud with sand is especially favorable and produces an increase in the animal population. The mud line near the edge of the continental shelf is called by Murray the great feeding ground of the ocean, to which cod and herring, mackerel and tunny, and even the whales, descend.

Facies in depositing shore communities

Although a general characterization of the fauna of the sea bottom with loose material may be made, its animal life is not uniform, but

* According to J. Wilhelmi,[87] the index forms of the mud facies in the Bay of Naples are *Plagiostomum girardi* (turbellarian); *Audouinia, Arenicola, Capitella capitata, Spio fuliginosus,* and *Spirographis* (annelids); *Asterias tenuispina* (starfish); *Bornia corbuloides, Capsa fragilis, Tapes aureus* (lamellibranchs); *Bulla striata* and *Doris verrucosa* (opisthobranchs); *Nebalia galatea* and *Brachynotus sexdentatus* (crustaceans); *Botryllus aurolineatus* and *Ciona* (tunicates); and among fishes *Mullus barbatus, Zeus faber,* and *Lophius piscatorius.*

changes from locality to locality in a notable way, even on extensive areas where the nature of the substratum and plant growth is essentially uniform. Within this biotope special facies are distinguishable,

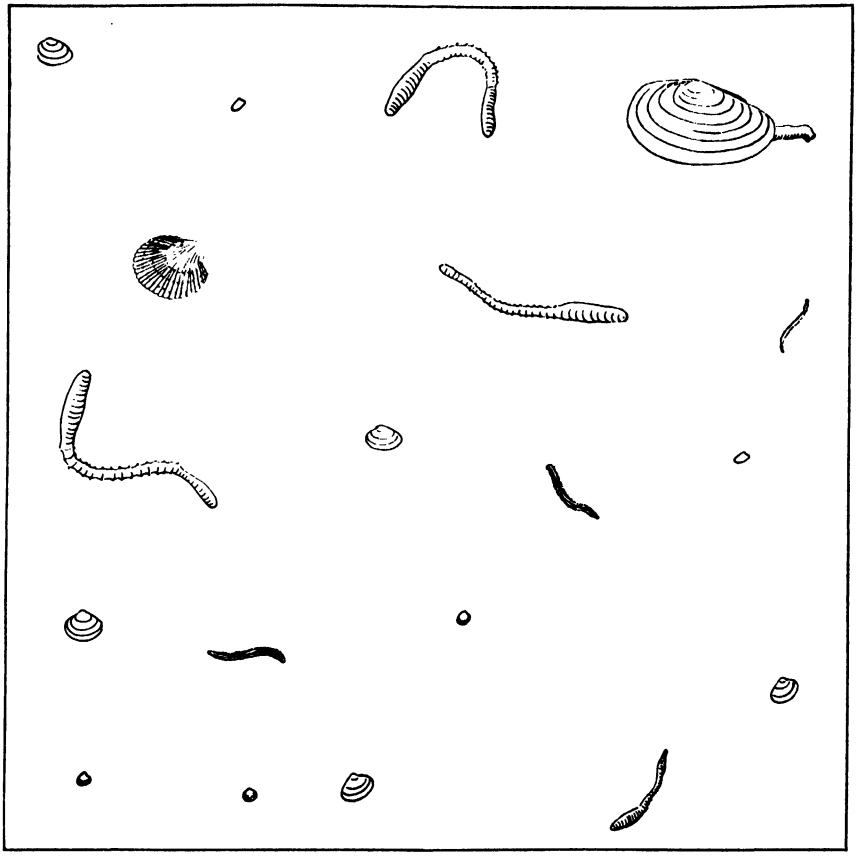


FIG. 31. Arrangement of animals on 0.25 sq.m. of sea bottom. I, *Macoma* community, at 0.3 m. depth, exposed at low tide, in the Ringkoebing Fjord. The inhabitants of this area include, among bivalve mollusks, 1 adult and 2 young *Mya arenaria;* 5 *Macoma baltica;* and 1 adult and 3 young *Cardium edule;* and among annelids 4 *Arenicola,* 1 *Aricia armiger,* 2 *Nephthys* sp. After Petersen.

which are repeated at other points when the same conditions are exactly repeated. A certain regularity in this diversified life is recognizable, especially a connection between these facies and the depth of the water. Other governing factors, as yet unknown, must also exist. Stuxberg [81] distinguished certain sections by the predominance of a single or of few species. C. G. J. Petersen [65] has described the com-

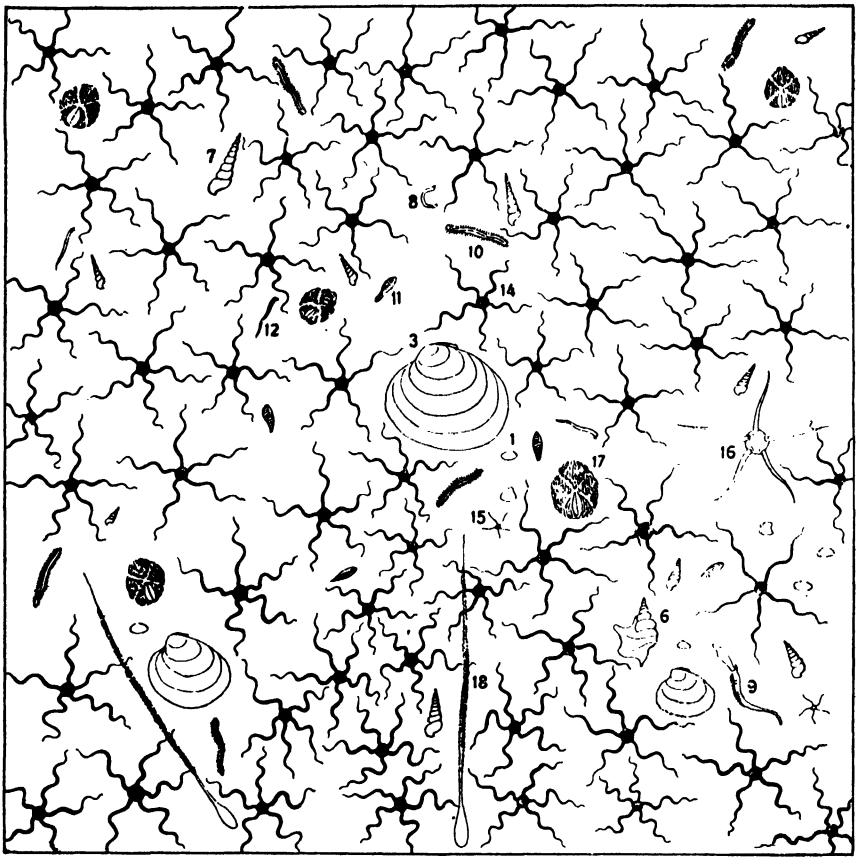


FIG. 32. Arrangement of animals on 0.25 sq.m. of sea bottom. II, *Echinocardium-Filiformis* community, at a depth of 20–22 m., in the Kattegat. The individuals, numbered for identification, and with the number of individuals, are listed below. Mollusks: (1) *Abra nitida*, 4; (2) *Corbula gibba*, 1; (3) *Cyprina islandica*, 3; (4) *Axinus flexuosus*, 1; (5) *Nucula tenuis*, 1; (6) *Aporrhais pes pelecani*, 1; (7) *Turitella terebra*, 10; (8) *Chaetoderma nitidulum*, 1; worms: (9) *Glycera* sp., 1; (10) *Nephthys* sp., 6; (11) *Brada* sp., 5; (12) *Terebellides stroemi*, 3; (13) a fragment of nemertine worm; ophiurids: (14) *Amphiura filiformis*, 60; (15) *Ophioglypha albida*, juv., 2; (16) *O. texturata*, 1; sea urchins: (17) *Echinocardium cordatum*, 5; pennatulids: (18) *Virgularia mirabilis*, 2. After Petersen.

position of eight types of the bottom biocoenosis in the ocean surrounding Denmark; Figs. 31–34 give a good representation of four

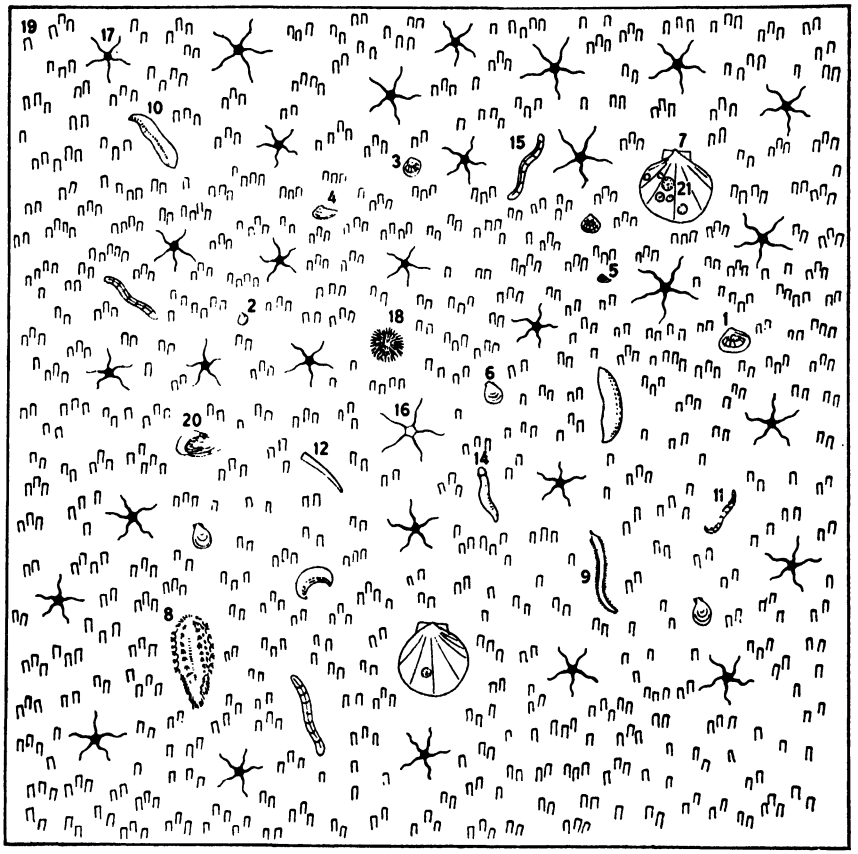


FIG. 33. Arrangement of animals on 0.25 sq.m. of sea bottom. III, *Haploops* community at a depth of 27 m. in the Kattegat. The inhabitants are: mollusks: (1) *Venus ovata*, 1; (2) *Cardium fasciatum*, 2; (3) *Axinus flexuosus*, 2; (4) *Leda pernula*, 1; (5) *L. minuta*, 1; (6) *Lima loscombi*, 3; (7) *Pecten septemradiatus*, 2; worms: (8) *Aphrodite aculeata*, 1; (9) *Glycera* sp., 1; (10) *Eumenia crassa*, 3; (11) fragment of a maldanid; (12) *Pectinoria auricoma*, 1; (13) a terebellid; (14) *Balanoglossus kupfferi*, 1; (15) nemertines, 3; ophiurids: (16) *Ophioglypha albida*, 1; (17) *O. robusta*, 30; sea urchins: (18) *Strongylocentrotus drobachiensis*, 1; crustaceans: (19) *Haploops tubicola* (see Fig. 27), 875; (20) *Morea loveni*, 1; (21) *Verruca stroemii* (on Pecten), 7. After Petersen.

of them. The index forms of the different facies belong to different groups of animals; lamellibranchs (Fig. 31), sea urchins and starfish (Figs. 32 and 34), crustaceans (Fig. 33), or annelids may fill this rôle,

and they are not necessarily the most abundant animals of the community. Some of these communities are rich in variety, up to 20 species, while others are poor (Fig. 31, with 6 species). In some, one species

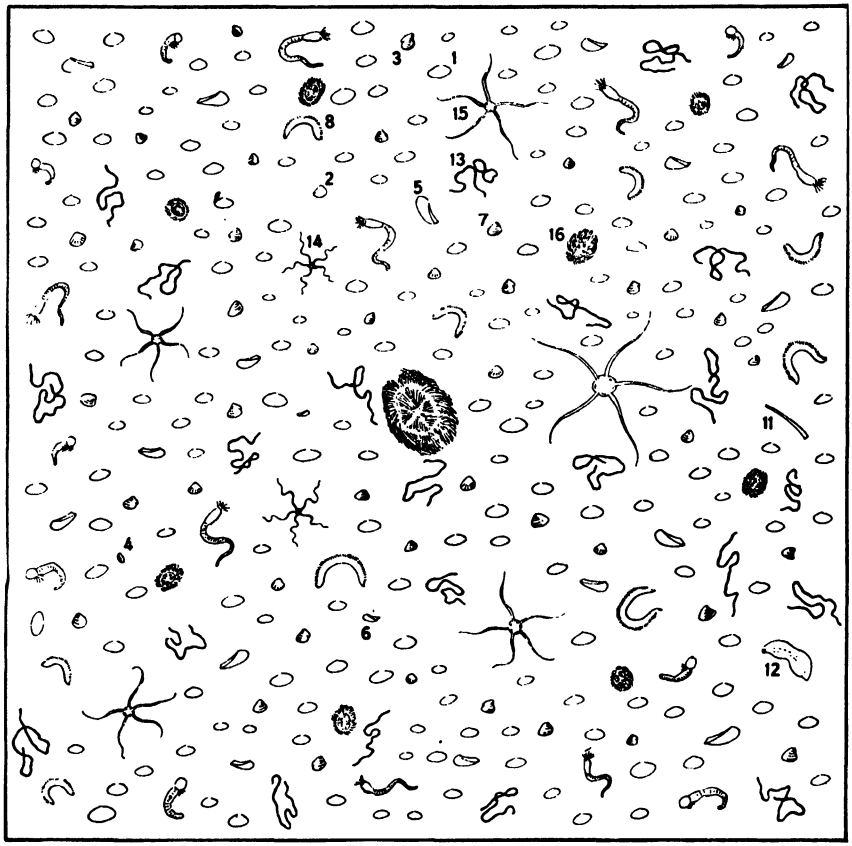


FIG. 34. Arrangement of animals on 0.25 sq.m. of sea bottom. IV, *Brissopsis-Sarsii* community, at a depth of 186 m., in the Skagerrak. The inhabitants are: mollusks: (1) *Abra nitida,* 179; (2) *Cardium minimum,* 11; (3) *Axinus flexuosus,* 20; (4) *Portlandia lucida,* 1; (5) *Leda pernula,* 17; (6) *L. minuta,* 1; (7) *Nucula tenuis,* 14; annelids: (8) *Aricia norvegica,* 9; (9) *Artacama proboscidea,* 8; (10) *Melinna cristata,* 8; (11) *Pectinaria auricoma,* 1; (12) *Eumenia crassa,* 1; (13) *Myriochele heeri,* countless; ophiurids: (14) *Amphiura elegans,* 2; (15) *Ophioglypha sarsii,* 5; sea urchins: (16) *Brissopsis lyrifera,* 9. After Petersen.

predominates, so that all others are overshadowed, for example, *Amphiura filiformis* (Fig. 32) and finally *Haploops,* with 875 specimens to 64 of the other species combined (Fig. 33). In others, a number of species are approximately equal in abundance. The facies

of the sea bottom bear some relation to the distribution of the fishes, certain fishes being found principally in or over similar areas, although never as index forms and always free to move over other types of bottom. These facies established by Petersen have a wider application than to the Danish waters, as shown by the application of Petersen's methods to the study of the animal communities of the Puget Sound benthos by Shelford [78] and his students, but further investigations are required to determine their validity.

The coastal conditions are not confined to the immediate vicinity of the coast but extend into shallow water far from shore, frequently to the edge of the continental shelf. The bottom of the North Sea [59] is predominantly loose, composed of sand, sandy ooze, and clay. Its life is characterized largely by the abundance of echinoderms; starfishes (*Asterias rubens, Astropecten irregularis*) occur at all depths, as do the irregular sea urchins *Echinocardium* and *Spatangus;* the ophiuran *Ophiura ciliaris* may literally cover the surface. Certain snails (*Neptunea, Sipho,* and *Buccinum*) are abundant and widely distributed. The higher Crustacea are few in kinds and in individuals, though the smaller amphipods and Cumacea are abundant, affording rich food for fishes, especially juvenile fishes, whose stomachs are often crammed with them. Where shells of mollusks are heaped up on the loose bottom, sessile animals take up residence, especially hydroid polyps, with their associates, small caprellids and nudibranchs, adding to the variety of animal life in this habitat. The fish fauna is rich in this region of shallow water, in general much more so than over deep water. Most so-called coastal fishes are caught above the continental shelf. One can gain an insight into the wealth of the fisheries of a country by merely examining a bathymetric chart.* [39]

Fauna of the tidal zone

From low tide mark upward the littoral fauna becomes more and more impoverished (Fig. 31), on account of less favorable conditions of life. The tides uncover a belt of varying width twice daily. Animals of this area must be able to withstand the temporary withdrawal of water; rains subject them to fresh water at times; they are exposed to the heat of the sun in the summer and to extremes of cold in winter. Food supply is also much less abundant than in and

* A number of European food fishes attain their greatest abundance in the North Sea, as for example *Gadus aeglefinus* and *G. merlangus, Pleuronectes platessa* and *P. microcephalus,* and *Rhombus maximus.*[59]

below the zone of plant growth. In consequence, only euryhaline and eurythermal animals are able to live within this belt of emergence.

A number of animals maintain themselves in this situation, the more easily as the stress of competition is reduced by the existence of physical and chemical restrictions. The biota varies with climate and with local ecological factors, particularly with the substratum. In biotopes in which burrowing is possible many burrowers living below low tide also dig themselves in between tide marks. This is true of burrowing sea anemones, of various kinds of worms, including diverse annelids, and of such mollusks as *Venus, Mya,* and the quite resistant *Cardium edule.* Zonation occurs correlated with the duration of exposure to the atmosphere in the short, intermediate, or long tidal cycles occurring during the year.[16] From the upper tide levels down, similar *Littorina,* balanoid, and laminarian zones have been described for the Pacific coast of North America [68] and for South Africa,[80] and can be recognized elsewhere sometimes with but slight modification. Additional zones may exist extending over long coastlines. Thus seven zones of algae grow one above the other along the shores of northern California and Oregon between the lowest of tidal low water and the highest high tide mark. The spray zone extends still higher.[16]

Basing his analysis upon his own extended study of the South African intertidal zonation in comparison with "the useful and interesting volume by Ricketts and Calvin entitled *Between Pacific Tides,*" Stephenson makes a summarizing comparison:

> The parallels between the two coasts as far as animals occupying similar "ecological niches" are concerned are amazingly close. Many of the photographs illustrating the Pacific coast fauna could be labelled with the names of South African species occupying similar habitats, without anyone but a specialist being the wiser. It is not that the same species occur on the two coasts—far from it—but that forms belonging to different species and often to different genera occupy similar habitats and have a similar appearance.

Vast numbers of small green turbellarian worms *Convoluta roscoffensis* are exposed at low tide along the coasts of Normandy, England, and the Channel Islands, and form dark green bands, often for many kilometers. By count, the numbers of these worms per square meter may be as high as 3,350,000. Light is required for the mutualistic algae-like flagellates contained in them.[40] The annelids *Arenicola, Nereis, Terebella,* and *Echiurus,* and the hemichordate *Balanoglossus* inhabit the intertidal beach, as do many sorts of crustaceans. Shallow tide pools retain shrimps and various other crustaceans, especially hermit crabs.

A number of species of the area exposed by the tides are so adapted to its special conditions that they are typically found in it; they are stenobathic and confined to shallow water. This applies to the above-mentioned *Convoluta;* the worm *Arenicola;* and the snails *Melampus* and the abundant *Littorina litorea.*

Where a sand beach is freely exposed to surf, so that the sand is continually stirred up and redeposited and the detritus particles washed out, the conditions for plant and animal life are unfavorable. Animal life is then usually wanting in the upper (terraqueous) levels and only appears in considerable amount when the wave motion is reduced, at considerable depths. The California pismo clam lives in this habitat.

Life of the spray zone

Marine life, finally, extends into a zone above high tide mark, where only spray and waves reach it, i.e., the supratidal zone. The marine animals that live in this situation have adopted an air-breathing existence and must be protected from drying out by a strong shell. Small quick-jumping amphipods (*Orchestia*) live beneath seaweed thrown up on the beach. Some of the related forms even extend further inland, like *Talitrus locusta.* Small snails are attached to the seaweed leaves. In the tropics the supratidal stage is characterized above all by the crabs *Grapsus* and *Ocypoda,* which are air-breathers, and the widely distributed hermit crab *Coenobita.*

Estuaries

Estuaries form a special biotope in the littoral zone.[39] Change and mixing of fresh and salt water and periodic stirring up by the tides produce special conditions. A river mouth at low tide has a median channel; the shores on each side are steep as high as ordinary tides reach, and more sloping above mean high tide, in the region of exceptional tides. On these slopes is deposited a sticky and often very dense mud in which a special fauna exists, composed of a mixture of fresh-water and marine animals. The list of marine animals is extremely small; it includes, in the northeastern Atlantic, the soft-shelled clam *Mya,* the annelid *Nereis cultrifera,* a few Gammaridae, and the ever-present beach crab *Carcinides maenas.* (See also Chapter 17.) Where seaweed is present, the fauna is enriched by the sponge *Suberites domuncula,* nudibranchs, and the spider and hermit crabs with sea anemones attached to their shells.

Such muddy bays, exposed to the tidal currents, are employed for the artificial culture of oysters in England, France, and on the Atlantic coast of North America. Oysters, otherwise inhabitants of solid bottom, adapt themselves well to mud, brackish water, and to shallow water. With careful protection from their enemies, cultivated oysters develop a form characterized by quality and size of soft parts, with a thin shell. These oyster beds require constant replenishment by brood oysters (oyster spat) from salt water; the fertility of the oysters in brackish-water beds is insufficient to maintain them. These beds, where a wealth of detritus is stirred up by the tides, with its attendant microfauna, are consequently essentially fattening establishments for the oysters.

Mangrove associations

A special facies of the estuarine habitat is represented in the tropics by the mangrove beach.[6,13a,30,42] The mangrove, with its stilt-like roots and a variety of plants with similar growth habit, especially *Sonneratia* (Myrtaceae), *Avicennia* (Verbenaceae), and *Aegiceras* (Myrsinaceae), is world-wide on quiet tropical coasts. The tangle of roots holds débris brought down by rains and floated in by the tide, until it decays. In and upon the mud is found a remarkable assemblage of marine, fresh-water, and terrestrial animals. The small actinian *Thelaceros rhizophorae* is found at the water's edge, in little pools near the mangrove roots. Between and upon the roots creep uncounted millions of crabs, usually adapted in coloration to that of the mangrove bark. The holes of the fiddler crab *Uca* are everywhere, descending to a depth of 75 cm. Hermit crabs live on bottom and roots. At ebb tide, ants abound on the mud, scavenging on the remains of marine life; their nests in the mangrove above mark the extreme height of the tide. Euryhaline lamellibranchs bury themselves in the mud, Psammobiidae and Solenidae from the sea and cyrenids from the fresh-water swamps. Various types of tree oysters attach themselves to the mangrove roots, in Java, for example, *Ostrea mytiloides.* The snails *Cerithium, Potamides,* and *Littorina* form a series successively more independent of the sea water, entering brackish water or becoming terrestrial. The fish called the mudskipper, *Periophthalmus,* is widespread on mangrove coasts, living more out of the water than in it. Its eyes are protected against drying (in the absence of eyelids) by a great development of the conjunctival sack.[5] They are placed on the dorsal side of the head, as in many amphibious animals (Fig. 35), so that vision above the water is possible when all the rest of the body

is submerged. Its food includes small insects as well as crabs. Supported on its tail and paired fins, it hops about on the mud and may climb the inclined branches of mangrove. A great number of birds, certain reptiles, and a few mammals (monkeys) frequent the mangrove flats for food, but have their residence in the adjoining forest.

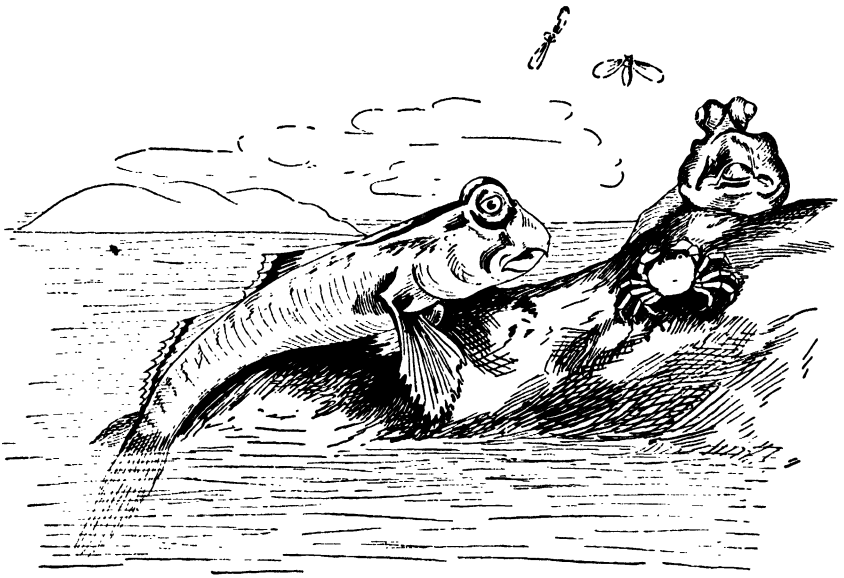


FIG. 35. *Periophthalmus koelreuteri*, the mudskipper, two-thirds natural size. After Hickson.

The mangrove strand has a very similar development of animal life in west Africa, the Indian and Pacific oceans, and in South America.

Littoral with solid substratum: eroding shores

The fauna of solid bottom, especially of rock, stands in sharp contrast with that of the loose substratum. This is especially obvious where single shells of mollusks, stones, rock outcrops, or harbor works and breakwaters are juxtaposed to the loose bottom. A quite different community of animals appears immediately on such a foothold. The submarine rocky bosses that project from the ooze of the quiet water in the Bay of Naples support a wholly different population from that of their surroundings. There are a few forms common to the two habitats, especially predaceous starfishes and crabs, and a few adaptable animals, like *Mytilus*. Altogether, however, the difference is radical and obvious.

Sessile forms are especially characteristic of the solid bottom. The majority of sponges and of sessile coelenterates are confined to rocks, scarcely requiring other protection against predators than their spicules or stinging cells and their powers of reproduction and regeneration. Hydroid polyps disappear as one leaves the coast and as the water deepens,[58] since in the quiet water of the deeps all available solid support is covered with ooze. Many tubicolous worms, especially those with calcareous tubes, require a solid basis. Bryozoa are predominantly rock dwellers; sand is not favorable for them, but their small size enables them to gain a foothold on the leaves of plants, shells of mollusks, or the carapaces of crustaceans. The great majority of simple and compound tunicates inhabit rock bottom.

Many of these sessile animals have the power of reproducing by budding, forming colonies of numerous individuals. Broad areas of a rock may thus be covered by a single species of animal. Hydroid polyps form miniature forests on stones and rocks; the beautiful orange coral *Astroides* covers the rocks just below low tide mark in the Mediterranean. The green and red sea anemones *Actinia equina* make a gaudy carpet on the rocks of Helgoland. Tunicates often occur in similarly thick masses. Tubicolous worms may cover wide areas; *Serpula* tubes may form a tangled web among which the gill-funnels appear like colored flowers; close to the surface in the North Atlantic and Mediterranean the leathery tubes of *Sabellaria* cover low rocks so thickly that the openings of the tubes are juxtaposed, and the surface appears like that of a honeycomb.

Of the mollusks, snails and chitons predominate on rocks, and lamellibranchs in muddy sand. The broad foot of snails functions better on solid material. Actinians, with their creeping foot, also are more numerous on rock. Echinoderms, with their ambulacral feet provided with sucking disks, are, in general, common on the rock habitat. Those that live on sand are adapted to it by changes in their ambulacral feet. Lamellibranchs that live on rock usually have no siphons, whereas their foot is provided with a byssal gland whose hardened secretion forms a fibrous attachment. The foot may be reduced in the rock-dwelling forms, never in the sand dwellers.

Some animals living on rock bottom have adopted the mode of protection furnished by boring into the substratum, so common among the sand inhabitants. Since this requires an enormous amount of work, relatively few animals have been able to acquire this habit, and these inhabit mainly limestone or tufa, or similar softer rock. Never-

theless, such rock-boring forms are found in a large number of animal groups. There are boring sponges; boring annelid worms from both Chaetopoda and Sipunculoidea;[25] the boring lamellibranchs are well known and are derived from various families, thus *Petricola, Venerupis, Eastonia, Saxicava, Gastrochaena, Pholas,* the "shipworm" *Teredo,* and *Lithodomus.* Sea urchins bore even into lava and metamorphic rock when exposed to wave action,[33] thus *Echinus militaris, Strongylocentrotus lividus* (which does not bore in the Mediterranean!), and species of *Arbacia, Cidaris,* and *Heterocentrotus.* These borings are often so numerous as to be separated only by thin walls; the external openings of the tubes are frequently narrower than the tube itself, the size of which is adjusted to the growth of the animal, so that they are confined to this location for life. Such intertidal borings are found only so placed that they retain water at ebb tide, and the sea urchins are enabled to live between tide marks, where at the surface they would be unable to withstand drying. Among barnacles, *Lithotrya* bores in rock, and *Alcippe* into small shells.

The holes provided by these rock-borers, like all other crevices, are made use of by other forms. The ark shell, *Barbatia barbata,* the peculiar echiurid worm *Bonellia,* and the small claw-snapping decapod *Alpheus* are especially common in the borings of *Pholas.*

The animals living unconcealed on rock surfaces are often provided with means of defense. The spicules of sponges and the stinging cells of the coelenterates have already been mentioned. Snail shells are thick-walled, tough, and often beset with spines. Shells of lamellibranchs are thick, arched, strengthened by corrugations, and often covered with folds or spines. Crustaceans have a thick, spiny shell. The name "echinoderm" indicates the nature of protection in this group, at least in the sea urchins and starfishes. These shell characters may be a response to the physical rather than to the biotic environment.

Other rock inhabitants obtain protection through protective resemblance; the *Octopus* sits in openings among the stones whose color is imitated by its skin, and the power of color change protects it when it changes location. Many fishes are able to adapt their coloration to that of the bottom. The scorpaenids, lying in wait for their prey, press themselves close to their support, and with their dermal appendages of varied form and their wonderful color resemblance, appear like pieces of alga-covered rock (Fig. 36). Many crustaceans, *Hyas, Inachus,* and *Maia,* for example, which maintain themselves among

rocks covered with other animals, have the extraordinary habit of attaching algae, sponges, polyps, and tunicates to their carapaces.[4] If one removes this covering, they will promptly replace it, as they must also do when they moult. Each will consequently adapt itself to its special surroundings; thus where the sea lettuce *Ulva* predominates, they will be clothed with it, while if a varied algal growth is present, their carapaces will reflect its variety. Crabs of the genus

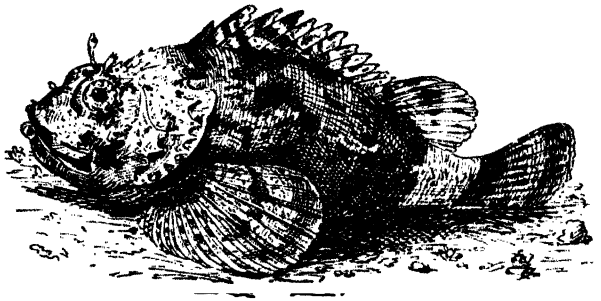


FIG. 36. Dragonhead *Scorpaena porcus*, one-third natural size. After "Aquarium neapolitanum."

Dromia bear a sponge that exactly covers them; they are thought to be protected by its inedibility. Hermit crabs living in snail shells to which sea anemones are attached belong in this category, being protected by the stinging cells of their messmates. Some sea urchins mask themselves similarly; *Toxopneustes brevispinosus* bears on its upper surface a number of shells, which are held fast by its tube feet, sometimes completely covering itself.[15,44,79]

As on sand bottom, plant growth begins near the low tide level in rocky areas wherever the surf is not too violent. As there is no opportunity for roots to penetrate, this growth is limited to algae. The upper levels, occasionally down to 10 m., are grown over with algae like *Sargassum* and *Fucus*. Below these come the sometimes gigantic *Laminaria*, extending to a depth of 30–40 m. These may be extraordinarily abundant and large. On the coast of Chile *Macrocystis* may reach the surface from a depth of 80 m., and the growth may be compared to that of a forest, as the stands of eelgrass compare with meadows.[12] At other places, brown and red and bright-colored calcareous algae may form a mixed growth.

These algal forests abound with animal life, even more than the eelgrass did in its prime. Hydroid polyps, calcareous and siliceous

sponges, tubicolous worms, Bryozoa, and tunicates grow on the leaf-like blades, as do small lamellibranchs with a byssal attachment. All sorts of small creatures occur there, turbellarian, nemertine, and chaetopod worms, snails and nudibranchs, small starfishes and sea urchins, and numerous crustaceans and pycnogonids. A number of small fishes feed here, and this is a normal habitat of oysters.

As on the sandy bottom, the fauna of rock bottom is unevenly distributed. Stretches relatively close together may exhibit considerable differences. Thus each of the coralline areas (Secche) of the rocky bosses on the bottom of the Bay of Naples has its own peculiarities. Lo Bianco [48] says that the Secca di Chiaja is rich in animals elsewhere rare, and that the somewhat deeper-lying Scogli coralliferi in the same area harbor a different association of animals. These differences are the more marked with greater geographic separation, especially below the laminarian zone. Sessile animal life, and its accompanying free-moving forms, is especially rich in deep sounds where a strong current keeps the bottom free from mud. Kükenthal [45] reports such a wealth of life from the West Indian waters near St. Thomas: "At times our great trawl was filled with hundred weight catches of tunicates, gorgonids, hydroids, sponges, and free-swimming forms." Schaudinn [72] reports similar conditions in the straits east of Spitzbergen.

The force of the surf is greater on rocky coasts than on sand beaches. This results in restriction of the fauna, which is greater the more open the coast and the stronger the tides. In the surf-beaten belt, and especially between tide marks, growth of algae is sparing or absent. All animals exposed to the surf are protected against being torn loose and crushed against the rock by special adaptations. They are mainly animals with a solid shell, especially mollusks and barnacles. Barnacles of the genus *Balanus* extend to the highest level, reaching the uppermost high tide mark. In localities like St. Malo, where the tides are especially high, they may be attached to the rocks many meters above the low tide mark, where they are reached by the high tide, and bathed in sea water for a few hours only twice a month. They are exposed to the summer sun and the cold of winter, but remain alive, protecting themselves against complete desiccation by the water retained within their shells. At a slightly lower level, snails of the genus *Littorina* are interspersed among the barnacles; *Nerita* holds a similar position in the Indian Ocean. Although these snails belong to different suborders of the gastropods, their similarity of form, produced by convergent adaptation to similar conditions, is

astonishing (Fig. 37). Below these appear limpets (*Patella*) and chitons (*Chiton*), with *Haliotis*, *Murex*, and *Trochus* at a still lower level. All these mollusks have a broad foot surface, with which they attach themselves to the rocks. The adhesion of *Patella* is supplemented by a glandular secretion and resists a pull of 3.7 kg. per sq. cm.[54] In addition, their shells are pressed tightly to their supporting surface; where the surface is uneven the shells of *Patella* acquire a corresponding irregularity at their edges [69] (Fig. 38), so that a given snail must retain its exact station, to which it returns after short excursions in search of its algal food. At such a permanent station the rock surface is smoothed, doubtless by the corrosive action of the secretion of the foot. Instances are known in which the secretion from the sole of *Chiton* pierced lead pipes 7 mm. in thickness. The form of the shell is also influenced by the strength of the surf.



FIG. 37. *Littorina rudis*, upper, European seas, and *Nerita funiculata*, lower, the Indian Ocean. Natural size.

At the *Fucus* level individuals of the edible mussel attach themselves to the rocks with the byssus; for the most part they do not reach the laminarian zone. These mussels thrive best where

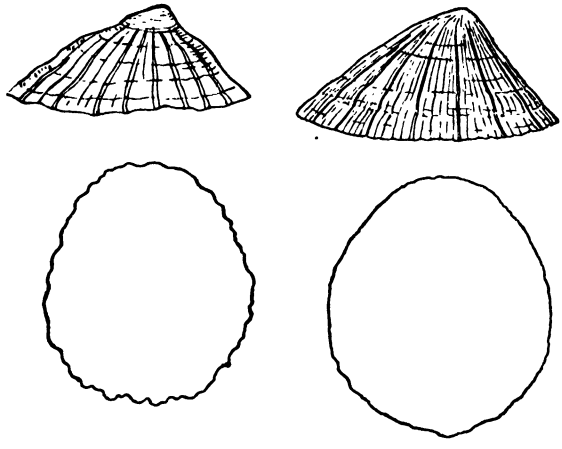


FIG. 38. Shell of *Patella vulgata* from the side, and outlines of the shell, from rough and smooth surfaces. After Russell.

they are most exposed to wave action, tending to be scarce or absent on sheltered cliffs and islands (Fig. 39).[26,38] This is remarkable, because *Mytilus* also thrives in places where the movement of water is relatively

slight, as in the brackish water at river mouths and in some bays. It is an extremely adaptable animal, and one may accordingly conclude that it is not the physical conditions but the biocoenotic relations that condition its abundance. In surf the individuals are small but thick-



FIG. 39. Distribution of some index forms in the littoral of the Island of Batz and the neighboring coast of Brittany. After Joubin.

shelled and with a strong byssus. Where wave action is weaker, algal growths of *Fucus* gain the ascendancy over them; at transitional areas thin patches of *Fucus* are interspersed with *Mytilus* colonies. At other places enemies, such as the starfish *Asterias* and the codling, keep them in check;[65] in the Bay of St. Malo, *Mytilus* has disappeared entirely with the increase of the octopus.[38] The surf zone, however, and also the brackish water, are closed to these predators, so that the mussel

can flourish there. It is not unlikely that exclusion of enemies and more favored competitors by wave action has operated to preserve a number of primitive forms; *Chiton*, and the snails *Patella, Fissurella, Nerita,* and *Haliotis,* are primitive in structure and confined to the surf zone.

The adaptation of *Littorina* to unfavorable conditions extends to its reproduction. *L. litorea* living near the low tide mark lays eggs that hatch into trochophore larvae and develop in turn into a veliger stage; in *L. obtusata,* living between the tide marks, the development is shortened; the young leave the eggs in the veliger stage; finally, in *L. rudis* and *L. neritoides,* which live at high tide mark, the larval stages are done away with, as these snails have become viviparous.[88] These progressive changes are marked by decreased fecundity.

The selective action of the surf shows itself in other ways. An isolated wave-beaten rock affords different habitat conditions on its various sides. The face toward the open sea receives the full shock of the waves. The opposite side is washed by the water as it streams backward, foaming and oxygenated but without destructive force, and hence favors numerous animals that require moving water. The outer face has only a few forms, the barnacle *Chthamalus stellatus* perhaps, and the common mussel, while the inner abounds with animal life. The same is true of groups of rocks and of larger islands similarly situated. The small island of Batz near Roscoff (Brittany) (Fig. 39) illustrates these conditions very satisfactorily. Its northwest coast is covered with barnacles and mussels, which are supplemented by *Haliotis* below low tide mark; its south coast, in quiet water very rich in oxygen, supports a flourishing animal life of different forms.[36] Hollows, cracks, and any protected sites on wave-beaten rocks afford a foothold to an assemblage of sessile animals and their free-living companions.

Severe conditions, which reduce the numbers of species in unfavorable sites to a few, eliminate the competition of other forms, so that those few flourish greatly. Möbius estimated the number of barnacles (*Balanus crenatus*) on a buoy at 10,000 per sq. m. Petersen [64] counted 3580 larger and 95 smaller mussels per sq. m.; these mussels form a connected strip half a meter wide exposed at low tide, on long stretches of the Scandinavian coast.

A supratidal stage, with specialized inhabitants, is present also on rock coasts. The spray forms small pools in hollows in the rock above high tide mark. In calm weather this water is warmed by the sun and concentrated by evaporation, while continued rains at other times

reduce its salinity. Only especially euryhaline and eurythermal animals are able to survive in these pools. A few rotifers, a few copepods and isopods, a few snails, and midge larvae *Chironomus frauenfeldi* are found in them. The conditions in such pools are the more unfavorable, the higher above tide mark they occur. Besides *Littorina,* small and active isopods of the genus *Ligia* occur on the spray-covered rocks above the water line.

Oysters and pearl oysters, which are of commercial importance, are generally more or less abundant on rocky coasts. Oysters require solid bottom on which to attach their shells. It is sufficient for them, to be sure, if stones or mollusk shells lie on the surface of more solid sand or mud. The Australian *Ostrea glomerata* even attaches itself to living snails (*Potamides ebeninus*); 4 or 5 individuals often fasten themselves to the same snail. With the growth of the oysters, their weight becomes too great; the snail is forced into the substratum, and dies. Oysters live on such supports on the banks of the shallow Holstein sea only 2 m. below low tide. The oyster banks of the deeper waters in the North Sea, between Helgoland and the Netherlands-Germany boundary, are also situated on coherent sand; they cover a breadth of 15–20 km. and lie at a depth of 34 to 42 m., affording a further example of the arrangement into communities described by Verrill,[85] Petersen,[65] and others.

The oysters on the Holstein banks are not close set, but spaced about a meter apart, as support is available, and are accompanied by a varied fauna of other mollusks,[56] hydroids, sea anemones, annelids, and crustaceans. *Ostrea glomerata,* in Queensland waters, contrasts with this type in occurring primarily on rocks, and forming reefs composed of solid masses of oysters that may be more than half a meter in thickness, the uppermost 20–30 cm. being living oysters, placed on the shells of their predecessors.[71] Where the sand or mud is subject to motion, oysters do not flourish, since it deposits on them and buries them; but active movement of the water is necessary to keep the detritus on which they feed in suspension. They are not sensitive to reduction of salinity.

The pearl oyster banks of tropical seas are also associated with rock bottom. On the coast of Ceylon [28] such banks are found at depths of 10 to 20 m., at places where sand and mollusk shells and organic materials have been consolidated by carbonate of lime, aided by Bryozoa and calcareous algae. There the pearl oysters *Pinctada vulgaris,* attached by byssal threads, are distributed uniformly over the rock; where they occur on bosses of calcareous algae or fragments

of coral, etc., on the neighboring sand flats, they are assembled in clusters and modify each other's growth (Fig. 40). A rich fauna lives among the pearl oysters; coral may compete with them for room; sponges and Alcyonaria are abundant; mollusk-eating starfishes such as *Astropecten hemprichii* and *Pentaceros lincki* feed on them; and annelids, bryozoans, and tunicates cover their shells. Nearness of

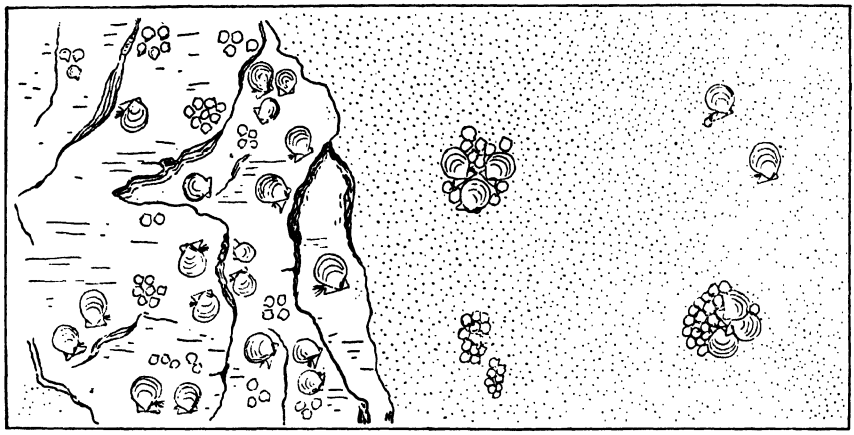


FIG. 40. Distribution of pearl oysters on rock bottom (left) and on sand bottom (right). After Herdman.

sandy areas may be fatal to the pearl banks if a storm stirs up the sand and redeposits it on them.

Coral reefs

Coral reefs form a special biotope in the rock-coast formation. These reefs are raised structures, extending from sea bottom to a little above low tide level, formed by living animals and consisting of their calcareous skeletons. Great masses of limestone are built up under the favorable temperature conditions of the tropical seas, to which the reef-building corals are confined.

The Madreporaria (reef corals proper) are the main component of the coral reefs; the lime skeletons deposited by their ectoderm form the foundation. Three families of reef corals are particularly important, the Poritidae (*Porites*, Fig. 41*a*), the Acroporidae (*Madrepora*, Fig. 41, below), and the Astraeidae (*Gonastraea, Coeloria*, Fig. 41*b*). The organ corals among Hexacorallae (Tubiporidae, Fig. 41*c*) must be added to these. So must the Milleporidae, belonging to another class of the coelenterates, known to the inhabitants of the Red

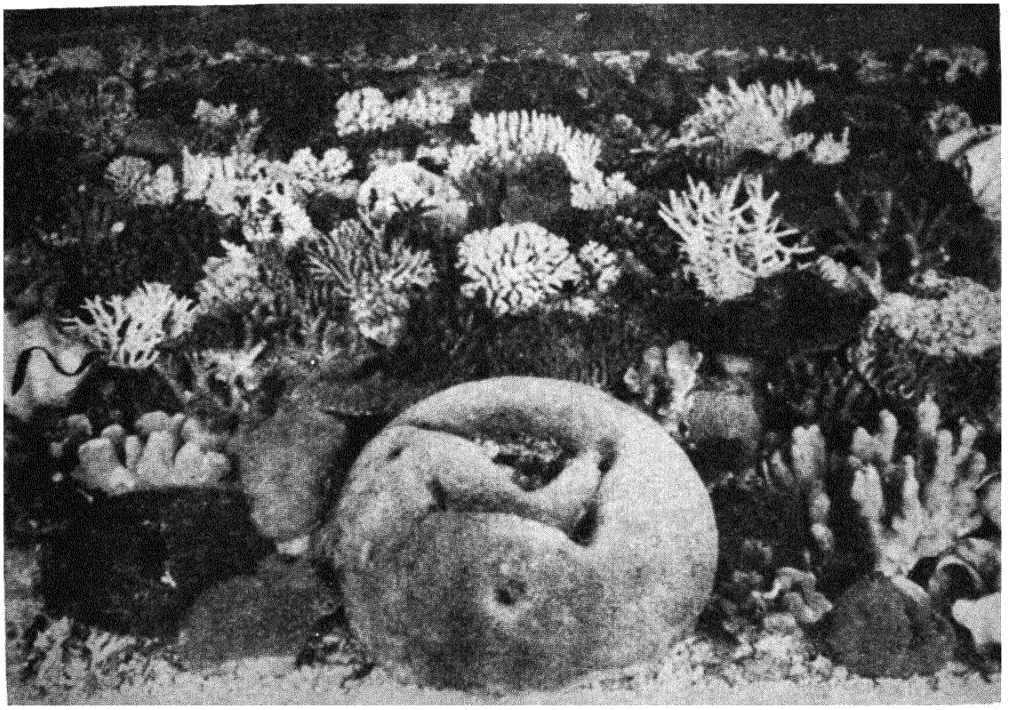


FIG. 41. Corals of the reef at Bake. A large *Astraea* (*b*) is in the middle foreground, above and to the left of which is an organ coral *Tubipora* (*c*); to the right and left are moderate-sized colonies of *Porites* (*a*), and the background is mainly filled with branched acroporids *Madrepora* and *Acropora*. Giant clams (*Tridacna*) may be seen at the right and left (*d*). After Wolf.

Sea area as "fire corals" on account of their stinging powers. These form massive branches by calcification of their ectodermal skeleton, an evolution convergent with that of the reef corals.

The calcareous algae are important in reef building everywhere; their bulk is composed of carbonate of lime up to 90%. Calcareous Bryozoa compete with them in places in growing over and cementing fragile or broken coral branches. The calcareous tubes of the serpulid worms play a similar part, sometimes an important one, as in Bermuda.[83] Some sessile mollusks, both lamellibranchs and gastropods, contribute to the accumulation of lime. Foraminifera, in spite of their minute size, also supply binding material, cementing fragments and filling holes. These usually subsidiary organisms are sometimes dominant in reef formation.

Reef corals are stenothermal, warmth-limited animals, and coral reefs are confined to warm seas. They flourish only in water above 20.5° C., which is almost confined to the tropics, approximately between 30° N. latitude and 30° S. (cf. map, Fig. 77). The Gulf Stream enables them to reach and form reefs at Bermuda in latitude 32° N. Even within the tropics, areas of cold currents, combined with the upwelling of cold water along west Africa and the west coast of South America, limit the occurrence of coral. The cold southward current on the east coast of Florida prevents their development, but they flourish on the west coast. On the other hand many corals are little sensitive to increase of temperature above their optimum. Coral polyps, withdrawn into their cups, may withstand a temperature of 56° C. in the direct sun, when they are exposed at low tide.

Within this tropical belt further subdivisions (with reference to the coral) may be made.[39] A narrower equatorial belt, with water above 23.4° C., harbors all the large branched forms, while the two bordering areas, with temperatures between 23.4° and 20.5°, have principally the encrusting forms, which are more resistant. The variety of species is also greater in warmer water. One hundred and eighty species of Madreporaria were found at Port Galero (Mindoro); 128 species have been listed from the very warm Red Sea; and 51 species are known from Zanzibar.[24, 41a, 49] On the Tortugas, at 25° N. latitude, the number of species is scarcely 30, and in the Bermuda reefs (latitude 32° N.) only 10 species of madrepores and 2 of millepores have been found.[57]

Stony corals exist, it is quite true, in higher latitudes. The solitary species *Flabellum* and *Caryophyllia* and the colonial *Astroides* occur in European waters, and *Astrangia* extends along the North American

coast from Florida to Cape Cod. Corals also appear in deep water as banks of considerable extent, though without forming reefs, as for example the "Coral Patch" in the Atlantic at a depth of 800 m., which drops off to 1000–1500 m. at its edges, covered with *Lophohelia prolifera* and other forms.[22] The same *Lophohelia* and *Amphelia ramea* appear on the Scandinavian coast north to the Lofoten Islands and are especially well developed in the Trondheim fiord, where they form banks at 200 m. depth, differing from reefs in that they do not rise to the surface.[7] Reef-building corals extend to a depth of 40–60 m., rarely down to 74 m.[84]

The growth of reef corals in waters close to the surface is intimately correlated with the penetration of light. Their polyps are filled with symbiotic alga-like flagellates, zoöxanthellae, either embedded in the body wall or free in the stomach. The zoöxanthellae were formerly considered to be the principal source of nutrition for corals in the photic zone. It now appears that corals are carnivorous and feed on zoöplankton at night. Digestion is rapid, and during the day the coelenteron is usually empty. In fact, starved coral polyps eject zoöxanthellae; their probable function is the removal of carbon dioxide and of the wastes from protein metabolism of the corals. In the relatively strong light of the upper four meters of water, the zoöxanthellae produce enough oxygen in photosynthesis to fill the oxygen needs of the corals.[20,31,89,90,91] Incidentally the presence of the zoöxanthellae produces the bright colors of the polyps, which may be yellow, yellowish-red, or red. Corals from deep water have colorless polyps.

Reef corals are sensitive to any decrease in salinity from the normal, though increase in this respect does not affect them, as is shown by their abundance in the Red Sea. Broad gaps in fringing reefs occur opposite river mouths, and the great gaps in the Australian barrier reef seem to be opposite the river mouths on the mainland. In spite of the aridity of the African coast of the Red Sea, its harbors, which represent gaps in the coral, are opposite the valleys that descend from the upper Egyptian mountains.[41] One may conclude from this fact that the rainfall in this region was greater in times not far past.

The sensitiveness of corals to river water is increased by the fact that they are adversely influenced by the mud and sand brought down by the floods. They are absent in the region of the mouth of the Amazon and are much reduced or absent in some areas in the Java Sea, on account of the sediment carried in by the rivers of the sur-

rounding large islands.[86] Coral reefs are absent in the neighborhood of active volcanoes, since ash deposits kill them.

A certain amount of movement of the water is also necessary to the corals, and this must be neither too active nor too slow. In deep bays and inlets where the tides are reduced, coral growth is weak. The best collecting and observing stations for the scientist are always on the sides of the reef, especially at capes that extend somewhat seaward,[30] and on barrier reefs and atolls, at the channels leading into the lagoon. Moderate motion of the water prevents deposition of mud, which is constantly formed by chemical and wave action and by the activity of the reef-boring animals. Such motion also distributes food and oxygen. Too much motion prevents the ciliate larvae from gaining a foothold and carries them away.

The rate of growth of corals is probably greatest near the surface. The diameter of a large madrepore on the wreck of a ship sunk 64 years before was 5 m., an average annual increase in diameter of 39 mm. on each side. Other estimates are lower, about 20 mm. for the more compact forms. The rate of growth of the Maldive reef is apparently 27–29 m. in 1000 years.[19] Charts of a reef may be wholly valueless after 20 years. Great blocks of hard coral, such as are produced by the Astraeae, may have an age of several hundred years.

Coral reefs frequently reach slightly above water level. Many kinds of coral are able to withstand a certain amount of exposure, so that the upper surface of the reef may be laid bare at ebb tide. Coral islands projecting above hightide mark are produced by the action of storms, which pile up loose blocks on the lowtide platform. These hold the erosion materials of the platform, small coral fragments and sand, and the accumulation may rise 1 to 2 m. above water level for stretches of varying extent. Seeds drift to this beach and find a foothold, and a vegetation may develop that increases in richness and variety with time. The cocoa palm thrives especially in this situation. A multitude of terrestrial invertebrates, hermit crabs, land crabs, insects, and snails, reach the new territory, as do birds. Finally man invades the island, bringing with him the animal and plant associates of human culture. It is not rare, however, for spring flood tides or great storms to wash all traces of life from such low islands into the sea, as in certain of the Tuamotus in 1878 and 1903.[76]

Arrangement of the types of corals in the reef is not uniform. At the upper rim in the surf-zone *Porites* (Fig. 42) and *Millepora* are the dominant genera. "These alone seem able to withstand the force of the waves at their outer border, and they form with the nullipores a

breakwater which prevents fragmentation by the waves" (Darwin). *Astraea* may also grow in shallow water and may be exposed at low tide without injury; it accordingly extends as a rule about 30 cm. above *Meandrina.*[37] The branched madrepores have a different habit of growth at different depths, more and more loosely branched as the depth increases, often within the same species, as for example in *Madrepora muricata* with its three forms *palmata, prolifera,* and *cervicornis* (Fig. 43). *M. scherzeriana* of the Red Sea varies similarly, as do some *Porites.* The madrepores are not true rock builders. "The cornerstones of the reef are supplied by the massive corals—the balls and pillars of *Porites,* the rounded walls of *Maeandrina,* and the great group of Astraeas."[41]



FIG. 42. *Porites* sp. After Vaughan.

Coral reefs are distinguished as fringing reefs, barrier reefs, and atolls, the last being ring-like coral islands.

Fringing reefs are juxtaposed to the coasts and follow their out-

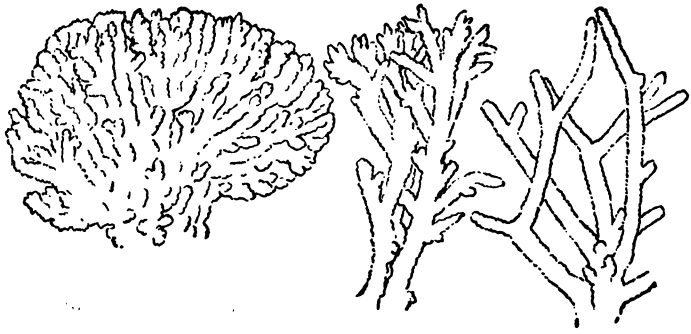


FIG. 43. Outlines of the habitat forms of *Madrepora muricata. a, forma palmata; b, forma prolifera; c, forma cervicornis.* After Vaughan.

lines. They may be reached dry-shod from the shore at low tide, when their platforms are exposed. They are often only a few meters wide, but may reach a breadth of a kilometer, according to the slope of the coast on which they are formed; the narrower reefs are on

steep slopes, the broad reefs on gentle ones, as for example at Dar es Salaam.[61]

Barrier reefs are separated from the coast by a canal or lagoon of varying width. Islands may be surrounded by a ring-like barrier reef (Fig. 44). Mainland coasts may be paralleled by them for great distances. The Great Barrier Reef of Australia extends for about 1900 km., the width of its lagoon varying from 38 to 150 km., its depth



FIG. 44. The island of Bora Bora, in the Society Islands, with its barrier reef. After Agassiz.

from 30 to 50 m. Such reefs have a steep outer and gentle inner slope.

Atolls are ring- or horseshoe-shaped reefs, extending only a few meters above sea level, and often more or less interrupted by passages (Fig. 45). The largest atoll, Sunadiva, is 42 by 32 miles, with a perimeter of 121 miles; it contains over a hundred subsidiary islets and a lagoon up to 100 m. deep that connects with the open sea by 40 channels.

Darwin [13] explained these varied reef formations by means of a comprehensive theory based on the following considerations: (1) that



FIG. 45. The atoll of Pinaki, Tuamotu Islands. After Agassiz.

reef corals flourish only to a depth of 40–60 m.; (2) that the growth is most rapid on the outer face of the reef; and (3) that variations in the level of the sea bottom take place. From the first consideration, reefs cannot rise to the surface from the oceanic depths but must be confined to submarine banks, such as the tops of submerged volcanos, or on the coast of existing land. On stationary and on rising coasts, the reefs are consequently of the fringing type (Fig. 46, I). But when

mainland coast or islands are sinking, the outer, more rapidly growing edge of the reef is separated more and more from the shore, and a channel or lagoon without corals is consequently produced between the reef and the original coast, i.e., a lagoon and barrier reef are formed (Fig. 46, II). When the submergence is long-continued, the island itself may disappear, and only the reef, now an atoll, remains (Fig. 46, III). "Atolls are the grave stones of sunken islands." All intergradations between barrier reefs surrounding islands and atolls may be found. Volcanic islands with surrounding reefs are found in the Gambier archipelago. In the Society Islands the progressive dis-

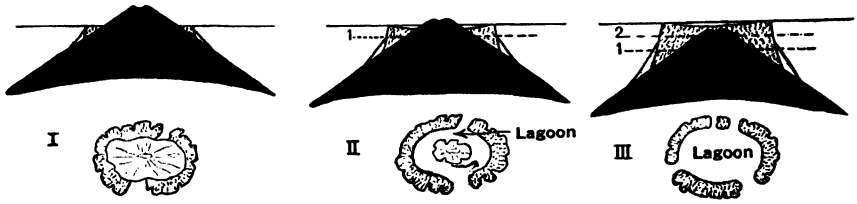


FIG. 46. Origin of various forms of coral reefs according to Darwin: I, fringing reef; II, barrier reef; III, atoll. Cross sections above, outline below, in each case. 1, 2, sea level in I and II respectively.

appearance of the volcanic peaks may be seen, as on Tapamano, about 100 km. west of Tahiti, where the central volcanic part is reduced to two hills, the highest of which is about 50 m. high; the volcanic peaks at Motu-iti, near Bora-bora, have disappeared, leaving only a low platform surrounded by a wreath of small islets.[76]

The Darwinian explanation, on account of its simplicity, found wide acceptance. Dana [10] believed that he could support it from his studies of Pacific reefs, and it still has numerous proponents. Exact investigations of many reefs, however, have shown that the situation is more complex. It is true that barrier reefs and atolls are in general absent along rising coasts, and that these have fringing reefs, as from Dar es Salaam to the Red Sea [9, 23, 61] and in the Sunda Islands. Barrier reefs and atolls, however, are not confined to areas of submergence, but may be formed where the shore line is stationary.

Careful observers who have dealt with this problem emphasize effects of aerial and wave erosion, boring of annelids and mollusks, browsing of certain fishes, and chemical solution of the calcium carbonate on the determination of the height and compactness of the reef and on the formation of lagoons. Semper [75] called attention to the fact that atolls, barrier reefs, and fringing reefs may occur in

the same region in relatively close juxtaposition. On Tahiti the north, west, and south sides are surrounded by a broad fringing reef, while on the east side, under the influence of the strong trades, a deep lagoon has been formed between reef and coast, whose origin through erosion may be plainly seen through its gradual transitions.[1] Similarly the broad fringing reefs of the Fijis may emerge into barrier reefs with narrow lagoons. The great effects of marine erosion are shown by the Metisbank in the Tonga Islands; in 1875 it was an island of 9 m. height above sea level; it was later raised to 40–50 m., and is now reduced to a submarine platform 30 m. below sea level.

These eroding influences are counteracted on one side by the growth of coral and on the other by the accumulation of coral sand brought in by waves and dust blown by the wind, which tend to fill the lagoons and produce extensions of the shore, shallows, islets, and secondary lagoons.

The abundance of concomitant factors and the various ways in which the balance may be established between the constructive and destructive agencies has as a consequence a great variety of appearance in the reefs of a single region, especially in the Indo-Pacific, according to local conditions. The variety of material of the shore, solid or loose volcanic material, tertiary limestone or modern coralline limestone, conglomerates, and breccias is a factor that affects reef building. Rapid uniform elevation, or interrupted or slow elevation, similarly produce varied results. Every coral reef is an individual formation, the product of a whole series of factors, and is understandable only from its own special history. The uniformity of the whole process postulated by Darwin is not valid in detail, but Davis [14] in a mature review of the whole problem in 1928 decided that in general Darwin's theory still represents the known facts better than any other proposed to date.

The original subsidence theory appears oversimplified and needs extension to cover the evidence that water levels have varied through other processes than simple submergence. Thus the so-called glacial control theory [8] takes cognizance of the Pleistocene ice age during which much water was piled up as ice on the land, and the ocean level was lowered sufficiently so that submarine platforms could be wave-eroded. Such platforms have since been covered by water released from glaciers to about the depth actually supporting coral reefs in certain regions.[19]

"Glacial control" is one of the theories of planation, all of which postulate the existence of a wave-cut platform upon which coral

reefs have developed.[8] Also, as others suggest and Darwin did not deny, reefs may form in areas in which the sea bottom becomes sufficiently elevated.[70] Such elevation might result (*a*) from crustal movement, (*b*) from submarine volcanic eruption, (*c*) from accumulation of skeletons of plankton organisms, (*d*) from the growth of deep-sea corals, or (*e*) from some combination of these possibilities.[70]

Boring through coral reefs

A test of these theories comes from evidence secured by borings, summarized in the table on p. 260. The simplified, over-brief, tabular summary shows that the three borings on Samoa reveal a wave-cut terrace in the underlying basalt. This platform lies within the depth to which the sea level might well have fallen during Pleistocene glaciation. Contours of the littoral sea bottom in the East Indies suggest that the lowering of the sea level there at that time was about 100 m. (= 328 feet).[74] Hence results from the Samoan borings not only show planation but can be used in support of Daly's theory of glacial control.

Subsidence may well have occurred in each of the other reefs tested. Some complications are furnished by the Bikini borings, since there is evidence that the interval from depths of 300–575 feet (91–175 m.) "was above sea level for an appreciable time after deposition. . . . Tertiary fossils have been identified from a depth of 930 feet, but the contact may lie above 725 feet and possibly as high as the 425-foot level" (130 m.). On the whole a period of elevation is suggested, and this possibility is supported by the fact that Plio-Pleistocene coral reefs exist on the island of Timor (East Indies) at an altitude of 1300 m. above sea level. "There are numerous instances of late tertiary and quaternary coral reefs being raised to great heights."[19,74] In summary, the data furnished by these borings give much support to the subsidence theory, though planation and elevation may also have been factors in supplying a suitable base on which coral reefs could grow.

Animals associated with coral reefs

The coral reef forms the background and basis for a wealth of animal life unequaled elsewhere even in tropical seas. Griffin reports from the coral reefs of Port Galera, Mindoro, 111 species of Alcyonaria, few starfish and sea urchins, but numerous brittle stars, crinoids, and holothurians; 70 species of chaetopod worms, 3 echiurids, and 10 sipunculids; and 200 to 250 species of crustaceans, among them 25 to 30

Location	Date	Depth Reached, in feet (number of wells in parentheses)	Geological Age	Reef Base	Indication
Funafuti Atoll, Ellice Islands [18]	1896–1898	(1) 1114	Recent	Not reached	Subsidence or talus
Samoa [8]	1920	(3) 68; 124; 124	Recent	68; 124; 124 ft.	Planation: wave-cut basalt terrace
Great Barrier Reef [67]	1926, 1937	(2) 600; 732	Recent	378; 506 ft.	Subsidence
Kita-Daito-Zima (North Borodina) [47]	1934–1936	(1) 1416	Above 340 ft. Plio-Pleistocene Below 1296 ft. Upper Oligocene	Not reached	Subsidence
Borneo Shelf Islet near Maratoea [47]	1947	(2) 856; 1407	Not stated	Probably not reached	Subsidence
Bikini Atoll, Marshall Islands [47]	1947	(5) 118; 190; 300; 1346; 2556	Recent Below 1020 ft. Tertiary Below 1790 ft. Lower Miocene	Not reached	Subsidence, then elevation, then subsidence

hermit crabs. Möbius estimates the number of molluscan species (without nudibranchs) on the reefs of Mahébourg, Mauritius, at 336. In general character this fauna associates it with the fauna of the rock bottom. The conditions that permit of such a rich development, in addition to the generally favorable tropical environment, are the abundance of food and adequate protection.

The reef corals with their symbiotic organisms are to be reckoned among the food producers, and are fed upon to some extent by the reef inhabitants. The colorful mixture of green, brown, and red algae supports another series of animals. The surf produces and brings detritus and plankton, which serve as food for others, and predators follow the herbivores, as everywhere.

The coral reef habitat offers much better protection and concealment than solid rock. It is permeated with pores and cavities like a sponge; there are broad caves and well-like hollows, connected with each other and with the sea; all these, with smaller cracks and interspaces, afford retreats and hiding places to associated animals. Even

the individual coral heads are porous, and when one is broken up a crowd of varied inhabitants scatters in all directions. As if there were not enough natural hollows, a whole series of forms bore into the coral. The examination of a solitary madrepore, located at a distance from the reef on sand bottom, shows how attractive it is to other animals. Much of the animal population of the surrounding area will be concentrated on and in it.[45]

There is scarcely a benthic group of animals not represented in the coral communities. It must suffice to emphasize the most important common characteristics. As in general on solid bottom, numerous sessile animals are present. In addition to the reef-building corals, others that merely inhabit the reef without contributing to its structure are present, such as the solitary proteoid *Fungia.* Sea anemones are numerous, among them the gigantic discosomatids with an oral surface 0.5, even 1.2 m. (*Stoichactis*), in diameter. Gorgonids may be abundant, especially in the West Indian reefs; they form a special gorgonid zone, below 10 m., in the Tortugas. Sponges of all sizes occur, up to the great Neptune's cup, *Poterion.*

Among the lamellibranchs here characterized by special thickness of shell are oysters, pearl oysters, and the spiny-shelled *Spondylus;* the gigantic *Tridacna,* which reaches a weight of 250 kg., is an index species of the Indo-Pacific reefs. A number of coral-boring forms are represented, such as *Lithodomus,* and others, like *Coralliophaga,* are grown over by coral. Numerous gastropods are sessile, like *Magilus,* which is remarkably transformed by its life in the coral; beginning as a snail with ordinary spiral shell, in cracks in the coral, it changes its direction of growth and extends the shell more or less in a straight line, as it becomes overgrown, in order to maintain its contact with the outer world, filling the older portion of the shell with lime (Fig. 17, p. 207). Serpulid worms are abundant on reefs and may play a part in their structure.

The snails of the coral biotope are remarkable. The distribution of the gastropods in the Indo-Pacific is governed by that of the coral reefs, on which the molluscan fauna is especially varied.[17] Besides the above-named *Magilus,* the family Coralliophilidae is especially adapted to life in the reefs, the different forms belonging to it having lost their radulae in adaptation to feeding on the coralline slime, for which teeth are not needed.

Some predaceous chaetopod worms, which live concealed in the reefs, are characterized by a remarkable mode of reproduction. In the palolo

worm, *Eunice viridis* (Fig. 47), of the South Seas the eggs and sperm are developed only in the posterior division of the body, and these parts are cast off when mature, when they leave the reef and swarm out into the open surface water. This occurs twice each year, at a predictable date, namely on the day before and the day of the last quarter of the moon in October and November.[48] The sea is then so filled with them that the natives gather them with baskets for a feast. *Eunice furcata* has the same habit in the Dry Tortugas.[53]

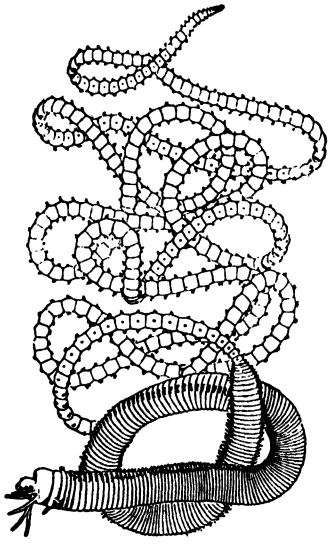


FIG. 47. Palolo worm *Eunice viridis*. The thick anterior end remains in the reef, and the more slender posterior portion breaks off and swarms in the open water as the palolo. After Woodworth.

Crustaceans are exceedingly abundant in the reefs, variously concealed in cracks and between the branches of the madrepores. The alpheids, or pistol crabs, small, long-tailed decapods that make a snapping sound with their claws (Fig. 48), are closely correlated with corals in their distribution. Out of 79 long-tailed decapods taken by Gardiner in the Maldive reefs, 76 were alpheids. Crabs are abundant, especially the small Cyclometopa. The family Trapeziidae (Fig. 49) is confined to coral reefs, where single species are restricted to single reefs and occur only on single kinds of corals, as *Trapezia rufomaculata* on *Pocillopora favosa* at a reef south of Dar es Salaam, and *Tr. guberrima* on *Madrepora haimei* on the Uyanga reef.[62]

The number of species of fishes found in coral reefs is large. "The coral reefs of the South Seas literally swarm with fishes. The larger species live in the deeper channels and swim in and out, exhibiting the most brilliant colors. The smaller species live on the surface of the reef and remain in tide-pools at low tide. Many of these fishes have a coloration like that of coral rocks, and remain in the protection of the coral. Others exhibit so-called warning colorations, with blue, scarlet, yellow and green sharply contrasted with their background." [35] Certain types of pattern and body form are repeated by genera of distinct families, sometimes so strikingly that such fishes were formerly classified in the same group; for example, the deep body form with

vertical black bands and long median fins extended backwards, as in many butterfly fishes (*Chaetodon*, Fig. 50*b*; *Holacanthus*, Fig. 51*a*) and pomacentrids (*Dascyllus*, Fig. 50*a*; and *Glyphidodon*). Species of the percoid genus *Serranus* and some labrids may resemble each other in their elongate elliptic body form, long, uniform dorsal fin, spotted or vertically banded body with many striped head markings, and the rounded or slightly concave tail fin. Families in which a uniform coloration is usual contain fishes with distinct patterns in the East Indies, as in the banded *Synaptura zebra* and the spotted muraenids.

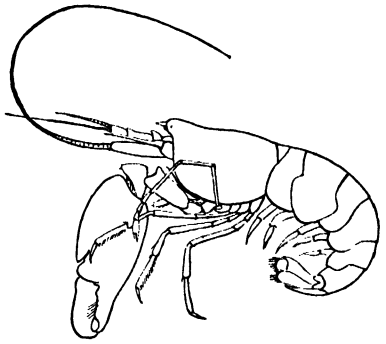


FIG. 48. Pistol crab *Alpheus bermudensis*. About twice natural size. After Spence Bate.

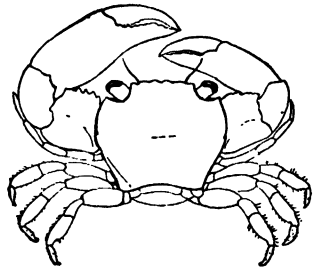


FIG. 49. *Trapezia rufopunctata* var. *intermedia*, natural size. After Miers.

Silver coloration, otherwise so widespread, is very rare among coral reef fishes.[50] Other fishes show convergent adaptation in consolidation of the teeth into a beak, enabling them to bite off small branches of coral. Among these are the pomacentrids (Fig. 50*a*), the sparids (Fig. 52*b*), and the suborder Plectognathi with the trigger fishes (*Balistes*, Fig. 50*c*), the trunk fishes, and the puffers (Fig. 52*a*, *Diodon* and *Tetrodon*). In spite of stony skeleton and stinging cells, these fishes browse on the coral; up to 1 kg. of coral, in rather large pieces, has been found in the stomach of *Diodon*.

Competition, amongst so great a number of animals in a limited habitat, is extreme. Protective devices are accordingly evident, more than elsewhere in the rock habitat. All the hiding places are utilized, including the disused holes of the deceased borers. Many forms permit themselves to be overgrown by coral (the snails *Magilus* and *Vermetus*, the lamellibranch *Coralliophaga*, and the annelid *Sipunculus*). Others bore into the coral—sea urchins, boring lamellibranchs, and the barnacle *Pyrgoma*. Crabs mask themselves with sponge.

Fishes and cephalopods change color in correlation with the background. Small shrimps and fishes (pomacentrids: *Amphiprion, Trachichthys,* and *Psenes*) [71] seek protection among the stinging tentacles of sea anemones (*Stoichactis* and others), which they resemble in

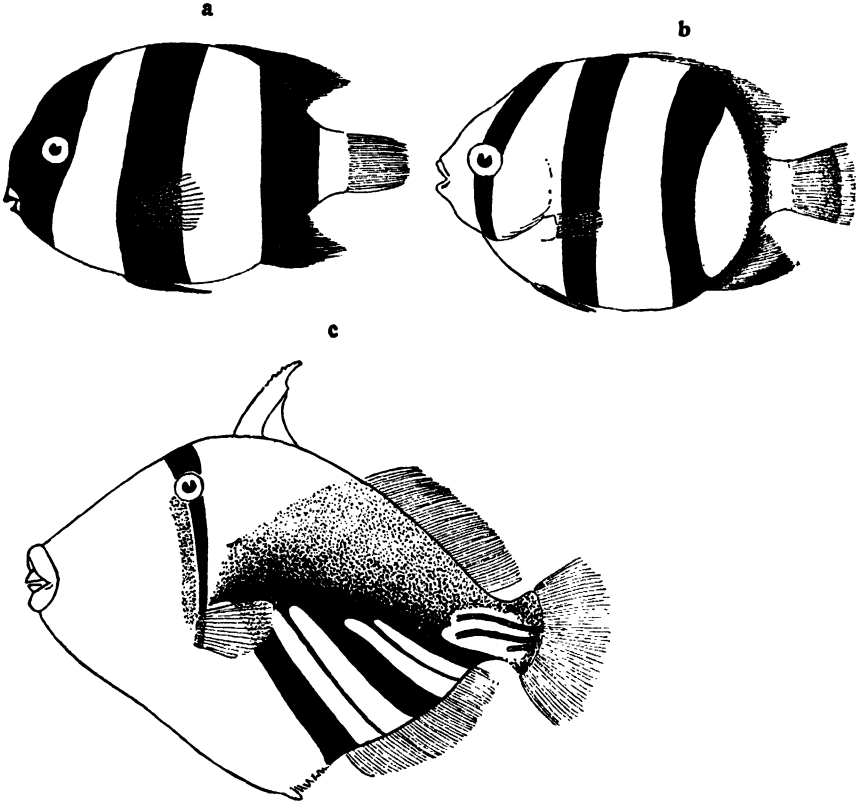


FIG. 50. Reef fishes with similar patterns: *a, Dascyllus aruanus,* a pomacentrid; *b, Chaetodon striatus,* a butterfly fish; and *c, Balistes aculeatus,* a trigger fish.

coloration, even seeking shelter in the enteric cavity. Trigger fishes lock themselves into crevices. The bright colors of some reef fishes may be interpreted as warning coloration; many such fishes are actually poisonous. This may also be the case with the opisthobranch snail *Bulla,* whose emerald green color, with orange spots, in addition to an unpleasant musk-like odor, indicate its unpalatability. The riot of color and pattern displayed by coral reef fishes may arise in part from the presence of rich food supplies and innumerable places of refuge, which permit colors to vary relatively unchecked by natural selection.

The richness of the reef fauna is not everywhere the same. The Tuamotu Archipelago, farthest east toward the open Pacific, shares the poverty of the latter. The number of species of corals is smaller

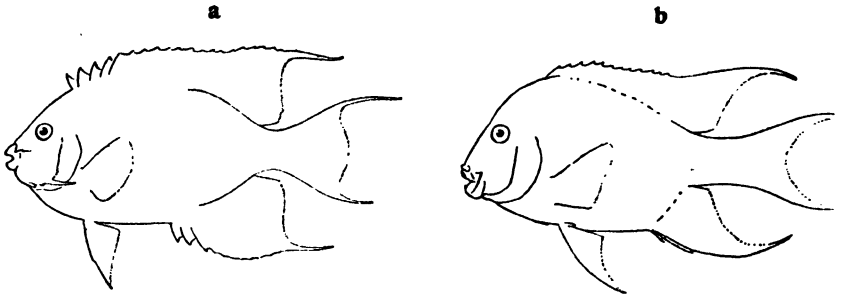


FIG. 51. Reef fishes with similar shape: *a, Holacanthus tricolor,* an angel fish; and *b, Microspathodon dorsalis,* a pomacentrid. After Jordan and Evermann.

than elsewhere in the same latitudes, and the accompanying fauna is similarly impoverished. The fleshy alcyonarians are notably absent, and the gorgonians are poorly developed; few sponges occur; and the

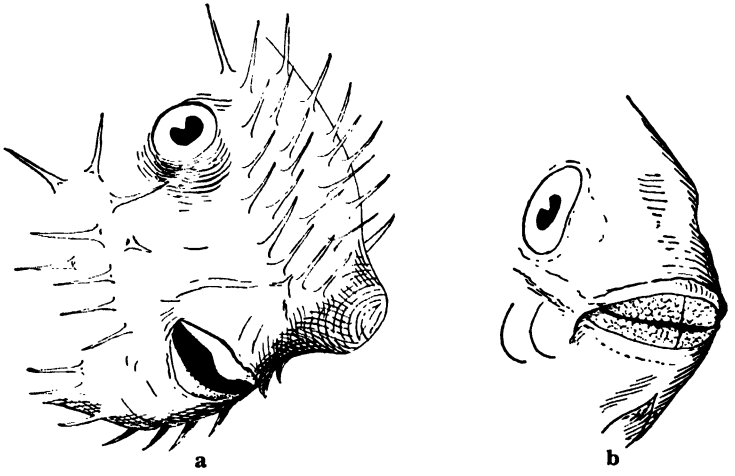


FIG. 52. Reef fishes with teeth fused into a beak: *a, Diodon hystrix,* a porcupine fish, and *b, Sparisoma aurofrenatum,* a parrot fish. After Jordan and Evermann.

Tridacna of 15 to 45 cm. are dwarfs in comparison with those of Queensland.[1] Gorgonians and alcyonarians are noticeably absent in Tahiti also. The rich fauna of Indo-Pacific fishes reaches its maximum in the East Indies and is much reduced in number of species in eastern Polynesia. The total effect of a coral reef is overpowering in its wealth

of life and splendor of color. The Dutch refer to them in the East Indies as "gardens." Haeckel speaks of "fascinating coral groves, where every animal becomes a flower."

In spite of many common characters, the general appearance of the reefs is not everywhere the same. While the reefs at Tur (Red Sea) are marked by the predominance of warm colors, yellow, orange, red, and brown, green is the dominant tone in the coral gardens of Ceylon, where yellowish green Alcyonaria accompany sea-green heteropores, malachite green Anthophyllae stand beside olive green millepores, and emerald green madrepores and astraeas beside brownish green montipores and maeandrinas.[27]

The animal life of the lagoons of barrier reefs and atolls is considerably different from that of the outer face of the reef. The corals themselves, in quiet water, have quite different habits of growth, and are often slender, branched, and fragile. They are less commonly continuous, but form spots and accumulations in limited areas. In the lagoons of the Marshall Islands, millepores are the most abundant corals, with *Porites* next. Solitary corals are frequent in the lagoons. The bottom of the lagoon is covered with coral sand and calcareous mud derived from the erosion on the reef, and this is probably one of the reasons for the failure of corals to flourish in the lagoons. The number of animals in the lagoon varies according to local conditions. Agassiz found the lagoons of Pinaki and Rangiroa rich in fishes. Fishes of the lagoon are mostly dull colored, in contrast with those of the reef.

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13. *The Biotic Divisions of the Ocean (Continued): the Pelagial*

AS IN THE BENTHAL, TWO VERTICAL ZONES MAY BE DISTINGUISHED IN THE pelagic communities, the lighted and the lightless, or abyssal zone. They are not sharply distinguished, although an ill-defined intermediate stage can be recognized. The depth to which light penetrates decreases from the tropics to the polar regions, and varies in each locality according to the time of year, depending on the angle of incidence. The lower limit, for practical purposes, lies between 200 to 600 m. Off Bermuda on "an exceedingly brilliant" day, Beebe [6,7] found light still visible to the eye at 571 m.; at 610 m. all daylight had vanished; earlier he had found no visibly detected light below 511 m.

The general discussion of the pelagial may best be restricted principally to the lighted zone, leaving the abyssal for treatment with the abyssal benthal (Chapter 14). The common character of all pelagic animals is their independence of the bottom, which means that they have the ability to maintain themselves in the open water without sinking. This capacity is variously developed. Some animals, like the ctenophores, never sink to the bottom; many elements in the pelagic fauna, however, are larvae of animals that spend their adult life in the benthal. In some cases the pelagic period is extremely short. Even unquestionably pelagic forms, such as the mackerels *Scomber scombrus,* are thought to spend part of the year resting on the bottom.

Flotation mechanisms

Living matter is heavier than sea water; its specific gravity ranges from 1.02 to 1.06, perhaps averaging about 1.04,[9] whereas the specific gravity of sea water varies between 1.02 and 1.03.[11a,36] Special adapta-

tions are consequently required to prevent animals from sinking. This distinguishes pelagic creatures from the animals of the benthal and gives them features in common that appear in various groups by convergent evolution.

The state of suspension may be regarded as a retarded sinking in which the rate approaches zero as a limit. The rate of sinking depends on various factors; it is reduced with reduction in specific gravity, and likewise with any increase in the resistance offered by the water. This resistance is the greater, the more water particles are displaced and the greater the sum of their paths described in such displacement; it varies also with the internal friction, or viscosity, of the water, which depends mainly on temperature and salinity.

Reduction in specific gravity may be made in many ways.[38] There may be economy in the use of hard skeletal or shell materials such as lime and silica. Pelagic relatives of benthic animals with a skeleton or shell are accordingly characterized by great reduction in such hard parts. The foraminiferan *Orbulina universa* from surface waters, has a very thin shell with walls from 1.28μ to 18μ, while specimens from the bottom have walls up to 24μ in thickness. The pelagic *Globigerina* are distinguished by thin-walled shells from the single benthic species, *Globigerina pachyderma,* whose name indicates its character. Calcium carbonate is also reduced in the shells of Foraminifera by increase in the size of the pores and by enlargement of the opening of the shell.[34] The shells of pelagic crustaceans are uncalcified or weakly calcified in comparison with those of their benthic relatives and have a higher fat content as well, as shown by analysis: [27]

		% Ash	% Fat
Benthic	*Nephrops*	33.79	2.67
	Carcinus	41.91	2.56
Littoral	*Crangon*	19.71	3.83
Neritic	*Mysis*	13.55	3.34
Pelagic	*Anomalocera*	6.61	5.73
	Fresh-water copepods	9.21	6.01

The pelagic sea cucumber *Pelagothuria* lacks the lime bodies invariably present in its relatives. Among pelagic snails the heteropods and pteropods have delicate shells or none at all. The shells of the pelagic lamellibranch *Planktomya* are uncalcified.[37] Similarly among the cephalopods, the benthic Sepiidae have a calcified internal shell, while the pelagic Loliginidae and Oigopsidae have the shell narrow, delicate, horn-like, and uncalcified. Among pelagic fishes, especially

among weak swimmers, the skeleton is weak, little calcified, or reduced, as in *Regalecus* and *Crystallogobius*. Reduction of weight is achieved by pelagic copepods by depositing their eggs singly instead of carrying the egg sacks with them.

The most widespread means of reducing specific gravity among pelagic marine animals is the taking up of large amounts of water. The absolute surplus of weight remains the same, but the relative difference is reduced. This water is ordinarily incorporated in the transparent jelly-like tissue, so abundant among marine animals. It is known as the mesogloea in coelenterates. Among medusae the amount of water may reach 96.5% in a variety of forms.[18] Siphonophores, heteropod and pteropod snails, Alciopidae and *Tomopteris* among annelids, and chaetognath worms have similar jelly-like tissue. Such jelly is widespread among the pelagic cephalopods. *Tremoctopus alberti* resembles a small transparent ball of jelly; the transparent *Alloposus mollis* has so soft a body that it is cut by the threads of a coarse net, the pieces passing through the meshes like jelly through a sieve; the decapod *Grimalditeuthis richardi* is so transparent that print may be read through its body.[20] The large vacuoles in the parenchyma of pelagic turbellarians of the genus *Haplodiscus* seem to be filled with jelly. The plankton fishes, *Crystallogobius* and *Aphia*, and the eel larvae, *Leptocephalus*, are also watery and transparent. Among the Salpae and Pyrosomae, the cellulose mantle is swollen with water. Invertebrate marine animals may take up water from their surroundings without injury since their body fluids are isotonic with sea water.

More effective than the addition of sea water is the storage of lighter materials, such as water of less salinity, fat, or even air. The fluid in the vacuoles of the extracapsular body of radiolarians, and the protoplasm of *Noctiluca*, have a lower specific gravity than sea water.[8, 33] The ctenophore *Beroë* is said to have a fluid of low specific gravity in the numerous vacuoles (of its cells), which may be emptied by muscular contraction at need.

The accumulation of fat is widely distributed among pelagic animals, and this lowers the general specific gravity. This is not uncommon even among pelagic Protozoa. Radiolaria contain oil drops in their intracapsular protoplasm, and the same is true of *Noctiluca*. More extensive accumulation of fat is found in pelagic crustaceans such as cladocerans and copepods (see table on p. 273). Numerous fat bodies are present in the mantle of *Planktomya* (which may be the larva of a mytilid). The selachians, and the cods (among bony fishes)

store food material in the form of fat in their livers. The eggs of many fishes are floated by the inclusion of large oil drops, as in numerous Clupeidae, mackerels, and flatfishes. Thick layers of fat enable the basking shark *Cetorhinus maximus* and the ocean sunfish *Mola mola* to sun themselves motionless on the surface of the sea. Similar accumulations of fat among warm-blooded marine animals, such as penguins, whales, and seals, serve also as insulation. The amount of fat varies with the season, and in non-polar regions it is usually true that there is more fat in the warmer season when the supporting power of the water is least.

The most effective means of all for reducing the excess of weight is the inclusion of air or other gases in the animal body. Among siphonophores, air sacs (pneumatophores) are present, which are filled with gas from a gas-producing gland. In *Velella,* which floats on the surface, branched air sacs are connected with the atmosphere and filled with air by rhythmic breathing motions. The cephalopods *Nautilus* and *Spirula* have a chambered shell with air in the chambers. The pelagic snail *Glaucus* (Fig. 53*a*) has intestinal gases that are supposed to play a similar part. An air sac is best developed among bony fishes, which usually have an air bladder whose gas content is under control, so that their weight may be exactly adjusted to that of the water displaced; thus their independence from the bottom is complete. The bony fishes are by far the most numerous of the vertebrate animals of the pelagial. One may say that the change from a littoral to a pelagic existence, where no place of rest is available, was made possible by the acquisition of an air bladder, for only the extremely powerful sharks and a few types of bony fishes without an air bladder are capable of the unceasing muscular exertion necessary to keep from sinking. The air bladder has also made the bony fishes more independent in the matter of body form, freeing them from the necessity of having flattened lower surfaces and large pectoral fins, so that they may be deep-bodied and even wedge-shaped ventrally, as the selachians never are.[17] Among the air-breathing vertebrates that have taken up a marine existence, such as sea turtles and certain snakes, and whales, sirenians, and seals, the lungs, in addition to their breathing function, serve the same purpose as does the air bladder of fishes.

These different means of reducing the density may occur in varied combinations, such as air chamber and jelly tissue in the siphonophores, and fat accumulation and air bladder in the moonfish. When an excess of density still is present, it must be overcome by increased

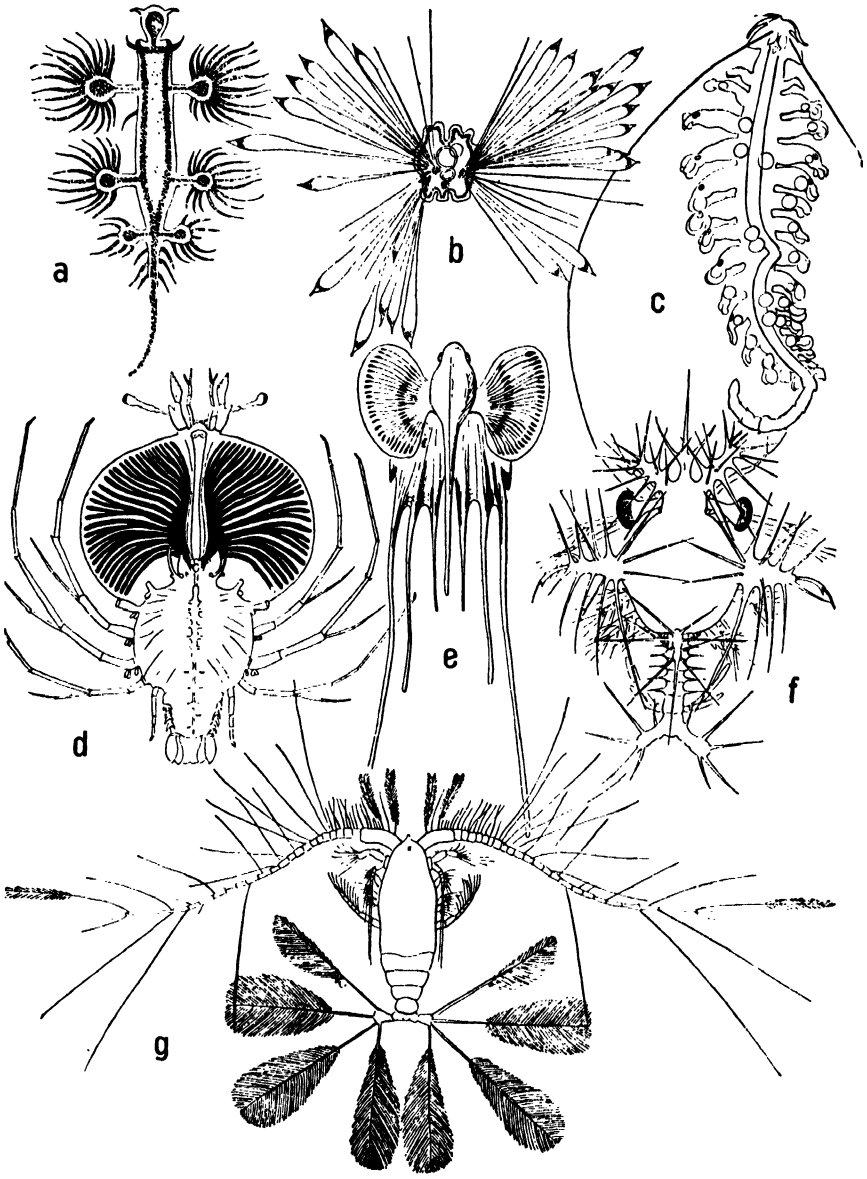


FIG. 53. Suspended or floating pelagic organisms with enlarged surfaces. *a*, *Glaucus atlanticus*, natural size; *b*, Maldanid larva (*"Mitraria müller"*), × 40; *c*, *Tomopteris euchaeta*, × 2½; *d*, *Phyllosoma* larva of *Palinurus*, slightly enlarged; *e*, Larva of *Lophius piscatorius*, somewhat enlarged; *f*, Larva of *Sergestes* (*Elaphocaris dohrni*) × 13; *g*, *Calocalanus pavo*, × 18. After Regne Animale, *a*; *Haecker*, *b*; Chun, *c*; Spence Bate, *d*, *f*; Agassiz, *e*; and Giesbrecht, *g*.

friction with the water and resistance offered by the surface. The amount of resistance in the water, aside from friction, depends on the sum of the distances to which the water particles are forced when the body is moved. The amount of such displacement is increased with increase in size in the horizontal plane of a sinking body. A sheet of any material will sink more slowly if laid in the water on its side than if placed edgewise. One may speak in this sense of the form resistance of a body, which increases with the increase of the horizontal surface. Such resistance to sinking may be actively increased by swimming.

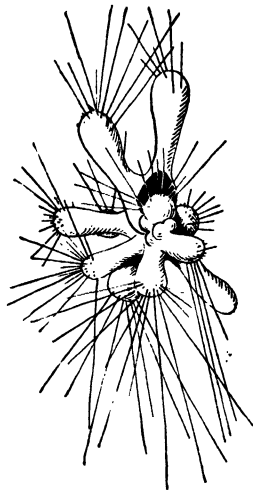


FIG. 54. *Hastigerina digitata*, a pelagic foraminifer. After Rhumbler.

The retardation of sinking by changes in form is a widespread phenomenon among pelagic invertebrates. It is possible to equalize only a small excess of weight in this manner and it is effective only for small animals, which have an intrinsically high surface-weight proportion. The simplest means of enlarging the ventral surface lies in the flattening of the body. *Leptodiscus*, the light-producing flagellate, most Hydromedusae and Scyphomedusae, the turbellarian *Haplodiscus*, the pelagic nemertines, the crustacean larva *Phyllosoma* (Fig. 53*d*), the copepod *Sapphirina*, and many others are thus flattened. Lateral projections, which may be branched in addition, often occur. Such apparatus is most developed among the Radiolaria and Foraminifera, in which the long pseudopodia are supplemented by spines of the test. Such "suspensory bristles" are notable in *Hastigerina* (Fig. 54) and *Globigerina* (Fig. 55). This means of support is less developed among the Metazoa; some of the most conspicuous examples, including annelid worms, their larvae, mollusks, crustaceans, and a fish larva, are shown in Fig. 53. Young transformed starfishes and sea urchins (Fig. 56) have relatively long tentacles and ambulacral feet, which make a free-floating life possible until their increase in weight outruns their enlargement of surface. In general this increase of surface by the development of projections is not widespread; it appears only among small and very small animals. The great majority of pelagic animals exist without this means of suspension.

Water resistance, produced by active swimming, is the most widespread means of preventing sinking. Such motion may consist

largely of force exerted opposite the direction of gravitational pull, as in the pteropods, or may be a small component of lateral motion,

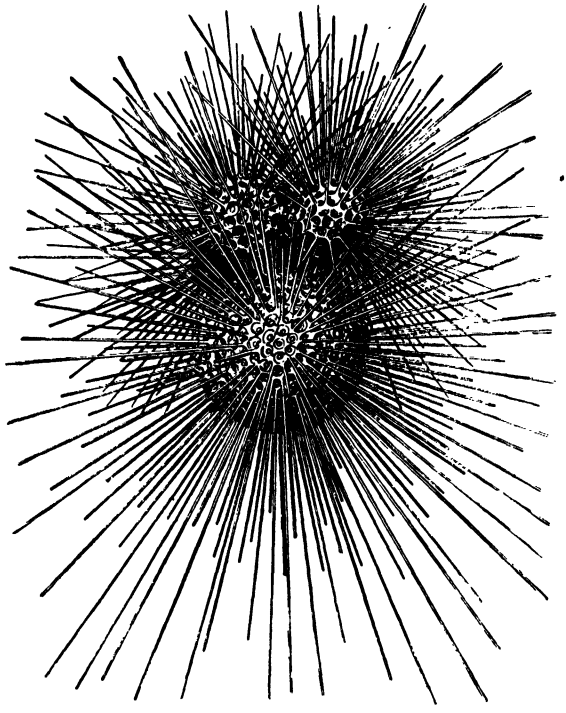


FIG. 55. *Globigerina bulloides*, a pelagic foraminifer. After Ziegler.

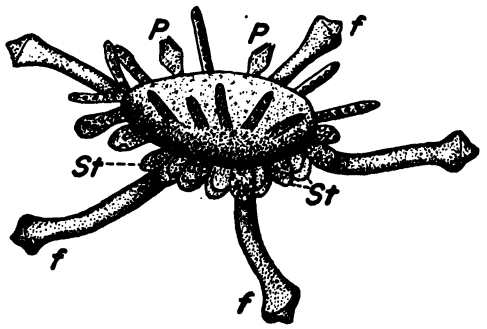


FIG. 56. Juvenile sea urchin *Arbacia pustulosa: f*, ambulacral feet; *p*, pedicellaria; *st*, spines. After Korschelt and Heider.

as in the sharks. The effectiveness of the reaction is measured by the size of the body and its rapidity of motion. The water resistance of a body is proportional to its projection on a plane at right angles

to the line of motion, and to the square of the speed with which the body moves.

Cilia and lashing hairs, on account of their small surface, are not

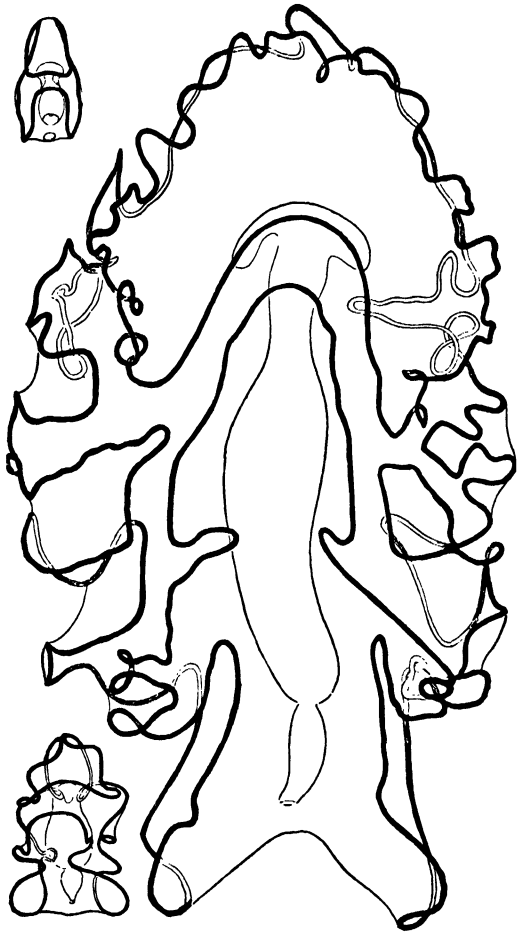


FIG. 57. Auricularia larvae with different lengths of larval life; the largest has the relatively longest ciliary band. × about 35 times. After Mortensen.

very effective and are found mainly among protozoans, among very small Metazoa, and among these especially in larval stages. Great numbers of cilia are required to support even small animals. In the almost microscopically small larvae of echinoderms, *Balanoglossus*, worms, etc., they are arranged in narrow rings or bands. When the larvae increase in size, further support can be gained only by rela-

tively great increase in the length of the bands of cilia. The larvae of echinoderms rarely reach any considerable size during their free-swimming stage; but in those that do, the bipinnarians and auricularians, reaching a length of about 5 mm., the ciliary bands are folded and bent in a remarkable way (Fig. 57). A more favorable arrangement is the distribution of the cilia over the whole body surface, but even so this device is suitable only for small animals. The disk-shaped pelagic turbellarian *Haplodiscus* has a diameter of only 1 mm., and another turbellarian in the North Sea, *Alaurina,* forms chains 0.9 to 2.5 mm. in length. Ctenophores, whose eight rows of swimming plates are composed of fused cilia of relatively great length, are forms with extreme development of gelatinous tissue.

Among larger pelagic animals, water resistance is uniformly produced by muscular work. The means used vary. A widespread method consists in the production of a stream of water, by the constriction of a tube or bell-shaped hollow body, the reaction from the ejected water driving the animal forward and upward. The bell shape prevails among the Hydromedusae and Scyphomedusae and in the swimming bells of siphonophores. It has been convergently developed among pelagic cephalopods by web-like membranes connecting the arms (*Amphitretus, Cirrothauma,* Fig. 58), and among pelagic holothurians by similar webs between the tentacles (Fig. 59). The contractile bodies of salpas and pyrosomas are more or less tube-shaped. This form of locomotion is highly developed by the squids, which outswim and catch fishes on which they feed.

Oar-shaped jointed limbs are a frequent form of swimming organ. Among pelagic annelids the parapodia are employed for this purpose (Alciopidae, *Tomopteris,* Fig. 53*c*). In pelagic crustaceans, a varying number of limbs are used; in small forms like the copepods (Fig. 60) and small larvae, the second pair of antennae fulfills this function and may be much enlarged; among schizopods and numerous pelagic amphipods, numerous limbs may be employed for swimming. The pelagic decapod crustaceans are distinguished from their benthic relatives by the broadening of two or four pairs of posterior thoracic limbs as, respectively, in *Sergestes* and *Polybius.*[16] Among the pteropods two parts of the foot are transformed into oars. Sea turtles and penguins row with their forelimbs.

Undulation of the body is the most common mode of swimming. Pelagic cephalopods and rays swim by the undulation of lateral fins, to which, in the former, is added the darting produced by sudden expulsion of water by the muscular mantle. In the heteropod snails

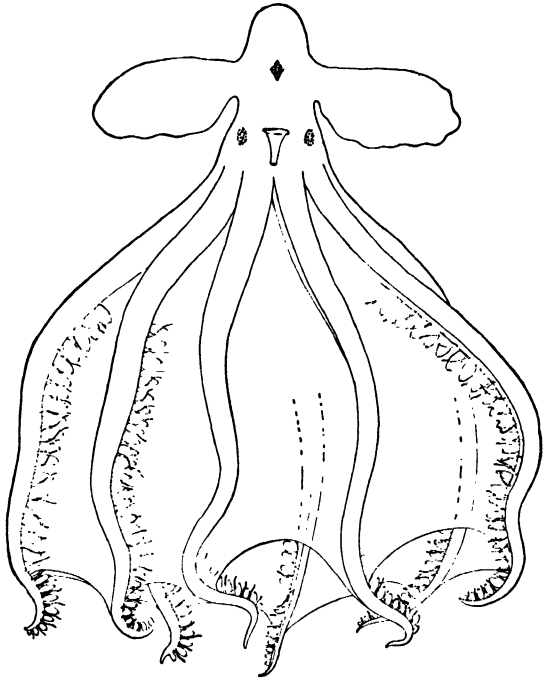


FIG. 58. *Cirrothauma murrayi*, a pelagic octopod. After Chun.

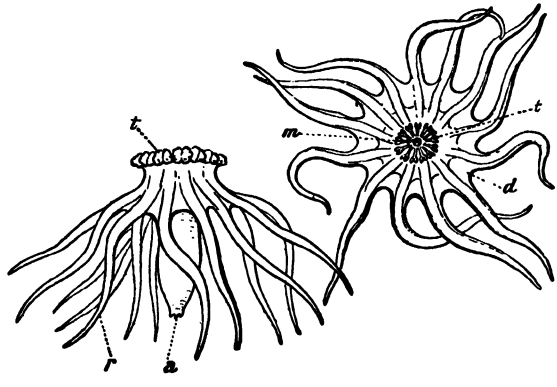


FIG. 59. *Pelagothuria natans*, a pelagic holothurian. *m*, mouth; *a*, anus; *t*, tentacle; *r*, ampullae; *d*, swimming membrane between the ampullae. After Ludwig.

a median ventral fin is undulated. In most fishes, whales, and seals the whole body or the posterior part of the body undulates. The resistance to the waves produced by these motions drives the fish forward, and the component acting on the lower surface neutralizes the force of gravity. Thus a special type of body form in large pelagic sharks, bony fishes without air bladders, porpoises, and seals, almost round with a slight ventral flattening, has been attained by convergence in these several groups.

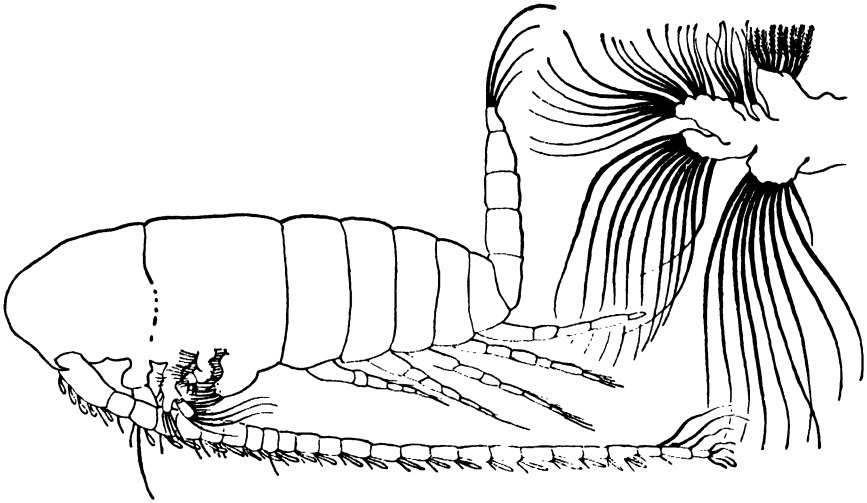


FIG. 60. The copepod *Calanus finmarchicus*, × 26. The antenna used as an oar at the left, the maxilla (greatly enlarged), with its bristles, at the right. After St. Brady.

Active motion is variously combined with other means of suspension. Swimming, as distinguished from motions that merely produce suspension, may be defined as motion sufficiently active to render the animal independent of the oceanic currents. Such swimming is never produced by cilia or by vibratory motion, but is always dependent on more typical muscular exertion. This increases proportionately with the size of the animal and is accordingly greater, as a rule, in larger animals. Small animals less than 1 cm. long (and hence all microscopic animals) are incapable of such swimming.

The effectiveness of muscular motion is such that other arrangements for suspension are rarely combined with it. The large pelagic rays (*Mobula* and *Manta*), reaching a breadth of 7 m., with their depressed bodies, perhaps form an exception. For the rest, among small free-swimming animals the suspensory processes are placed in

the plane of motion (for example, in *Calocalanus,* Fig. 53g); thus they do not obstruct the motion and combine the function of aiding suspension with that of a rudder.[43,44] In the swiftest of the swimmers, such as the blue shark and the mackerels, every unevenness of the body is removed, and in the mackerels the body fins fold into grooves when not in use.

Plankton and nekton

Pelagic animals may be grouped according to their ability to swim freely, independent of oceanic currents, or according to their dependence on the latter; the free-swimming forms are called nekton as distinguished from the passively floating or suspended plankton. It is evident that no sharp division between these groups exists, but they merit discussion as including assemblages of animals with much in common. Some modern students use the term *seston* to apply to all swimming or floating bodies in the water, alive or dead; the nonliving seston is then called *tripton;* the living seston associated intimately with the surface film is called *neuston.*

Plankton includes all those animals and plants that drift aimlessly, i.e., those whose independent movements are insignificant in comparison with the movement of the water. Most of them are small or microscopic, and all microscopic animals that are pelagic belong to the plankton. The converse is not true, as many larger animals with muscular movement are also included in this category, such as the jellyfish *Cyanea arctica,* which reaches a diameter of 2 m. The giant shark *Cetorhinus maximus* is so very dependent on the Atlantic currents that it might almost be included with the plankton. In quiet water even small animals may be capable of directed movements, especially vertical ones, such as a nocturnal rise to the surface. A practical definition of plankton includes those forms that are unable to escape the ordinary plankton net by their own movements. Plankton animals may be assorted according to size as nannoplankton, microplankton, mesoplankton, and megaloplankton. The minute nannoplankton escaped observation until it was discovered in the feeding apparatus of the appendiculates. It is now secured by filtration or centrifuging. The definition of these several sizes of plankton is arbitrary.

Nekton is composed of free-swimming forms, which are mainly independent of wind and current. Complete independence of currents is reached only by certain fishes, some cephalopods, the marine reptiles, and the homoiothermal marine birds and mammals. Both plank-

ton and nekton include predaceous as well as herbivorous forms and cannot be distinguished according to their food habits.

The viscosity of water, which is of such great importance in reducing the rate of sinking, is not uniform. It depends chiefly on the temperature, less markedly on the salinity of the water. Other conditions being equal, it is only half at 25° what it is at 0°. The conditions for suspension of organisms are consequently more favorable in the cold waters of the polar regions and of the oceanic depths than in the warm tropical waters.

The radiolarians of the family Challengeridae (Fig. 61) are assorted vertically according to size, the smaller ones in the warmer surface waters, the larger ones below. Thus the average sizes in millimeters of the following forms may be grouped according to depth: [15]

50–400 m.		400–1500 m.		1500–5000 m.	
Challengeria xiphodon	0.11 mm.	*Ch. bethelli*	0.215 mm.	*Pharyngella gastrula*	0.33 mm.
" *swirei*	0.11 "	" *slogetti*	0.25 "	*Ch. thomsoni*	0.35 "
" *harstoni*	0.16 "	" *tizardi*	0.28 "	" *naresi*	0.58 "

The same is true of other radiolarians, for example, *Aulacantha scolymantha.* This seems like a mechanical sifting, a sinking of the animals to the depths at which they can maintain themselves. Numerous Metazoa exhibit the same phenomenon. The arrowworm *Sagitta hexaptera,* for example, which inhabits the lighted pelagial, is larger and more mature the deeper the source of specimens.[35] The little fish *Cyclothone microdon* increases in size with depth, specimens from 500-m. depth averaging 30 mm., from 1500-m., 60 mm.; and specimens from the same depth in the southern part of the North Atlantic are much smaller than the northern ones. There is similar sifting by size in the shrimp *Acanthephyra.* Among the pelagic cephalopods the smaller forms are found only at the surface, while the larger inhabit the oceanic depths. Pelagic dinoflagellates like *Ceratium* form longer processes in warm than in cold water. Such feather-like processes as are found in *Calocalanus* (Fig. 53g) occur in warm-water copepods but not in polar forms. Ability to float seems to be the governing factor in the composition of the surface fauna of the tropical and subtropical Atlantic, with its siphonophores, medusae, salpas, and pyrosomas. Among larger fishes, only specialized forms like *Mola* with its thick layer of fat, or active swimmers, like the sharks, are found at the surface; other fishes are represented mostly by juveniles. Such mechanical relations with depth throw light upon the occurrence of sur-

face forms in the Norwegian seas, such as the pteropod *Clione*, the medusa *Aglantha*, and the copepod *Calanus*, which occur also at

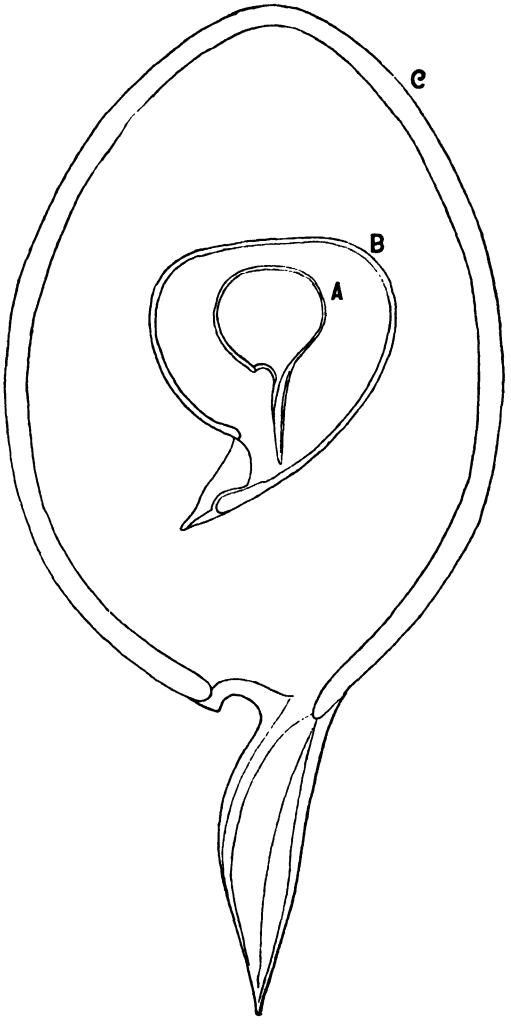


FIG. 61. Various sizes of *Challengeria* species according to the depths at which they occur: *A*, *Challengeria xiphodon*; *B*, *Ch. slogetti*; *C*, *Ch. naresi*. × 140. After Haecker.

depths of 750 to 1000 m. in the warmer part of the Atlantic, where the viscosity is the same as that of the surface waters near Norway.[30]

The variation of viscosity with temperature may bear upon the fact that many pelagic animals are smaller in warm seas than in cold.

This may be referable to direct action of the lower temperature, as it applies also to the benthic animals, but it involves nonetheless a coincident adaptation on the part of the pelagic fauna. The fishes *Cyclothone microdon* and *C. signata* in the vicinity of the Canary Islands are notably smaller than at the same depths in the North Atlantic,[30] and the arrowworm *Sagitta bipunctata* reaches a length of 12 mm. in the Mediterranean and of 44 mm. in the Arctic. This matter evidently requires consideration in connection with the size relations discussed in Chapter 10.

Special means of securing food are required by pelagic animals, since their food differs in a number of ways from that of benthic types. There are no great accumulations of detritus such as occur on the sea bottom, and there are none of the many-celled algae and vascular plants. The basic food supply is the plant portion of the plankton, that endless number of single-celled algae, such as are found in the nannoplankton of the ocean. Lohmann found, in the Bay of Kiel, that for every metazoan (such as an ephyra or *Sagitta*) there were 1000 protozoan and 7000 protophytan cells, and these figures are low.[25] The devourers of these plankton algae are in part small animals, such as radiolarians, Foraminifera, copepods, etc., but they also include larger ones that have solved the problem of securing large numbers of the small forms. The larger plankton animals, small Metazoa up to the size of pteropods, form the food of the larger pelagic animals. In order to secure their food, which is minute compared with themselves, the plankton feeders require special apparatus, convergently evolved from different origins into similar structures with like functions.

Lohmann [24] divides plankton feeders into three groups: those that feed by means of tentacles, those that produce a current of water, and those that hunt actively. The tentacle feeders are the most primitive type; they feel about for their food while otherwise remaining at rest. Radiolaria and Foraminifera do this with their radiating pseudopods, which paralyze their minute food by a poison. The long tentacles of siphonophores (up to 30 m.) serve the same purpose. The cephalopod *Chiroteuthis* has its sucking disks evolved into sticky threads, from which the food is removed by the specially adapted lips.[21]

A most singular means of securing food is found in animals that strain out the living forms from a stream of water that they produce themselves. Self-produced nets or screens perform this function. The bristles of the mouth parts of Cladocera and copepods (Fig. 60), the

slime bands in the body cavities of salpas and pyrosomas, the remarkable apparatus of the appendiculates, built up out of jelly-threads (Fig. 62), the screen-like gill strainers of the plankton-eating fishes, such as the herring or the giant sharks, and the baleen of the toothless whales, all illustrate this means of food-getting. The effectiveness of this apparatus is shown by the fact already stated that a whole new world of minute plankton creatures, the nannoplankton, which had escaped the finest silk nets, was discovered by examination of the

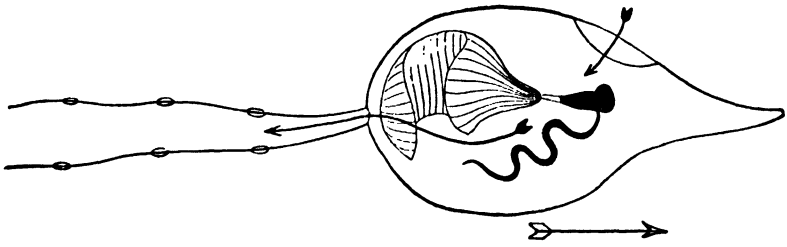


FIG. 62. The appendiculate *Oikopleura albicans* (black) in its house. To the left of the animal is the permanently outspread net. The black arrows show the direction of the currents of water produced by the undulation of the tail. The light arrow beneath points in the direction in which the animal moves. After Lohmann.

appendiculate sieve and by the presence in the stomach of a single herring of 60,895 small copepods.[20]

Predaceous animals, which hunt for their prey by active movement and find it by means of their sensory organs, do not present any structures peculiar to the pelagial.

Pelagic and benthic formations compared

The special adaptations required by the pelagial give its fauna a somewhat different composition from that of the benthal. The groups absent in the pelagial are the sponges, ascidians, brachiopods, and bryozoans. Large groups are represented by only a few specialized forms. There are a few pelagic actinians; echinoderms are represented by *Pelagothuria* and larval stages; and with the exception of the Chaetognatha, worms are few. Lamellibranchs are represented only by *Planktomya*, and snails only by a few opisthobranchiates and the specialized heteropods and pteropods. Radiolarians, medusae (with the exception of *Lucernaria*), siphonophores, most ctenophores, chaetognath worms, heteropods, pteropods, salpas, and appendiculates are all exclusively pelagic. The copepod crustaceans predominate, com-

posing 90% of the whole fauna, with schizopod, decapod, and hyperine forms in addition. Next come the pteropods, siphonophores, and chaetognath worms; cephalopods and fishes are also an important element.

Distribution of pelagic animals

The free suspension of pelagic animals favors the wide distribution, not only of active swimmers like tuna, bonito, and mackerel, which occur in all the oceans, but also of many with poor powers of swimming, such as the deep-sea fish *Ceratias couesii*, and others. Most of the important genera of sharks are found in both the Atlantic and Indo-Pacific. Many planktonic forms have the same distribution. The Acanthometridae (Radiolaria) are astonishingly similar in the warmer parts of the oceans of both hemispheres.[32] The siphonophores of the two oceans are often distinguished only by trivial characters; pelagic turbellarians are represented in both by the same species. The same is true of most species of the pteropod genera *Hyalaea* and *Cleodora*, and of the heteropods *Atlanta peroni* and *Oxygyrus keraudreni*. No pelagic forms appear to have been discovered in one ocean that are not represented by parallel forms in the other.

The pelagic life of the larvae of many benthic animals is of great importance to their distribution. The length of larval life becomes a governing factor in the extent of the distribution of such forms, varying from 20 to 60 days in the echinoderms to 4 to 7 days in brachiopods, sea anemones, corals, annelids, and snails. Hedley has shown that in Polynesia the gastropod genera *Mitra*, *Conus*, and *Cypraea*, which have a pelagic trochophore larva, are more widely spread than *Melo* and *Voluta*, from whose large-yolked eggs the young snails appear in a benthic juvenile stage.

Variations in environmental conditions are less frequent and less abrupt in the open sea than in the shore waters or on land. Nevertheless, the conditions are not uniform, and pelagic life is accordingly not uniformly distributed. The short-lived and rapidly multiplying nannoplankton affords the best index to the existing conditions. Its distribution is neither fortuitous nor uniform, but ecologic, i.e., dependent on environmental conditions. Each smallest portion of the ocean has at all times a population of nannoplankton and microplankton that is an exact reflection of the environmental conditions.[25] Long-lived animals can exist for periods of time in unfavorable localities, as in polar seas, drawing upon their stored supplies. But as these are also ultimately dependent on the plant plankton, the animals are abundant

where the plankton is at least periodically rich. The extremes of density of life in the pelagial are shown in the poorest catch of plankton, 763 organisms per liter in the tropical Atlantic, as compared with a maximum of 76,915 in a liter in the cold water of the North Atlantic.

The study of pelagic distribution on this basis has just begun. Lohmann [26] divided the pelagial into rich and poor sections according to the existence of more or less than 1000 nannoplanktonic organisms per liter. In the rich areas the distribution is not uniform, as numerous distinct aggregations of especial density of life appear. The rich domain of pelagic plankton is the upper 100 m. of the sea water, since the plant element in it is dependent on light, and the impoverishment of the plankton begins below this level. The basis of study of plankton distribution in this direction lies in the construction of lines of equal plankton development or "isoplankts," especially for equal amounts of the plankton as a whole and for certain outstanding species.[25]

Among longer-lived animals, there are vast aggregations, as in the schools of herring, cod, mackerel, and other fishes wandering to feeding grounds or breeding places. Such aggregations also appear in less active forms, such as the numbers of *Salpa fusiformis* that are developed annually in July and August north of the Hebrides, and the more accidental accumulations on the borders of currents and in bays. The former have been distinguished by Apstein as "production," the latter as "swarm" aggregations. The great numbers of the northern copepod *Calanus finmarchicus* (Fig. 60) may color wide stretches of the sea brown. The siphonophore *Velella* forms swarms of enormous extent. Such an accumulation observed by the German Plankton expedition in the Atlantic extended for 300 km. Salpas and pyrosomas, ctenophores and siphonophores, and even globigerinas are found in great masses, especially in places where currents rich in plankton meet.[42]

So-called "animal streams" may appear in both open sea and near coasts, sometimes with a good deal of regularity, in which animals of varied kinds are so abundant that one can dip a soup of plankton. These streams may be distinguished by a smooth oily appearance of the surface and may extend for more than a kilometer, with a breadth of 5 to 10 m. Their appearance may be dependent on wind and current; they appear in the harbor of Messina, for example, twice daily.[1, 14]

The composition of the plankton varies with time as well as with locality. It is usually composed of a great number of different animals, but at a given place and special time a single species may flour-

ish to such an extent that it predominates, and one speaks of monotonous plankton. This is especially a phenomenon of shallow seas; in the North Sea a pteropod or copepod, and in warm seas a salpa, may predominate. Such plankton may be dominated either by mature or by larval animals. Seasonal variation in composition of the plankton is important in temperate and cold seas. The maxima and minima of different organisms depend in different ways on the temperature and may alternate in the single elements so that a varied plankton

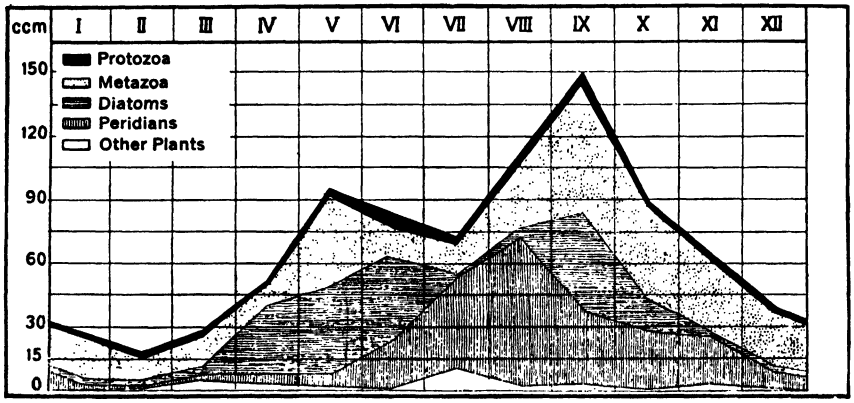


FIG. 63. Curves of volume of various groups of organisms in the total plankton at Laboe, in the Bay of Kiel, during the year. After Lohmann.

may have very different compositions at different seasons (Fig. 63). Changes may take place too rapidly to permit comparative studies by one ocean-going vessel. Perhaps, in time, such plankton comparisons in distant regions may be made by cooperative effort or by the use of adequately equipped airplane expeditions.

There is even a difference in the composition of the surface plankton between day and night. At night numerous deep-sea forms come to the surface, even from great depths, to return before daybreak. These are followed by predatory forms that live on them. Schools of herring come to the surface at night, but remain at considerable depths during the day.

Important and readily understandable differences exist between the pelagial of the deep sea and that of shallow seas; one may distinguish between these as oceanic and neritic pelagial. The oceanic pelagic life is made up of animals independent of the bottom throughout their development; these animals are called holopelagic or holoplanktonic. To this group belong all radiolarians, many Foraminifera,

the medusae without a sessile stage (many Hydromedusae but few Scyphomedusae, among the latter *Pelagia noctiluca*), most siphonophores and ctenophores, the chaetognath worms, copepods and hyperines among crustaceans, heteropods and pteropods, appendiculates, salpas, pyrosomas, some sharks, a great number of bony fishes with air bladders, and some without, and finally the Cetacea.

The neritic pelagial includes, in addition to holopelagic forms, animals dependent on the bottom during part of their existence; to these the terms hemipelagic or meroplanktonic are applied. To this group belong all the medusae with alternating generations, the larvae of numberless benthonic animals, and the floating eggs of many fishes. The water fleas of the genera *Podon* and *Evadne,* whose eggs sink to the bottom, and the ostracod *Philomedes brenda,* which comes to the surface in May to breed, are hemipelagic. Hemipelagic life includes many cephalopods (*Sepiola,* for example), most sharks and rays, and many bony fishes, even some active swimmers like *Julis* and *Coris,* which rest on the bottom at night. Finally, the neritic pelagial includes the sea turtles and seals, and especially the walrus, which feeds on benthic animals. The time as well as the season of dependence on the bottom vary with the different animals, so that periodic changes in the composition of the neritic pelagial are much more pronounced than in the oceanic.

The neritic pelagial is bounded in general by the 200-m. contour, and thus includes banks as well as coastal waters. This boundary is the obvious result of dependence on the bottom. The inhabitants of the neritic and oceanic pelagial are mixed at the boundary, and currents carry the neritic forms out and the oceanic ones in, generally to their destruction, although the eels are a marked exception. To what extent the holopelagic animals are destroyed by modified physical conditions, such as greater turbidity of the water, in the neritic area and to what extent they are destroyed by biotic competition is not known. Deep bays, fiords, lagoons of coral reefs, etc., operate like traps, in which large numbers of macroplankton, such as salpas and medusae, accumulate at certain seasons. In the spring of 1900, velellas, physalias, and ianthinas had been driven into the Bay of Naples in such numbers that they covered millions of square meters; all were stranded and destroyed by the beginning of May.[22] Both oceanic and neritic plankton suffer in storms and are driven ashore in great masses. Windrows of dead velellas more than half a meter high and a kilometer in length appear on the coast of the Riviera after storms; in

August 1883, the beach at Kristineberg, Gulmar Fjord, Sweden, was covered with a thick glowing mass of the protozoan *Noctiluca,*[40] and in September 1893, the water at that place was a thick greenish broth of the holopelagic copepod *Anomalocera patersoni.*

Oceanic areas are poor in life, and neritic ones rich, the differences between them being greater than that between the polar and tropical Atlantic.[25] The reason lies in the better food supply provided by coastal plant detritus, and the richer fertilization of the water in the vicinity of land, which make possible a greater development of plant plankton. Plankton bacteria are much less abundant in the open ocean than near land. An increase in the animal population follows directly. It is the richer food supply that keeps various holopelagic animals, which have been able to adapt themselves to the change, in the neritic area. The number of appendiculates in a tenth of a cubic meter of water may reach 600 in shallow water, while it sinks to 13 in the water of the open ocean.[23]

The population of the pelagial is a well-characterized association almost entirely self-sustaining, and hence rather sharply distinguished from neighboring associations. The food chain here represented extends from the small single-celled algae to the larger fish and toothed whales, as already shown. The dependence of various elements of the food chain on a preceding one conditions the distribution of the larger forms. The mackerel fishery at the mouth of the English Channel depends on the amount of animal plankton, especially copepods; corresponding to variations in the plankton, it was good in 1905, poor in 1906, and good again in 1907.[10] The appearance of the herring on the north coast of Iceland is dependent on the summer development of the copepod *Calanus.* The complicated wanderings of the herring, aside from their breeding movements, are probably a response to the distribution of their food supply. The distribution of whales[70] is also dominated by food supply. The baleen whales are at home in the arctic and antarctic seas, where such an excess of plankton develops at certain seasons. The coastal waters, rich in plankton and small fishes, harbor the humpbacked whales *Megaptera.* In open, warm seas the plankton lies at a deeper level and is followed by large crustaceans and cephalopods. Giant squids, in turn, are found in the stomachs of the sperm whale *Physeter macrocephalus,* which is able to reach great depths (up to 750 m.).

Pelagic biotopes

Distinct biotopes within the great extent of the pelagial are only vaguely differentiated. Perhaps the most important differences are those between the oceanic currents, the eddying areas, and the great oceanic water masses.

Oceanic currents are obviously of primary importance in the distribution of pelagic animals, and many free-swimming forms are also influenced by them. The action of the currents differs according to their course. The current may return to its source, forming a closed circuit, or may come to an end. At the present time only the surface currents are well known, and the currents of the depths are only beginning to be studied with reference to their special faunae and effects on distribution.

A closed current returns its animals to the same position and environment. The distribution of the developmental stages of *Calanus finmarchicus* in the Norwegian Sea affords an example.[12] Great numbers of adult animals with eggs appear in spring in the diatom beds near the Shetland and Faeroes islands; carried away by flow of the Gulf Stream, the larvae emerging from these eggs gradually grow, while the adults die out; these then develop, farther north, into "juniors"; the current then returns from Jan Mayen, and the number of juniors lessens as that of adults increases; they apparently winter in deep water and re-enter the circuit at the Faeroes in spring, when the warm water of the Gulf Stream brings them to sexual maturity. These animals thus are carried through an extensive temperature range and must be to a considerable degree eurythermal. This is still more strikingly a requirement in the great closed circuits of the North and South Atlantic. The latter carries water from the neighborhood of the equator to the 48th parallel of south latitude, and organisms in it, especially in its peripheral portion, are exposed to a considerable range of temperature variation. The plankton in such a current requires several months and even years to return to its origin, about 1¼ years in the North Atlantic Current and 2¼ in the South Atlantic. Among short-lived plankton animals many generations, even hundreds of generations, are included in this period. Larger animals with longer periods of development are also exposed to considerable differences in successive generations. Lohmann [25] believes that regular differences, "cyclomorphoses," are connected with this cycle, corresponding in coccolithophorids, peridinians, and zoöflagellates with the seasonal forms in fresh-water animals. These relations require further investigation.

The conditions are quite different for organisms in the non-circulating currents, which either carry warm water into a cold region, as does the Gulf Stream or the Japan Current, or cold water into warm, like the Labrador Current or the Humboldt Current. The distance reached depends on the season, so that index forms of cold water such as *Oikopleura labradoriensis* and *Frittilaria borealis* reach the North Sea in spring, whereas in the summer warm-water forms such as *Physophora hydrostatica* are carried to the Lofoten Islands.[11] These foreigners suffer in the new environment, are unable to breed, and ultimately die. The contrasts are especially notable where a warm and cold current meet. On many banks there may be rapid and extensive displacements of water and consequent extreme fluctuations of temperature. Fewkes [13] noted a variation of 5.5° between two successive tides in Narrangansett Bay, caused by change in the relative predominance of the Gulf Stream and Labrador currents. There may be a great mortality in the plankton at such places, as on the New England Banks, the Agulhas Bank, the Spitzbergen Bank, or at the juncture of the Japan Current and the cold Ojashio on the east coast of Japan. Murray showed that the deposits of pelagic Foraminifera on the sea bottom were greatest where currents of different temperature met. Unusual westward extension of the cold waters over the warmer southern New England Banks in 1882 caused extensive destruction of the tilefish *Lopholatilus chamaeleonticeps,* which did not reappear for many years,[19] and the southern forms of plankton formerly abundant in that area on the border of the Gulf Stream also disappeared. Such massive destruction provides food for the bottom fauna, and, by its disintegration, for pelagic life wherever the resulting food substances are brought to the lighted zone.

The plankton carried along by the current becomes mixed with that from other sources, so that its composition changes with the progress of the current. Such currents have a characteristic fauna, varying with their origin, and are the better defined, the more the current differs in physical and chemical characters from the neighboring waters. The Guinea Current, which flows from west to east near the equator, is sharply distinguished from the adjacent north and south equatorial currents by vast amounts of the schizophycean *Trichodesmium* and by the appearance of neritic forms like the appendiculate *Oikopleura dioica* and the peridinean *Prosocentrum micans.* The life of the Labrador Current differs from that of the adjacent Gulf Stream. An index form for the Polar Current north of Iceland is the copepod *Calanus hyperboreus,* whereas in the Nor-

wegian Sea it is *C. finmarchicus.* A characteristic animal of the North Atlantic Current, rarely found outside its limits, is the basking shark *Cetorhinus maximus.*

Great numbers of animals may accumulate at the borders of currents, just as débris is carried into quiet bays by flood water in streams. A cloud of *Salpa flagellifera* 100 m. long has been encountered on the border of the Benguela Current,[3, 4, 30] and certain stations on the borders of great currents are especially rich in pteropods.[39] Beebe [5] describes masses of floating débris and associated wealth of life in a current rip some 200 miles southeast of Cocos Island in the eastern Pacific.

Algae provided with floating bladders are carried off by the oceanic currents and accumulate in the quiet eddies in great amounts. In the eddy of the North Atlantic Current the weed is *Sargassum bacciferum;* in the Indo-Pacific there are other species of *Sargassum,* and in the South Pacific *Macrocystis pyrifera.* The weed is carried back and forth by wind and may reenter the current for a second circuit. Such accumulations of seaweed form a special biotope in the pelagial.

A Sargassum community

The best-known example of such an eddy is the Atlantic Sargasso Sea.[2] The *Sargassum* comes from the coasts of the Caribbean islands and is carried away by the strong Florida Current, especially during the hurricane season. The masses of *Sargassum* are separated out to the right of the current, and continue to grow, without reproducing, until the bladder-like floats disintegrate and the weed sinks to the bottom. The weed affords a base for a curious nomadic fauna [41] of littoral origin, coming from the original home of the *Sargassum,* but enabled by it to live a littoral life on the high seas. Various adaptations are necessary, such as attachment to the weed, and, in the more free-swimming forms, provision for the young by nest-building, or care of the young. Some of these forms, such as the fish *Pterophryne histrio,* are common on the Gulf Coast. Others, like the small crab *Planes minutus,* are widespread on floating bodies of every kind; the shrimp *Leander tenuicornis* is also found in the Pacific. Others appear to have become specifically transformed (such as the shrimp *Latreutes ensiferus*) and are confined to the Sargasso Sea.[31] The change to this half pelagic existence being impossible for some of the original inhabitants of the seaweed, its fauna in the Sargasso Sea is poor in species. Besides a few species of algae there are 16 animals directly attached to the weed, 10 hydroids, 2 polychaetes, 2 bryozoans,

1 cirripede, 1 ascidian,[16a] and in addition to these such small forms as turbellarians, snails, and fishes live in or rest upon the weed. The number of individuals of the Sargasso animals is fairly large. These animals are wholly dependent on the weed and constitute a pseudobenthos (Fig. 64). The bryozoan *Membranipora* is abundant, as are the spiral calcareous tubes of the annelid *Spirorbis*. The most frequent hydroids are *Clytia* and *Laomedea*. A small sessile ascidian (*Diplosoma*) is present. The nudibranch *Scyllaea pelagica* creeps over the weed, and the weak-swimming crab *Planes minutus* uses it as a resting place. The Sargasso fish *Pterophryne* makes a nest among the "leaves" by cementing them together with mucus. The weed is yellowish brown, spotted with white by the *Membranipora* and *Spirorbis*. Many of the Sargasso animals are similarly white-spotted on a yellowish brown ground color; they may have remarkable weed-like appendages. This is especially true of the fishes (pipefish and sea horse, besides *Pterophryne*) and the nudibranch, as well as certain crustaceans.[30] The enemies against which this coloration may protect them are doubtless the sharp-sighted birds.[41]



FIG. 64. Floating piece of sargassum, covered with the hydroids *Aglaophenia* and *Clytia*, the bryozoan *Membranipora*, and the tube building worm *Spirorbis*. After Hentschel.

A number of unexplained faunal parallels exist between the fauna of this area and that of the Mediterranean, such as similar compositions of the nannoplankton, similar radiolarians, with *Lithoptera fenestrata* known only from these two regions; other species with sim-

ilar distribution include the annelid *Alciope contrainii,* and the copepod *Copilia mediterranea.*

For the rest, the Sargasso Sea is characterized by poverty of plankton. Its water is remarkably clear; the Secchi disk is visible to 66 m. depth as compared with 33 m. in the Mediterranean, 20 m. in the North Sea, and 13 m. in the Baltic. Among the few abundant forms are the water flea *Evadne spinifera* and the larvae of the forms living on the weed. The high temperature of the water at considerable depths is a notable characteristic. At 200 m. the temperature is 18°; at 400 m., 16°—about 4° higher than in corresponding depths in the adjacent waters. This is explained by the fact that on account of its greater density surface water is here being carried down to the oceanic depths, compensating in part for the upwelling currents on leeward coasts, and this also explains the poverty of life in general in the Sargasso Sea (Chapter 11).

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14. *The Abyssal Benthic and Pelagic Communities of the Sea*

THE DEPTH OF PENETRATION OF LIGHT INTO SEA WATER HAS BEEN DISCUSSED previously (p. 185). It is important to note that it is the threshold values for optic sensation and for plant assimilation that are important for animal distribution rather than the minute amounts of light present at great depths.[16] The lighted stratum at a given locality varies in depth diurnally and annually and also varies notably with the latitude for different localities. Any sharp delimitation is made still more impossible by the varying threshold values for different animals and plants. The lighted stratum is commonly divided into a euphotic stage (0–80 m.) and a dysphotic stage (80–600 m.). It does not seem practical to attempt a further subdivision of the lightless lower stratum, in which even the great increase in pressure seems to have little effect on distribution.

The penetration of light directly governs the presence of plants. In both the benthal and the pelagial they are principally developed in the upper stage of the lighted stratum, and extend to greater depths in the tropical than in the polar oceans.

Lohmann's figures[24] for nannoplankton, primarily composed of plants, are as follows:

Average Numbers of Single Organisms per Liter

	Depth				
	0 m.	50 m.	100 m.	200 m.	400 m.
(*a*) In cool water	21,601	6,245	2,039	317	140
Ratio	100	29	9.5	1.5	0.5
(*b*) In warm water	2,486	2,335	1,059	193	46
Ratio	100	94	42	8	2
Ratio (*a*) to (*b*):	8.8	2.6	1.9	1.6	3.0

Greater depths are reached only by the protected spores and dead remains of plants. A great number of animals directly dependent on living chlorophyll-bearing plants for their food are thus confined to the euphotic stage.

The amount of water in the abyssal stratum exceeds that in the lighted one. Of the total surface of the oceans the following percentages correspond to various depths:

	15.59%	19.34%	58.42%	6.5%
Depths of	0–1820 m.	1820–3640 m.	3640–5460 m.	5460–7280 m.

The whole region below, say, 400 m. exhibits a much greater uniformity of environment than the much smaller lighted stratum—absence of sunlight, constant low temperature, decreasing with depth, and almost complete absence of motion; the subantarctic intermediate water at depths of 1000 to 2000 m. moves north near Bermuda at the slow rate of 400 to 500 m. per day.[8] The animal life of this vast area, however, is by no means uniform, but divides into pelagic and benthic in the same way as the lighted stratum. Nevertheless, a number of special characters are common to abyssal animals of both divisions.

Both number of specimens and number of species regularly decrease with depth, in the benthal as well as in the pelagial; this is clearly shown in the total collection of the *Challenger* expedition.[25] More species of animals were secured in the uppermost 180 m. than in the rest of the ocean together (see table, p. 32). The vertical net hauls of the *Michael Sars* produced 10 fishes and 11 shrimps from 4500 m. to 1500 m. (i.e., in a vertical distance of 3000 m.); in contrast, in the 900 m. from 1350 to 450 m., 44 fishes and 35 shrimps were secured. The Foraminifera collected by the *Gazelle* [12] were as follows:

Depth in meters	0–100	100–500	500–1000	1000–2000
Number of species	138	352	132	147
Depth in meters	2000–3000	3000–4000	4000–5000	5000–6000
Number of species	53	79	38	19

The great depths of more than 4500 m. are poor in life, and the most successful dredge-hauls secure only a few specimens. Beebe's [3] direct observations down to 924 m. indicate that there is a greater amount of fish and large invertebrate life at this depth than is demonstrated

by net catches. His findings, however, do not alter the conclusions just given.

Animals are frequently not confined to any given depth, in which case they may be referred to as eurybathic as contrasted with stenobathic forms. Thus of 20 chaetopod worms [13] that descend below 1800 m., 12 also occur in the upper 180 m. *Echinocardium australe* ranges from 0 to 4900 m.; the bivalve mollusk *Scrobicularia longicallus* ranges from 36 to 4400 m.; the snail *Natica groenlandica,* from 4 to 2300 m.; and the shrimp *Gennadas parvus,* from 600 to 5600 m. Examples of stenobathic forms, aside from purely littoral or purely surface animals, are few. The ascidians *Caesira eugyroides* from 450 to 540 m., *Pyrosoma elongatum* between 750 and 1500 m., and the fish *Argyropelecus hemigymnus* from 150 to 500 m., may be mentioned.

The abyssal benthic community

The sunless benthal exhibits different habitats corresponding to the different biotopes of the littoral, principally based on differences in the substratum. Rock bottom is present in deep water only at very isolated places where special conditions cause a current at depths of more than 400 m. (see p. 192). With these exceptions the bottom of the sea is covered with deposited materials, of varied origin and composition. Murray distinguishes terrigenous and pelagic deposits, the former derived from land areas and made up of decomposed rock, principally quartz sand. Such materials are in general deposited near land, but they may occasionally be carried to great distances by icebergs, though not in sufficient quantity to produce a uniform deposit. The coarser deposits are laid down closer to the land, and abyssal terrigenous deposits consist only of the finest materials. Even the largest rivers carry little of such material beyond the border of the continental shelf at a depth of 200 m.

The sea-bottom deposits

Deposits beneath the open ocean contrast with terrigenous ones in that many are composed of the calcareous or siliceous skeletons of pelagic organisms; their nature varies with locality and with depth. The various types of bottom deposits intergrade with one another; those based on marine organisms do not predominate in the continental shelf. Deposits of terrigenous origin are built up with comparative rapidity and tend to be bluish, blackish, greenish, or gray in color. Pelagic deposits are built up more slowly and are red, brown, yellow,

or white.[33] Murray distinguishes pteropod ooze and *Globigerina* ooze as calcareous, and diatomaceous and radiolarian ooze as siliceous. The calcareous deposits are developed especially in subtropical and tropical regions, where lime deposition by animals is facilitated. The siliceous deposits appear in polar regions and in regions where an abundant influx of argillaceous material supplies the plankton with silica, as in the East Indies. At very great depths the pressure prevents the deposition of either lime or silica, which are redissolved, and the only deposit is a red clay, the product of the decomposition of volcanic materials. Pteropod ooze is found in relatively shallow water and relatively small areas. *Globigerina* ooze is widespread, covering 29.2% of the ocean bottom (105,000,000 sq. km.), and is second only to red clay in extent. It prevails especially in the North Atlantic, broken only by isolated areas of red clay, which is the typical deposit of the Pacific.

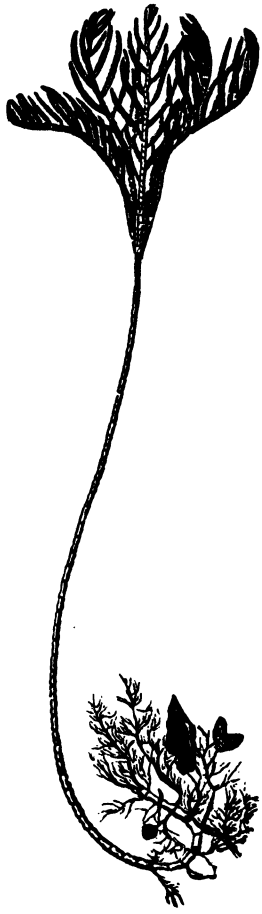


FIG. 65. *Rhizocrinus lofotensis*, a stalked crinoid of the deep sea. After Boas.

Globigerina ooze, on account of its lime content, is especially favorable to the development of animal life. At certain of the *Challenger's* stations in the Indian Ocean, where diatom skeletons composed the principal deposit, the higher animals contained only small amounts of lime in their shells. Thus among the echinoderms there are some very thin-shelled and irregular sea urchins and an excess of holothurians.[35] Life on the red clay is everywhere poorly developed, consisting of shell-less holothurians and worms. This fact may be in part due to the great depths in which the clay is found.

The terrigenous deposits vary in nature. In the East Indian waters, where such deposits are abundant, they may have a rich fauna. On the contrary, Chun reports that the river mud of the Gulf of Guinea is poor in animal life. Single groups may thrive on a special type of bottom. The glass sponges (Hexactinellidae) [29] with their siliceous skeleton do best on siliceous deposits, diatomaceous

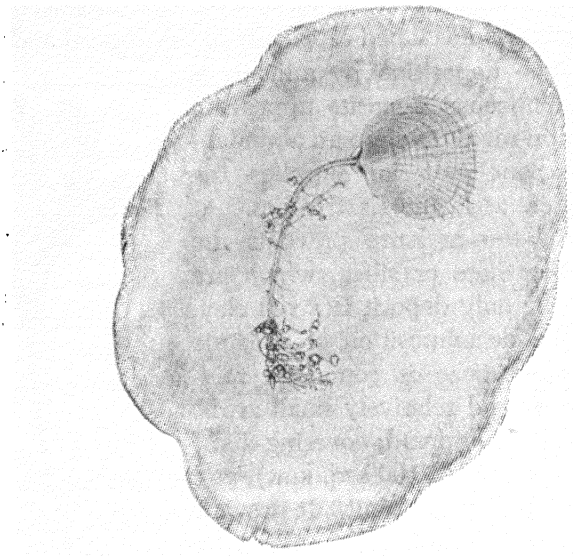


FIG. 66. *Chlidonophora chuni,* a long stalked brachiopod from the deep sea. After Blochmann.

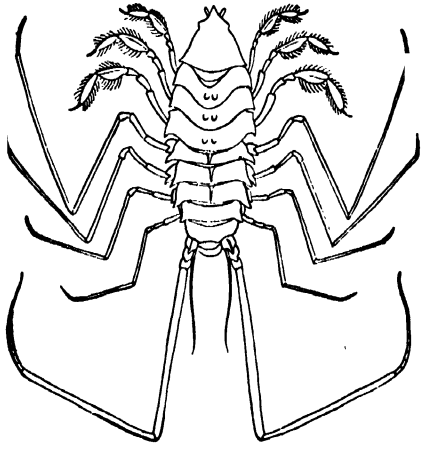


FIG. 67. Deep-sea isopod *Eurycope novae-zelandiae* from 2000-m. depth, on blue ooze. After Beddard.

ooze ranking first, radiolarian ooze next, and blue, deep-sea ooze, third; the last is a quartzitic terrigenous deposit.

Deep-sea ooze may be compared in appearance and consistency to butter in summer. Animals living on it require some means of support. An enlargement of surface, and, in animals with legs, a distribution of the weight to widely separated points, are associated adaptations. Thus flattened forms such as *Sperosoma grimaldi* are found among abyssal sea urchins. Holothurians have a specially broadened sole.

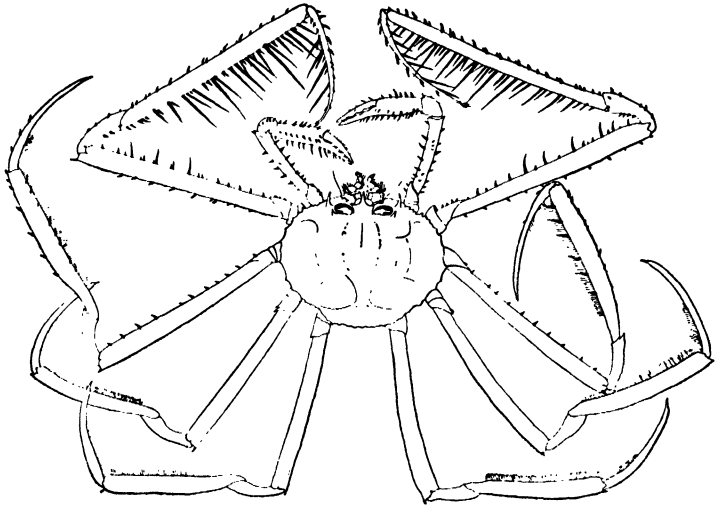


FIG. 68. Deep-sea crab *Platymaia wyville-thomsoni* from 275–800 m., one-third natural size. After Doflein.

Almost all deep-sea sponges are stalked or provided at the base with brushes or collars of spines.[35] The root-like growths at the base of the stems of stalked forms serve the same purpose, as in the hydroid polyp *Branchiocerianthus*, horn corals such as *Chrysogorgia*, and certain crinoids (Fig. 65) and brachiopods (Fig. 66). As compared with their relatives elsewhere, crustaceans living on the ooze usually have very long limbs, the terminal joints of which are expanded by hairs to increase their supporting surface (Figs. 67–68).

The abyssal pelagic community

The upper limit of the sunless pelagial varies from 200 to 600 m. in depth according to the latitude. No sharp faunal division at this point is possible, especially as many of the inhabitants of the abyssal waters rise to the surface at night, while others undergo their develop-

ment at the surface. There are forms that remain permanently in the abyssal waters; thus whereas 90% of the fish larvae and juvenile fishes collected by the *Michael Sars* in the Atlantic were caught in depths of 0–150 m., *Alepocephalus* appears to develop entirely below the lighted level. It is unusual for a surface animal to develop in the depths. The siphonophore *Velella,* whose larvae are taken at depths of 1000 m., is such an exception.

Nocturnal net hauls on the surface frequently obtain fishes with every mark of the inhabitant of abyssal waters. In the herring fishery, the bottom trawl is used by day and surface nets at night. Cod caught on hooks at depths of 360 m. by day feed on cephalopods (*Ommastrephes*) which are taken at the surface at night. Smaller animals also make these periodic ascents and descents. The details have been ascertained for *Calanus finmarchicus.*[15] During the day, from 6 A.M. to 6 P.M. it is taken at 350- to 450-m. depth; from 6 to 8 P.M. it is uniformly distributed from 350 m. to the surface; about midnight the whole population accumulates between 46 and 3 m., and between 4 and 6 A.M. the majority are at a depth of 180 m. The composition of the surface plankton in consequence varies from night to day. Animals of deep water may come to the surface for egg-laying. *Nautilus,* an archaic cephalopod, an inhabitant of great deeps, breeds in shallow water near Amboina from May to September.[31]

Abyssal characters common to pelagial and benthal

In spite of the interdigitation of the deep-sea fauna with that of the lighted zone, the peculiarities of the environment to which all deep-sea creatures are subject result in many parallel adaptations. The peculiarities consist in the nature of the food, the absence of light, the stillness of the water, the low temperature, and the great pressure, the uniformity of these factors being more marked than in the rest of the ocean.

Living plants are not available to deep-sea animals as food. The food of the deep-sea forms, except as they prey upon each other, is derived from the bodies of the surface plants and animals that sink to the bottom, and on the falling excrement of the surface animals. Herbivores are consequently wanting in the deep-sea fauna proper; only scavengers and predators are represented. Food falls like gentle rain into the depths, its abundance depending on the number of animals in the upper zones. The rate of sinking of the food materials is slow. A salpa of 5-cm. length sinks 40 cm. in 20 seconds, at which rate it would require 2 days and 7 hours to reach a depth of 4000 m. The low

temperatures of the deeper water prevent decomposition, even in this time. The greater abundance of neritic than of pelagic animals, plus additions brought in by streams and winds from land, produces a greater supply of food in the littoral depths, and hence a greater concentration of animals, than is to be found in the depths beneath the open ocean.[2] The falling food supply is continually diminished on its way by various animals of the intermediate zones, so that under equal conditions the deeper the sea, the less of this food supply reaches the bottom. This must be one of the reasons for the reduction of population density with depth.

The remnant of the falling food material accumulates on the bottom, where it forms the food supply of the benthic animals of the deep sea. Numerous species of Foraminifera live on it. Many echinoderms have the same feeding habit in the lighted zone, so that their evolutionary transition to the abyssal benthal was simple; holothurians are the most abundant deep-sea animals.[26] Many snails adopt similar feeding habits, for example, the Trochidae. Their digestive tract is elongated, their radula reduced, and the excretory tube is elongated and carries the excreta away from the feeding ground. The Pleurotomidae have given up their predaceous habits in the deep sea.[9] Amphipods and isopods are already detritus feeders and flourish in the deep sea. Hydroid polyps, sponges, lamellibranchs, worms, and cirripedes live on the detritus, which is collected by self-made water currents.

Predaceous deep-sea forms require little comment. Some fishes are characterized by extraordinarily wide mouths and very strong dentition, their distensible stomachs sometimes containing prey larger than themselves (*Melanocetus, Saccopharynx, Eupharynx*). In general the predaceous animals of the depths display few special characters and no special superiority on account of the greater severity of competition. There is a notable increase in the number of structures that are interpreted as lures, and these may bear special lights.

Deep-sea animals are usually small in comparison with their relatives at the surface. Lamellibranchs and snails are often minute, and rarely reach moderate size. Fishes are relatively small; *Chimaera,* a meter in length, is large; the shark *Scapanorhynchus,* several meters long, is an exception. The reason may lie in the scarcity of food. The relatively gigantic size of a few deep-sea forms, in comparison with the size of their relatives in shallow water, is the more conspicuous. Long duration of growth correlated with postponement of

sexual maturity, conditioned in turn by low temperature, has been suggested as an explanation.

The density of the animal population on or near the bottom in deeper water is unknown. There is a definite, positive correlation between the amount of life at these depths and the development of phytoplankton at the surface. The ultimate source of food for these deep-dwelling animals appears to be from (*a*) surface organisms or their excreta, which sink, or (*b*) the utilization of dissolved substances. Plankton organisms cannot reach the bottom at great depth in significant amounts, but the excreta and bodies of large animals must provide a considerable amount of food. Calculations of the number of whales dying in Antarctic waters support this contention. In a column of water taken at 5400-m. depth off Bermuda, Krogh found that the concentration of nitrogen and carbon was constant from surface to bottom at 0.244 and 2.35 gm. per cu. m., respectively. These quantities are approximately 300 times the average amounts in the dry substance of all the marine organisms present on the average in a cubic meter of water.

The theory of Pütter that organisms take such dissolved nutriment directly from the water may hold for smaller forms such as bacteria and for some small protozoans. The small number of bacteria in sea water argues against their having a high food value; those in the bottom ooze may be present in high enough numbers to have significance as food for protozoans that are also able to utilize dissolved substances, at least to some extent, and to feed upon other minute particles. These microorganisms, together with the particles falling from upper levels, probably constitute the base of the food pyramid in the deep waters.[20]

Bioluminescence

The production of light by deep-sea animals is to be regarded as an adaptation to the absence of sunlight. Light production is by no means confined to the animals of the deep sea, for pelagic animals of diverse groups give off light in sufficient quantity to produce the bioluminescence of the surface of the sea. The protozoan *Noctiluca,* with *Pyrocystis* in the tropics, the jellyfishes *Cyanea* and *Pelagia,* the ctenophores *Beroë* and *Cestus,* copepods among crustaceans, *Phyllirhoë* among snails, and *Pyrosoma* among tunicates are examples. Some shallow-water fishes have light-producing organs in which luminescent bacteria are contained in a palisade of tiny tubules. The lights can be concealed or opened to flash like so many fireflies.

They seem to be a social signal in the pelagic schooling *Anomalops.*[16a] Animals that live in the dark may show no tendency toward light production. Cave animals exhibit only a single known light-producing form, a dipterous larva (see Chapter 27), although there are a number of bioluminescent forms among terrestrial animals, including an earthworm and the various light-producing insects; light production may nevertheless be said to be especially characteristic of deep-sea animals.

The production of light by animals of the littoral benthos is exceptional (*Pholas, Chaetopterus*); the abyssal benthos swarms with light producers. The largest number is perhaps supplied by alcyonarian coelenterates—Alcyonidae, Pennatulidae, and Gorgonidae. Echinoderms have the starfish *Brisinga* and *Freyella,* and annelids are represented by *Chaetopterus* and *Polynoë.* All these have usually a continuous light, whose clarity and beauty of color delight every observer. De Folin [15a] expresses his impressions of nocturnal dredging as follows: "How great was our astonishment when a great number of bouquet-like gorgonids were taken from the net; these sent forth flashes of light so bright that the 20 torches lighting the work paled into insignificance as soon as the polyps were near them. From every point of the main stems and branches beams of light radiated, whose intensity became less, then increased, passing from violet to purple, from red to orange, from blue to various tones of green, and sometimes to the white of flowing iron. Meanwhile the predominant color was plainly green, the others appearing momentarily and melting quickly into the general color." In all these animals the power of light production is not confined to special organs, but is more or less diffused over the body.

Bioluminescence is more common among fishes, crustaceans, and cephalopods of the mesopelagic zone, occupying the twilight region of the sea, than in the lighted surface zone above or the bathypelagic region below.[36] No less than 44 per cent of the fishes of depths beyond 900 m. are light producers.[27] It is estimated that two-thirds of all bathypelagic fish species and over 96 per cent of the individuals are luminous. By direct observations, Beebe [3] found the first animal lights at 207 m. and thereafter in slowly increasing numbers down to the greatest depth reached, 924 m. Diffuse luminescence occurs among the macrurids, which give off light-producing mucus from their skin glands. For the most part, however, the pelagic forms have special luminescent organs under the control of the nervous system. In some forms these organs are simple in structure and are mere ac-

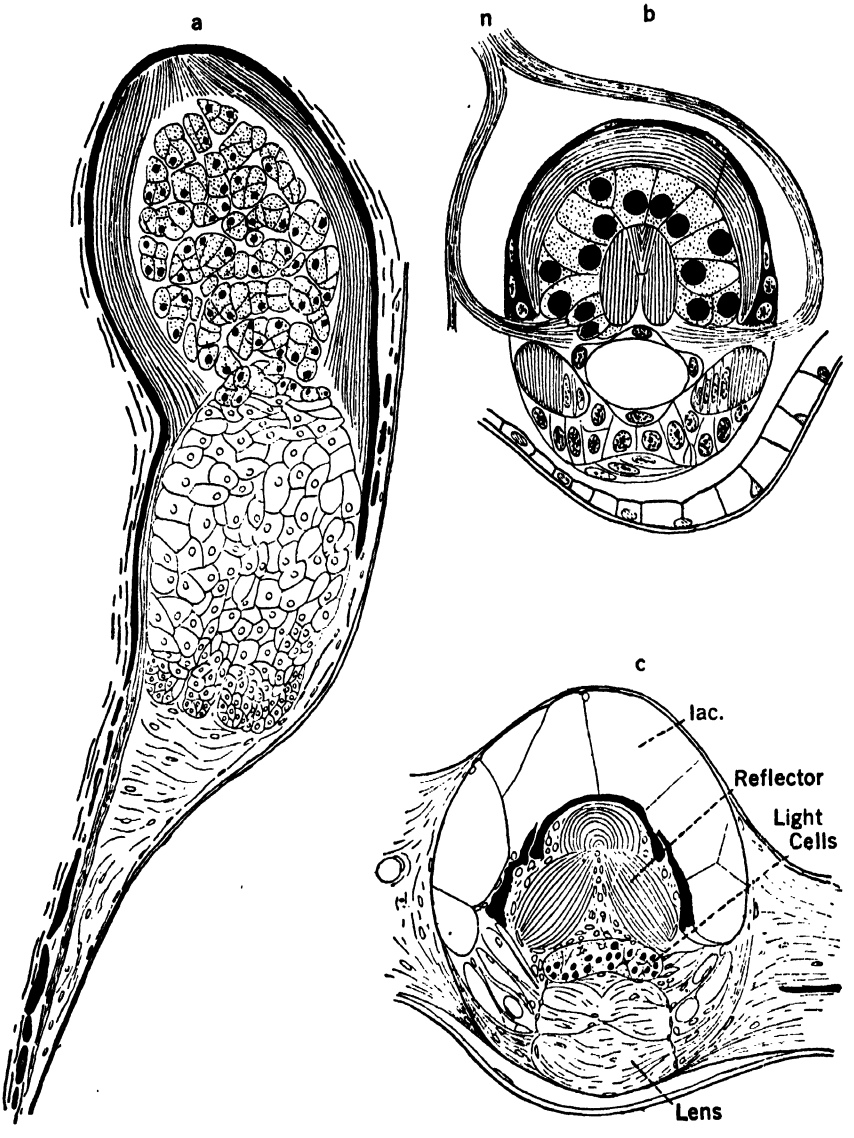


FIG. 69. Light organs of deep-sea animals: *a*, of a fish (*Argyropelecus affinis*); *b*, of a schizopod crustacean (*Nematoscelis mantis*); and *c*, of an octopod (*Abraliopsis morisii*). Light cells stippled; reflector lined, backed by a pigmented layer, black. A lens of varying structure in front of the light cells, made up of cells in *a*, homogeneous in *b*, fibrillous in *c;* in *b*, with an afferent nerve, *n;* in *c*, *lac.* = lacunae. *a* after Brauer; *b* and *c* after Chun.

cumulations of gland cells with a luminescent secretion. In other groups the structure becomes more complex and reaches its highest degree among Euphausidae (Crustacea), cephalopods, and bony fishes. Convergence in the evolution of these organs in such diverse groups is notable. Behind the group of light-producing cells is located a tapetum, in the form of a concave reflector, covered over by a pigment layer. An outer lens is present, formed in different ways in the different animals (Fig. 69). Independent convergent origin of light organs may be seen within groups of cephalopods and fishes. It is notable that light production is unknown among the cephalopods and fishes of shallow water. The deep-sea members of the Iniomi (lantern fishes) have luminescent organs, which are absent in the few coastal forms. Many luminescent cephalopods and fishes maintain themselves in the transition zone between the lighted and the abyssal pelagial.

What may be the function of this bioluminescence? The attraction of prey must be considered as the primary possibility in the benthic forms. In pelagic animals, the highly developed light organs must have other uses. Many are grouped around the mouth, and again suggest a use as food lures. It is probably equally important that their characteristic arrangement makes possible a recognition of the sexes, and of the species in gregarious forms. This helps explain the great variety in arrangement of the light organs and in the color of the light emitted, but scarcely touches the problem of bioluminescence of alcyonarians and other sessile forms.

The sunless depths of the sea are consequently not without light. Thousands upon thousands of luminescent animals provide torches that light the abyssal depths. This light is not uniformly distributed. Oases of light occur where there are forests of gorgonians or meadows of alcyonarians. In comparison with sunlight, this light is weak at best and does not reach far into the water, but it does enable animals to direct their motions by means of their eyes. Some of the relationships are indirect; thus a hermit crab is known that carries luminescent actinians on its borrowed shell.[2] The development of bioluminescence explains the fact that degeneration and loss of eyes is less general in the abyssal fauna than in caves.

Eyes in relation to depth

Oddly enough, the eyes of bottom-dwelling fishes may be well developed even though their own light-producing organs are lacking. Apparently these fishes use the light given off by benthic invertebrates.[33]

The eyes of many mesopelagic animals are especially large (Fig. 70*a*), much larger than in their relatives of the upper or lower depth zones. These animals live near the upper limit of the sunless depths and thus correspond to the nocturnal or twilight terrestrial animals with large eyes, such as geckoes, owls, and tarsiers. A number of decapod crustaceans exhibit this peculiarity (Fig. 71*d*),[2] as do many amphipods (Fig. 71*a*), schizopods (Fig. 71*b*), and sergestids. Their eyes are divided into a dorsal portion with upward-directed elongate and little divergent facets, whereas the lateral portion has shorter and strongly divergent elements. Such eyes are otherwise unknown in these groups. Numerous fishes of the border zone of the abyssal also have enlarged eyes, for example, *Brama longipinnis*, *Aphanopus carbo*, and *Regalecus*. Certain mesopelagic cephalopods like *Chiroteuthis* and *Pterygioteuthis*, have very large eyes; but their habits are insufficiently known to make it certain that this is in adaptation to mesopelagic life.

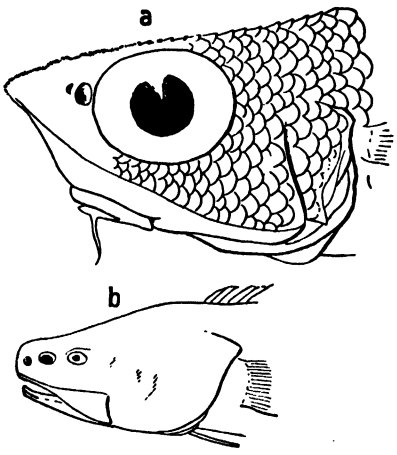


FIG. 70. *a*, *Macrurus fasciatus* from 250-m. depth; *b*, *Bathyonus taenia* from 4500-m. depth. After Günther.

Enlargement of the lens alone, instead of enlargement of the whole eye, affords a second type of adaptation to the dim light, exhibited by the so-called telescopic eyes (Fig. 72). These are found only in the smaller fishes, of which the largest, *Gigantura chuni* (Fig. 73*b*), measures 11.8 cm. Such telescopic eyes (really tubular) have developed independently in five different orders and eight suborders of fishes. A deep-sea cephalopod also has eyes of this type.[2,7,21] The similarity of the frontal eyes of pelagic deep-sea crustaceans is only apparent, although there is also a relative enlargement of the light-gathering surface. As a further adaptation to the small amount of abyssal light, the retina of the deep-sea fishes of all groups has specialized light-sensitive rods; the cones are largely or wholly absent.[5,36]

There are eyeless animals in the deep sea, but their number in the pelagic formation is small. Eyeless animals and those with reduced eyes are numerous in the abyssal benthos. The deep-sea

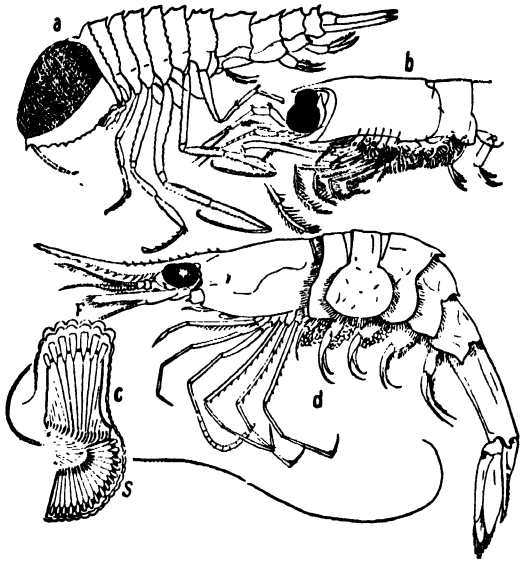


FIG. 71. Deep-sea crustaceans with enlarged eyes. *a*, a hyperine, ***Cyrtisoma spinosum***; *b*, an euphausid, ***Thysanoessa gregaria***; *c*, eye of an euphausid, ***Stylocheiron mastigophorum***, in vertical section, in which *F* is the anterior and *S* the lateral eye; *d*, a caridid, ***Pandalus magnoculus***. *a*, *b*, and *d* from the ***Challenger*** report; *c* after Chun.

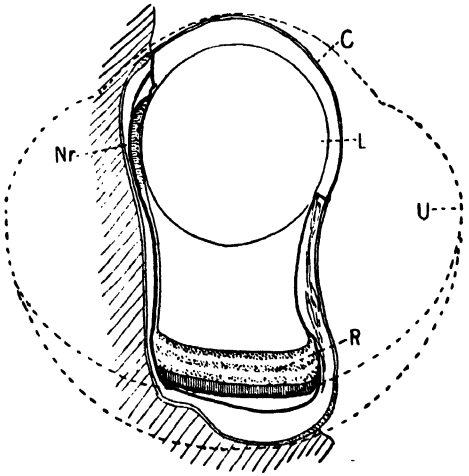


FIG. 72. Telescopic eye of the deep-sea fish ***Argyropelecus*** in transverse section, with the dotted outline, *U*, of a normal eye for comparison. *C*, cornea; *L*, lens; *R*, retina; *Nr*, pigmentary layer. After Brauer.

pectens and *Eulima* and *Fusus* are eyeless. The eyes of benthic crustaceans are frequently reduced, both in number of facets and in amount of pigment present. Doflein [11] found all crabs from considerable depths with fewer facets in their eyes than the related littoral forms, and 20 per cent of the higher Crustacea in the catch of the *Investigator* had pigmentless or reduced eyes. Among some crabs reduction of the eyes with increasing depth is found within the same

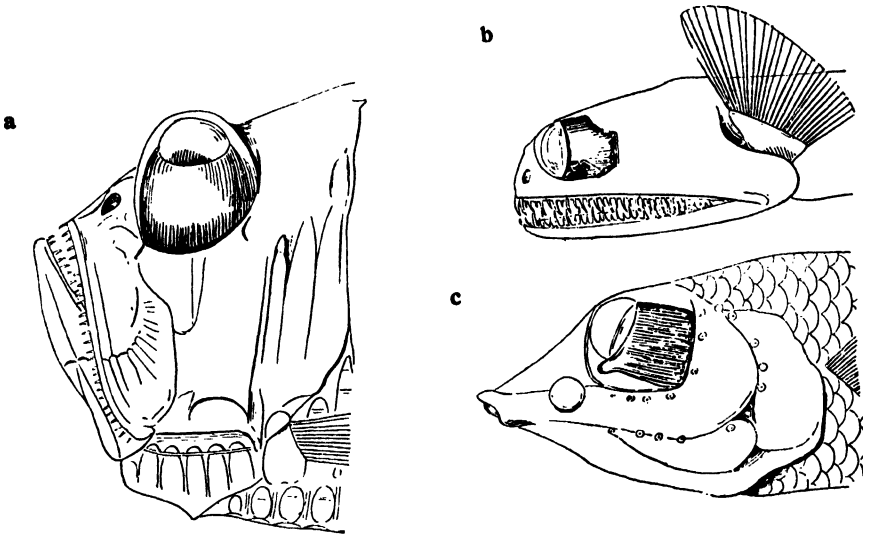


FIG. 73. Telescopic eyes of deep-sea fishes of various families: *a, Argyropelecus affinis; b, Gigantura chuni; c, Winteria telescopa.* After Brauer.

species.[2] Fishes and cephalopods rarely exhibit complete degeneration of the eyes. An eyeless cephalopod, *Cirrothauma murrayi,* is known from a depth of 1500 m. Among fishes the *Macrurus* species of the *Challenger* collection may be sorted as to depth according to the size of their eyes. Those with large eyes live in the twilight zone, those with smaller eyes in more considerable depths.

In correlation with the difficulty of orientation by sight in the dim light, numerous deep-sea crustaceans and fishes have antennae of unusual length in comparison with those of their relatives in the lighted zone. *Sergestes magnificus* (from 800 to 1200 m.) has antennae three times the length of the body; *Arachnomysis,* with well-developed eyes, has antennae four times the length of the body; in the isopod, *Munnopsis longicornis* (600–800 m. depth), the antennae are more than eight times the body length, and in the shrimp *Aristaeus* they measure

10 to 12 times the length of the body. In numerous fishes, such as *Bathypterois* (Fig. 74), single rays of the various fins serve as feelers and are longer than the body. High development of the lateral

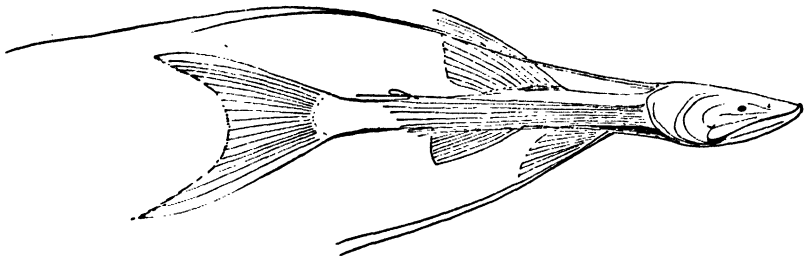


FIG. 74. *Bathypterois longicauda* from 4600-m. depth in the south Pacific. After Günther.

line system is also notable in many deep-sea fishes. Similar development of the organs of touch and smell is found in cave animals (cf. Chapter 27).

Coloration in relation to illumination [26]

The protective colorations of the animals of the lighted benthal region have been discussed previously. They are extremely varied, in correlation with the variety of background on which the animals live. The colorations of pelagic animals in the lighted zone are much less varied. The plankton animals are in the main transparent, in part owing to the high water content of their bodies. For the rest, blue is the dominant color, as in the siphonophore *Velella,* on the edge of the disk of the medusa *Rhizostoma,* in the copepod *Anomalocera,* the decapod *Virbius,* and in the snail *Glaucus* (Fig. 53*a*). The dorsal half of pelagic juvenile fishes (*Mullus*) and of adult fishes like sardines, mackerels, and the flying fishes, is blue. The dark brown back of the herring is invisible from the surface, and only the silvery gleams from their sides make them visible. In the lower stages of the lighted zone, with dim light, the fishes are predominantly silvery.

In greater depths, where sunlight is absent and where a uniform ooze covers the bottom, colorations are much more uniform. There is a decided predominance of red colorations in all tones, besides dark brown, dark violet, and black. The absence of red light in depths even of 50 m. makes red appear as black, as shown by Fol in diving experiments in the Mediterranean. Some Foraminifera of the deep sea are striking for their dark reddish violet and black coloration. In the

abyssal benthal are red hydroid polyps, such as the gigantic *Branchiocerianthus imperator,* bright red sea anemones, and intensely red alcyonarians, in contrast with the yellow, green, and brown forms of the littoral.[2,7,21] The starfish of the deep sea are red, orange, or terra cotta in color. Red cephalopods are not rare, and red crustaceans are abundant. The shells of snails and lamellibranchs, however, are mostly colorless or have pale coloration. The same colorations are found in the lightless pelagial. The scyphomedusan *Atolla* has increasingly dark coloration with depth, in contrast with its glass-like relatives of the surface. The bathypelagic larvae of *Velella* are red. The deep-sea nemertean (*Pelagonemertes*), some arrowworms, and a number of pelagic cephalopods are red; the deep-sea pelagic holothurian *Pelagothuria* (Fig. 59) is deep rose. Many deep-sea copepods are dark violet. Almost all decapod crustaceans below 750 m. in the tropics, 500 m. in the temperate zones, and 200 m. in polar seas are uniformly red. The abyssal fishes are mostly dark violet or black, and red is a rare color among them. *Cyclothone microdon,* from deep water, is black, while *C. signata,* whose lower limit coincides with the upward range of the former species, is light-colored. There are also, to be sure, colorless animals in the abyssal pelagial such as the crustacean *Sergestes magnificus,* the annelid *Tomopteris* (Fig. 53*c*), and the fish *Bathypterois longicauda* (Fig. 74).

Body form and skeleton

In depths below 100 m. the water has little motion. This makes possible structural forms impossible in rapidly or violently moving water. Delicate, slender, long-stalked animals or animals with an ungainly walk on stilt-like legs are not uncommon. The wonderfully fragile glass sponges (Hexactinellidae), the long-stemmed crinoids, and long-legged crabs like *Kaempfferia* require quiet water. Fishes with tails drawn out into long points, such as *Chimaera* (Fig. 75), the bony fishes, *Gigantura,* Macruridae (Fig. 76), and Gastrostomidae, are characteristic of the abyssal waters. Compressed forms such as the deep-sea shark, *Chlamydoselachus,* and the band-like fishes *Regalecus* and *Trachypterus,* are likewise characteristic of the depths, in correlation with their weak powers of locomotion. The absence of water movement also makes possible the survival of many forms with weak and fragile skeletons, whose presence is associated with the difficulty of lime formation.

The drop of temperature with depth leads to uniform low temperatures in the great depths of the abyssal ocean. The difficulty in

the formation of lime produced by the low temperatures in the polar seas (see p. 207) is thus repeated in the deep sea. Accordingly, animals belonging to groups with a strong calcareous skeleton or shell in the warmer waters are found with weakly or completely non-calcareous skeletons in the deep sea. Thus calcareous sponges are wanting below

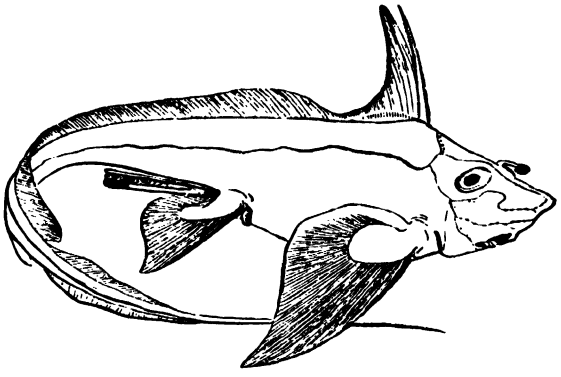


FIG. 75. *Chimaera monstrosa.* After Boas.

300 m. Numerous echinoderms, such as the echinothurid sea urchins, have a leathery non-calcareous skeleton; the starfish *Brisinga* has a reduced skeleton; and the pelagic deep-sea holothurian, *Pelagothuria,* has no calcium bodies in its skin. Numerous deep-sea barnacles of the genus *Scalpellum* have an incompletely calcified shell. Such forms all

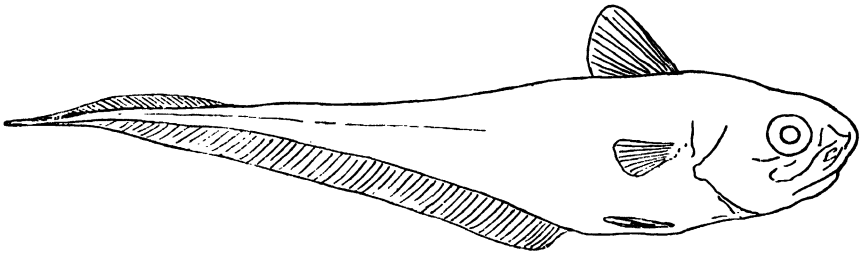


FIG. 76. *Macrurus rupestris.* After Hentschel.

belong to great depths, mostly below 1250 m. Even in the same species, the skeleton may be reduced in deep water; *Scalpellum stearnsi* in 200–450 m., with a normal shell, is identical with S. *polymorphum* from below 400 m., with a reduced shell.[18] Mollusk shells from great depths are mostly fragile. Many deep-sea fishes exhibit

uncalcified or weakly calcified skeletons, as in *Chimaera.* Some deep-sea forms, on the contrary, are not deficient in calcium carbonate.

Faunal affinities of abyssal animals

The occurrence of surface forms of polar seas in deep waters in the warmer zones, where they are absent at the surface, is explained by the temperature relations. Among many animals the connection between the polar surface forms and the tropical abyssal ones can be followed continuously. This is true of many snails and bivalves of the northern Atlantic, living in the Arctic littoral to a depth of 50 m.; they may be followed at steadily increasing depths on both sides of the ocean, to the Canaries and St. Helena (to 2000 m.) and to the West Indies and Pernambuco (to 800 m.).[23] The northern starfish *Brisinga* is found in the abyssal Indian Ocean, which also has characteristic northern snails of the families Pleurotomidae, Trochidae, and Naticidae. The lamellibranch genera *Yoldia, Nucula, Lima,* and *Abra* are littoral in the Arctic, abyssal in warm seas; the same is true of decapod crabs;[2,17] typical northern genera of shrimps,* of crabs,† and of anomurans‡ inhabit the deep sea in low latitudes. The deep-sea genera of shrimps, *Hymenodora* and *Pontophilus,* have at least one or a few species near the surface in the Arctic Ocean. The sharks have similar distributions, especially among the Squalacea; *Centroscyllium* is also found nearer the surface in polar waters than in the tropics.[14] The great majority of deep-sea fishes, however, do not enter polar surface waters.[4] On the whole, the difference between littoral and abyssal animal life is greater in the tropics than in arctic seas; for the most part abyssal fishes are archaic.[36]

Uniformity in abyssal waters

Uniformity of environmental conditions in the deep sea is greater than in any other division of the ocean. At great depths the water is uniformly cold, with little motion, without sunlight, the bottom covered with ooze whose main variation is chemical and which is uniform over wide areas even in this respect. The bottom is smooth, without holes or cracks, since there are no modeling forces in play. With environmental barriers wanting, the deep-sea fauna is characterized by great uniformity over extremely wide areas, and it was even supposed at one time that it was essentially uniform throughout the

* *Crangon, Pandalus, Pasiphaea.*
† *Homola, Latreillia, Maia.*
‡ *Lithodes.*

oceans. The increase in our knowledge of deep-sea life has shown that the uniformity, though great, is not world-wide. Faunistic differences are less marked in the abyssal benthal and pelagial than in the lighted benthal or even in the lighted pelagial, and the great number of animals of various groups found in the depths of all oceans makes any faunal division of the abyssal oceans more or less vague. It is predominantly the bathypelagic animals that exhibit such wide distributions, but widespread benthic ones are not wanting. The medusae *Atolla* and *Periphylla* are known from all seas. Numerous sea urchins of great depths are common to the Atlantic and Indo-Pacific.[10] The deep-sea ostracod *Gigantocypris* is known from the Atlantic and Indian oceans. Ortmann[28] enumerates 49 species of world-wide deep-sea decapod crustaceans belonging both to the pelagic and benthic habitats. A number of abyssal lamellibranchs such as *Silenia sarsii* and *Semele profunda* have a very wide distribution. The cephalopods *Calliteuthis reversa, Mastigoteuthis flammea, Toxeuma belone,* and others, are known from the Atlantic and Indian oceans; *Spirula* is known from the Pacific as well. Of 130 bathypelagic genera of fishes a fourth are known from three oceans and another fourth from two. Numerous species also have the same distribution, as *Chimaera monstrosa* or *Cyclothone microdon,* in all seas, and *Malacosteus indicus, Cyema atrum, Melanocetus krechi,* and others, from the Atlantic and Indian oceans. It is to be watched whether the number of the deep-sea forms known to be widespread will be increased as our knowledge grows concerning the deep sea, its water masses, and slow-drifting currents.

On the other hand, faunal differences may appear even when there are no demonstrable barriers. Of the 272 species taken by the *Challenger* near Kerguelen, from depths greater than 2300 m., 60% were unknown from other regions. Of 523 species dredged from depths of more than 1800 m. south of the tropic of Capricorn, only 36% were known from other regions.[25] The Sunda Archipelago on one hand and the Gulf of Bengal and Oman on the other exhibit two distinct deep-sea faunae of holothurians, though their genera and families are much the same.[19] The 21 North Atlantic species of sea urchins and the 28 west African forms have only 10 species in common. The east and west Atlantic in the abyssal zone have a total of 74 species of sea urchins, but only 24 are common to both areas. The decapod crustaceans exhibit similar differences in the North and subtropical Atlantic.[26] Although most species of the deep-sea fish *Cyclothone* are sub-

tropical, *C. livida* occurs only on the west African coast, where it is abundant.

Local specialization accordingly takes place also in the deep sea. Such differentiation is further increased where there are great barriers that are insurmountable for many animals. The Faeroe Ridge between the Norwegian Sea and the Atlantic, and its continuation in the direction of the northeast corner of Scotland, the Wyville-Thomson Ridge, is such a barrier. The effect of the latter is the more notable as it extends as a narrow ridge, whose deepest point is 556 m. below the surface, between depths of more than 1000 m. on each side. North of this ridge the temperature drops much faster with depth than it does to the south (Fig. 16) so that in the Faeroe-Shetland channel, at depths of 1100 m., a temperature of −0.41° prevails, and scarcely a degree farther to the south, at an equal depth, the temperature is about 6°. At the deepest point on the ridge, the temperature is +7.5°, so that for stenothermal cold-water forms this ridge is an impassable barrier. This barrier shuts out the whole of the Atlantic deep-sea fauna from the Norwegian Sea; the only exchange of forms possible is in the uppermost zone. Murray records 385 species of animals from both sides of the barrier, of which only 48 (12%) are common to both the warmer Atlantic and the colder Norwegian Sea. No Atlantic abyssal species of fishes are found in the northern ocean. The genera *Cyclothone* and *Macrurus,* which play an important rôle in the Atlantic, are wholly wanting, while in the Norwegian Sea *Lycodes* (related to the "eel mother" *Zoarces*) predominates, with only a few special forms in the Atlantic. Just south of the ridge are found animals that range to the Canary Islands; a few kilometers to the north occur forms that extend to Spitzbergen and even farther.[26] Similar differences are also shown in the benthic fauna of the two sides of the ridge.

Abyssal animals reviewed

Although a considerable number of the deep-sea animals are eurybathic and range upward into the lighted zone, and although the peculiar adaptations to the deep-sea environment are by no means general, so that a special character of deep-sea life can be asserted only with reservations, the composition of the deep-sea community, according to the groups of animals represented, is so different from that of the lighted zones in the ocean that there is a recognizable peculiarity in this respect. A rapid review of the deep-sea fauna shows this plainly. Among the radiolarians, *Nasselaria* and *Phaeodaria* outnumber the *Spumelaria* and *Acantharia* with increasing depth, and

the family Challengeridae is confined to the abyssal pelagial. Foraminifera are abundant in the abyssal benthal, especially imperforate forms with sandy shells. The *Globigerina* ooze is composed of the dead shells of the relatively few surface forms, which predominate on the sea bottom on account of their great numbers in the lighted zone. Among coelenterates, Hydrozoa are scarce in the abyssal. The stony corals of deep water are completely different from the reef corals and are almost always simple. Sessile Alcyonaria, like *Mopsea* and *Primnoa,* are not rare. Certain sea pens (*Umbellula*) reach great depths. The abyssal sponge fauna is composed of siliceous sponges, and among these the glass sponges are almost confined to the lightless depths. Turbellarians appear to be absent. The *Challenger* Expedition secured only six species of nemerteans from the sea floor, while the family Pelagonemertinidae is represented by numerous genera and species in the abyssal pelagial, to which it is confined.[6]

The number of annelids is relatively small, and among them are only the tubicolous forms that feed on detritus; predaceous forms are rare. The Gephyrea of the deep sea are also tube-dwellers such as *Phascolosoma.* Among crustaceans the barnacles are represented primarily by the genera *Verruca* and *Scalpellum,* which are mainly abyssal though not wholly absent from the upper zones. Isopods and amphipods are relatively well developed, with numerous species. Stomatopods seem to be wholly absent. Numerous deep-sea decapod crustaceans are known, although the brachyuran crabs do not go below 800 m.; the family Eryonidae is now confined to the deep sea; Anomura are not rare; Galatheidae are for the most part deep-sea forms; Paguridae (hermit crabs) are represented by a number of peculiar genera. Pantopoda are poorly represented, only 6 of the 27 genera being known from the abyssal. Among mollusks, about half the species of scaphopods are deep-sea forms. Lamellibranchs are few and snails still fewer; they have no characteristic abyssal genera.

The number of abyssal cephalopods is relatively large, the benthic forms fewer than the bathypelagic. Of Bryozoa, the chilostomes have numerous abyssal representatives, some going to great depths, *Farciminaria delicatissima* to more than 5000 m. Cyclostomes and ctenostomes are poorly represented. The most abundant deep-sea animals are echinoderms. Of 49 genera of holothurians discussed in the *Challenger* Reports, 19 are littoral, 20 are abyssal, and 10 are found in both zones; the family Elasipodidae is confined to the deep sea with the exception of two species; it has 66 abyssal species, double the

number of the abyssal species of other families.[32,34] Among starfishes, 272 species out of 832 descend below 400 m.[32] The proportion of abyssal sea urchins and brittle stars is somewhat smaller. The stalked crinoids are almost wholly confined to the deep sea. Tunicates are few in the deep sea, with the exception of ascidians, which have 12 genera confined to the abyssal, while 28 of the 91 genera reach depths below 800 m. The number of deep-sea fishes enumerated by Brauer [4] is 309 genera with 1007 species, of which 131 genera and 397 species are pelagic. In the groups represented, this fauna differs conspicuously from that of the lighted zones; few spiny-rayed fishes reach the depths, and lophobranchiates and plectognathids are wanting.

Archaic forms in abyssal waters

The necessity for special adaptation for life in the deep sea, of which only a certain proportion of animals are capable, produces the relative poverty of the deep-sea fauna. While the struggle with the physical environmental forces is increased, the competition between species is diminished. This is consequently one of the places where ancient types have been able to maintain themselves. Such archaic forms are not absent from the lighted zone—as illustrated by the horseshoe crab, the brachiopod *Lingula*, and amphioxus—but they are relatively more abundant in the abyssal depths. Many of the deep-sea stony corals are closely related to Mesozoic and early Tertiary forms. The sea-urchin families Salenidae, Echinothuridae, and Ananchytidae, which reached their maximum development in the Cretaceous, were thought to be extinct until the dredge brought living representatives to light from the deep sea. Of the more recent Clypeastridae, which originated in the Cretaceous, only the two oldest genera, *Echinocyamus* and *Fibularia*, go deeper than 400 m. A. Agassiz [1] remarks that the forms with greatest range in depth are also those with greatest span in time; the living littoral forms extend only into the late Tertiary. Stalked crinoids, which were numerous and widespread in the earlier geological periods, are now confined to the deep sea. The cephalopods *Spirula* and *Nautilus* belong to the deep sea, though *Nautilus* may rise to the surface. Among abyssal decapod crabs the representatives of the otherwise Triassic family Eryonidae (*Willemoesia*, for example) are notable, as is the great number of such primitive groups as the Peneidae and Caridae. Among fishes the chimaeras, and the shark *Chlamydoselachus*, related to the Devonian *Cladodus*, may be named as archaic. Among the bony fishes, forms with soft rays predominate in the abyssal, as they do in fresh water.

The more recent spiny-rayed fishes have as yet scarcely found their way into the depths.

Although there is this easily recognized archaic element of the abyssal fauna, the ancient character does not apply to the whole, as it does for example to the land fauna in Australia. The deep sea is not isolated, and the way into the depths is continuously available to animals of the lighted zone. The genus of crabs *Ethusa,* in which the same species exhibits reduction of eyes with depth, has been regarded as an example of a form in process of descent into the abyssal habitat.[30] In some forms renewed speciation appears to have taken place in the abyssal zone; Kükenthal[22] regards the higher development of the deep-water gorgonians as evidence of more recent origin, and he maintains that the gorgonians of the littoral belong to more primitive genera.

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15. *Geographic Divisions of the Animal Communities of the Sea*

UNLIKE MANY OF THE BIOTIC DIVISIONS OF THE LAND, THE ANIMAL COMmunities of the sea are not separated into irregularly placed subdivisions but rather extend as broad zones. Although physiographic divisions can be recognized, these separate the animal communities of the lesser seas, gulfs, and bays from the oceans proper instead of coinciding with the geographic divisions between the oceans. In these smaller bodies of water such as the Mediterranean, Baltic, or Black seas, there are distinct peculiarities in temperature, especially in gradation with depth, in salt content, and in the accumulation of chemicals in the water, which condition the development of recognizable animal communities. These are the more distinct when such land-locked seas are connected with the ocean proper only through narrow and shallow straits such as the Straits of Gibraltar. Within the oceans similar differences may occur in the littoral regions, especially near the mouths of great rivers such as the Amazon or the Congo. The geographic distribution of the animal communities of the oceanic pelagial are, in the final analysis, determined primarily by temperature. In littoral areas the relationships are frequently complicated by depth, type of bottom, presence of fresh water, and similar factors.

The major animal communities of the sea are the most extensive of life zones; they may be compared to the climatic zones of the continents, but far surpass them in area and in homogeneity of environmental factors and of associated biota. The distinctions to be made are extremely simple and consist most plainly in a subdivision of the animal communities of the ocean into those of warm and of cold waters, very roughly corresponding with the tropical and subtropical areas on the one hand and the cooler waters on the other.

The boundaries between these vast areas are not determined by latitude, and run entirely independent of the conventional tropics of Capricorn and Cancer. They are much more closely correlated with the isotherms of the surface waters; in fact, Meisenheimer's divisions based primarily on the limits of the tropical pteropods coincide in the North Atlantic with the 15° isotherm and in the South Atlantic

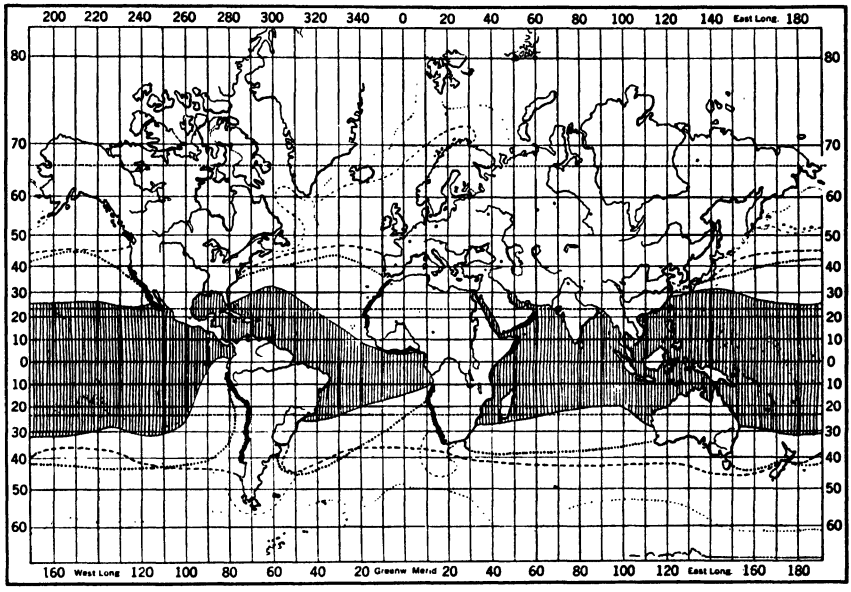


FIG. 77. Limits of the warm water region: heavily dotted line according to Ortmann, heavy broken line according to Meisenheimer; polar limits of the transition zone, lightly dotted line after Ortmann, light broken line after Meisenheimer. Distribution of reef corals vertically ruled, after Joubin. Upwelling cold bottom water, heavy coast line.

with that of 17° (Fig. 77). Ortmann [24,31] sets somewhat different boundaries on the basis of the distribution of the fairly constant high temperatures in which the warmth-limited, stenothermal tropical life can exist. His boundary lines therefore bend far toward the equator along the west coast of South America and of Africa on account of the cold Antarctic currents and the upwelling of water from the cold ocean depths. As shown in Fig. 77, the boundary lines of these two investigators differ essentially in that according to Meisenheimer the tropical animal communities of the Atlantic and Indian oceans are united around South Africa, whereas, according to Ortmann, they are entirely separated.

Both the warm and the cold belts of the sea can be subdivided. Marine animals react to an equatorial belt of water with a temperature above 25° as distinct from cooler tropical waters lying on either side with temperatures from 20 to 25°. Similarly there are recognizably different animal communities in the cold-water areas around the poles with temperatures below 10° as distinguished from those of the less cold waters with temperatures between 10 and 15°. Indeed, in the best-studied region, the North Atlantic, other subdivisions can be made; for example, the animal communities of the cold waters can be separated into arctic and boreal communities, both distinguished by characteristic dominant animals.

The boundaries between different temperature areas are usually not sharply defined either physically or biotically, yet in the open ocean and apart from regions where opposed currents meet, relatively narrow strips can be located in which water temperatures and their accompanying animal communities change more abruptly than in adjoining regions. The location of all these boundaries shifts with the season; warm streams augment their area in summer and are pushed back by the advancing cold in winter. Such phenomena are particularly noticeable in terminating streams, such as the well-known Gulf Stream, but they apply also to circular currents. Pelagic animals are able to follow these shifts to some extent, but littoral animals are less motile as a rule and often exhibit special adaptations.

Tropical marine communities

The influence of temperature on marine animals has already been discussed and needs only a brief summary. The warm waters of the equatorial belt lack that distinct seasonal periodicity found toward the poles. This allows the development of an extensive warmth-limited stenothermal community. As a result of the continuous high temperatures metabolism and growth rates are accelerated, and generations follow each other in quick succession. This is best seen in the smaller plankton organisms. An equal mass of plankton at any given time would mean more food for the plankton feeders per week in the tropics than in colder water. The speeding up of life histories favors the appearance of mutations, and perhaps the higher temperatures are less rigidly selective than the low temperatures obtaining in polar seas. At any rate, as has been stated previously, the tropical waters are rich in genera and species but have a smaller number of individuals per species than are found elsewhere. This condition is especially noticeable among the pelagic animal com-

munities. The tropical waters are therefore rich in index forms, even among the invertebrates, while the communities of the colder waters may be distinguished rather by their negative characters.[15]

We have also seen that a different stratification of animal life occurs in the tropical as compared with colder waters, particularly in that the depth penetrated by surface pelagic forms is greater, with a consequent lack of concentration in the surface waters. This may well be a basic reason why, except in a favorable region such as that established by the cold Humboldt Current, and the upwelling water mass along the coast of Chile and Peru, the number of sea birds that secure their food from the uppermost surface water is so much less in the tropics than in polar seas. The absence of seals in the tropics may have been originally determined by this same phenomenon.

When tropical pelagic communities are examined, it is found that about 20 species of Foraminifera occur there, while only one or two dwarf species are found in polar waters. The Siphonophora, with few exceptions, are confined to the tropics. The Geryonidae among the Hydromedusae and the Charybdeidae among the Scyphomedusae live only in warm seas. Of crustaceans, the species of the copepod genus *Copilia,* which accumulate toward the equator, most of the Euphausiacea, most of the *Sergestes,* as well as the shrimp *Lucifer,* are present only in the warm water. Of mollusks, all heteropods, most pteropods, and the pelagic snails *Ianthina* and *Phylliroë,* are limited to warm water. Among tunicates the Pyrosomatidae belong to the warm waters entirely, as do the salpas with few exceptions. Thirty species of Appendicularia in the Atlantic, representing 7 to 8 genera, occur in the warm zone, as against 3 species (of 2 genera) in the cold, and the latter are specifically different. The tropical plankton includes numerous free-swimming larvae of forms of echinoderms, mollusks, annelids, and others, which are entirely absent in cold water. Finally, the flying fishes (*Exocoetus* and its relatives) are strikingly characteristic of warm seas. It is characteristic of the shifting boundaries of the warm-water belt that the northern limit for flying fish extends about 5 to 8° latitude farther north in the northern summer than in the northern winter. The absence of flying fishes in cold seas may well be associated with the adverse effect of too rapid cooling produced by the swift movement of the moist animals through cold air.

It is worth noting that in spite of the complete separation of the warm-water belt into two subdivisions, the Atlantic and Indo-Pacific, separated by the continents of Africa and America, the pelagic animal

life limited to warm water shows a great agreement in both areas. Thus, for the copepod species occurring in both, part are identical * and part of them are closely related species that vicariate in the two regions,† a similar situation exists among the schizopod and decapod crustaceans; [29] most of the salpas, and certainly the most abundant species, are present in both oceans. The significance of the connection of the two oceans in the region of Central America during Tertiary times in this regard is evident.

Although the pelagic animals serve adequately to separate the tropical animal communities from those of cooler waters, the warm seas are particularly distinguished by the reef corals. They are limited in their distribution to a mean temperature of at least 20°, and their variety increases in higher mean temperatures. The area of distribution of these corals is indicated in Fig. 77; the boundaries lie within the limits of the tropical belt; the southern limit coincides somewhat with Ortmann's southern border of the warm-water zone, but the northern limits are independent of it, particularly in the Atlantic.

Polar marine communities

A direct result of the winter freezing appears in the absence of algae and of sessile animals in the littoral formations of the Arctic Sea to a depth of 6 m.; only bare rocks are to be seen, from which the drifting ice masses have scraped off all life. Below the limits of ice action, on the other hand, plants and animals are present in abundance, often in larger numbers than in the adjacent boreal zone, a little to the southward.

Because of the low temperature, fecundity is reduced, and, correlated with this fact is an increased size of egg (compare p. 198). The suppression of free-swimming larval forms is a result, especially among the benthic animals. The descendants therefore remain in the immediate vicinity of their parents; thus enormous aggregations of single species occur in many places, as is well known in arctic seas. For example, in the sea along east Spitzbergen, sedentary annelids (*Scione lobata, Thelepus cincinnatus*) are found together in patches; in the Barents Sea, the *Michael Sars* brought up more than a ton of the siliceous sponge, *Geodia,* with a single haul of the dredge; at another time, near Jan Mayen, more than a barrel of the scallop, *Pecten*

* *Corycaeus lautus, C. speciosus; Calanus robustus, C. vulgaris; Heterochaeta papilligera.*

† Like *Corycaeus clausii* and *C. vitreus.*[7]

groenlandicus, was similarly taken; other accounts mention large catches of feather stars, *Antedon eschrichtii.*

The composition of the cold-water fauna is different from that of the tropics in many respects. The number of animal species that can live in the surface water of both the polar and the tropical seas is small. The fauna of the polar seas shows throughout the influence of environmental selection as compared with that of the tropics. Though not so numerous as the warmth-limited types characteristic of the tropics, still many genera and species find their most favorable conditions for existence in these colder waters. Such groups are the Hydrozoa among the coelenterates and the Holothuria among the echinoderms. Siliceous sponges occur especially in antarctic seas. On the other hand, the scarcity of higher crustaceans is striking; of the decapods, only a few species of shrimps are present in the higher latitudes.* [26] Hermit crabs and true crabs seem to be entirely absent.

The polar plankton is distinguished by the great scarcity of free-swimming larvae. It also differs from the warm-water plankton in its distinctive copepods, some of which appear in enormous numbers of individuals, such as the large *Calanus hyperboreus* (9 mm. long) in the Arctic Sea, the great abundance of which is responsible in a large measure for the wealth of animal life in the Arctic. Scarcely less characteristic are the hyperiids and schizopods, and great quantities of various species of pteropod snails among the mollusks. Hydromedusae are much more abundant in cold seas than in warm water. The abundance of diatoms in the polar seas furnishes many plankton animals both in the north and the south with siliceous skeletal material, used, for example, by many radiolarians (species of *Aulocleptes*) and a number of ciliates (*Lamprotintinnus*).[20]

The density of population of the pelagic animal life shows characteristic differences. At least in the Atlantic, cold waters are richer in life in general and in animal life in particular than warm water. Lohmann [21] obtained an average count of 2500 organisms in 1 liter of cold water and only 700 in warm water above 20°, a fact at least of value as a ratio. Hensen summarizes the results of the investigations to date by saying that the arctic areas are richer in plankton in the summer and the tropical areas are meager throughout the entire year. At any rate, a very definite periodicity exists in the plankton of the polar areas. At the Gauss Station in the Antarctic, the volume

* In the Arctic, *Sclerocrangon ferox, Bythocaris* and *Hymenodora glacialis;* in the Antarctic, *Crangon antarcticus* and *Choriomus antarcticus.*

of plankton varied in the following proportions during the course of the year: it showed its minimum in winter (June to December), increased sevenfold in January, increased to twenty-five fold in February, and reached its high point in March when it was fifty times greater than in winter; decreased in April to twenty times its lowest volume, and returned to minimum volume again in May. In the North Sea, a vertical pull of a net through which 1000 tons of water was seined brought up about 400 *Calanus* in February and about 4,000,000 in April.[17] The enormous increase in summer is naturally determined in large part by the strength and duration of the light; a thorough light penetration of at least the surface layers for about 20 hours in summer must be extremely favorable for the development of the phytoplankton, and thereby much food is provided for a rich fauna; in winter, on the other hand, plant life is entirely wanting because of lack of light, and only dormant stages survive. Foodstuffs necessary to the plants accumulate, while animals dependent upon plants survive only by reason of stored reserves. Whether the entire year's production of the polar sea is greater than that of the tropical cannot yet be stated with certainty. Hensen is inclined to believe that it is, but his evidence is inconclusive.

The abundance of the lower forms of animal life in the upper strata of cold seas attracts a large number of bird and mammal predators; these are lacking in the tropical seas or occur sparingly, or in limited regions with special conditions. Sharks occupy a similar place in the food chain in the warm-water pelagial. The birds, which breed in enormous numbers along the coasts of the polar seas, on islands and cliffs, during the warmer seasons, are entirely dependent upon the sea for their nourishment. Many, especially the diving birds like the eider ducks (*Somateria*), feed on benthic animals; others such as penguins feed on pelagic fishes and on plankton. Some of the mammals of the polar seas, such as the whalebone whales or the crab-eating seals (*Lobodon carcinophaga*), which feed upon Euphausidae, and the Weddel seal, live on plankton; others, like the walrus, depend on benthic life for food. Still others are active predators, and live mainly on cuttlefishes and fishes. Better testimony could scarcely be given for the abundance of life in the polar seas during the summers than the immense numbers of these birds and mammals that found their sustenance there before their decimation by man. Thus, according to Heuglin, 700 walruses were killed in a few hours on Bear Island in 1606, and fully 900 the following year, and the former

vast abundance of the fur seals on the Arctic islands is one of the most notable of animal phenomena.

Comparisons of the animal communities of tropical seas with those of polar regions have been made primarily on the basis of the situation in the Atlantic, where relationships are best known. Even here the difference in density of population in warm and cold waters need not be related to temperature alone. Unusually large amounts of plankton from the tropical Indian Ocean are reported.[5,13] In comparison with the equatorial Atlantic, the Indian and Arctic oceans and also the Antarctic have a greater development of coast line and are relatively more shallow. Similar relations prevail in the East Indian Archipelago and undoubtedly affect the development of pelagic life. Comparisons of the animal life of tropical and polar seas demonstrate marked differences, but, as is to be expected, the animal communities of cool and temperate areas, while fairly closely allied to those of higher latitudes, are not sharply differentiated from those of tropical and subtropical waters. The greater temperature variations in the North Atlantic, amounting in the southwestern portion of the North Sea to 9° even on the bottom, and in the shallow coastal waters of less than 20-m. depth to 15° or more, favor the development of eurythermal animals that may even invade the colder seas and thrive better there on account of the greater uniformity in conditions. In addition to the Arctic area in the North Atlantic, with a temperature below 2°, a boreal area with surface temperature of 2–8° and a temperate area with a surface temperature above 8° have been distinguished, each characterized by dominant forms. It would require too much space to consider these subdivisions, which are well discussed by Ekman.[9]

Bipolarity

The investigations of marine life stimulated by the *Challenger* Expedition (1872–1876) disclosed what seemed to be a surprising number of animal species found in Arctic and Antarctic waters and unknown from intervening seas. Such distributions led to an active discussion of the phenomenon of "bipolarity." By extension of ideas, bipolarity came to mean any northern and southern distribution discontinuous across the tropics.

Early lists of bipolar animals were focussed especially on the existence of identical species in two widely separated populations, and led to attempts to account theoretically for the present discontinuity of their ranges. The relict hypothesis of Théel[39] (1886) elaborated by

Pfeffer [33] (1891) explained the known discontinuities by the supposition of world-wide uniformity of climatic conditions and of animal life in the Cretaceous seas, with subsequent evolution predominant in the equatorial or low-latitude seas, and thus with survival of the ancient forms in the waters of high latitudes.

Ortmann (1896,[30] 1899 [32]), opposed the structure of hypothesis built on the reported facts of species bipolarity, and D'Arcy Thompson (1898 [40]) presented a sharp critique of the suppositions of specific identity. It could be shown that in most of the forms in question the evidence of identity was extremely inadequate. Since the turn of the century, furthermore, there have been continuing discoveries of supposedly "bipolar" animals at greater depths (and absent at the surface) in equatorial waters. These have reduced the necessity for a relict hypothesis, and it was this continuous connection of the two polar seas through the colder water at considerable depths in the equatorial zone that had been pointed out by Ortmann in his so-called "Migration Hypothesis." The residual series of species thought to be bipolar is critically examined by Ekman [9] (1935, pp. 327–329), who points out that actual disjunction of range remains to be proved for even this list. The unsatisfactory nature of the examples of bipolar forms cited at the species level is illustrated by the North Atlantic ascidians, *Didemnum albidum* and *Botryllus schlosseri*, which are reported also from New Zealand seas. Such examples recall the isolated occurrence of the horseshoe crabs in the western North Atlantic and the tropical East Indies rather than any distributional phenomenon properly to be referred to as "bipolarity."

Turning to bipolar genera, in which a series of Arctic and a series of Antarctic species form what is evidently a natural group, it is quite evident that a genuinely bipolar distribution is demonstrable in a considerable series of forms. The examples cited by Ekman are the Hydroid genera *Lampra, Myriothela, Grammaria,* and *Sclaginopsis,* the trachymedusae *Ptychogastria* and *Botrynema,* the gephyrean *Priapulus,* the euphausian *Thysanoëssa,* the cephalopod *Bathypolypus,* the sardine *Sardina,* and the entire group of stalked medusae, the order Stauromedusae. Even in groups that are widely distributed there may appear geminate species that are respectively Arctic and Antarctic, as in the hydromedusan *Bougainvillia.* That the modern separated distributions represent an earlier continuity is evident from any evolutionary consideration, and the resultant forms are thus both relicts in the sense of Pfeffer and the results of "migration" in the sense of Ortmann.

The phenomena of bipolarity have an ecological aspect somewhat independent of the systematic relations of the species or their geological history. If the deep-water equatorial forms are found at the surface in both the Arctic and Antarctic, the phenomenon is certainly one of "bipolarity" and one of essential interest to ecological animal distribution. The parallel development of great masses of plankton in the long summer in Arctic and Antarctic seas, with complex attendant food chains, is not less interesting for the fact that the seals of the two regions belong to different genera or that there may be distinct types of whales. Finally, there remains the development of parallel cold-water "varieties" that may equally as well be independently derived from the intervening warm-water form or relict populations of the primary form from which the warm-water form has evolved.

Animal communities of seas, bays, and gulfs

As stated at the beginning of the present chapter, the physical conditions of the partially separated seas, bays, and gulfs are associated with the lessened interchange of their water with those of the main ocean. Important differences in temperature, salinity, and other conditions are found in each such sea or bay; such differences tend to separate its animal communities, not only from those of the ocean proper, but from other, similarly characterized subdivisions.

The peculiarities of the lesser seas rest primarily on their salt content, which is regulated by the ratio between influx of fresh water and evaporation. The tropical areas of the ocean show a noticeable increase in salt content as a result of increased evaporation; in the polar seas, on the other hand, a decrease in salinity takes place in the summer because of the small amount of evaporation and the huge amount of water melted from ice and snow. The salt content of the ocean and of various bays and land-locked seas has been given previously (p. 203), and is summarized for the Baltic Sea by the lines of equal salinity in Fig. 79.

Temperature distribution in small seas frequently differs greatly from that of the ocean. The temperature of the surface layer is not much different from that in the neighboring part of the ocean, although the highest surface temperature always occurs in the lesser seas, reaching 34.3° in the middle part of the Red Sea and 35.6° in the Persian Gulf,[18] whereas in the open ocean the summer temperature in some places rises to 29°, and near coasts and in the western Pacific to 32°. Further, the decrease in temperature according to depth is

different in many small seas from that in the ocean. The low temperature of the abyssal water masses is explained by the slow creep of the denser polar waters along the bottom. But if the entrance to a deep sea such as the Mediterranean (see Fig. 15) is closed for the deep water by a bank or shallow strait, the cold water from the depths of the ocean cannot enter and the temperature of the restricted sea bottom remains constantly at that of the lower layer of the inflowing ocean water. In the Red Sea, the temperature of 21.5° extends from a depth of 700 m. to its greatest depth at 2190 m., whereas in the ocean at such depths the average temperature is 2.11°. Similarly, in the Sulu Sea, the temperature from a depth of 800 m. to the bottom (more than 4000 m.) remains at 10.3°.

The Gulf of California is somewhat comparable to the Red Sea in general climate, shape, and distance from the equator, though it opens farther to the north. The two bodies of water are quite unlike hyrographically in that the Gulf of California is in connection with the adjacent ocean down to nearly 3000 m., whereas the greatest depth of the sill at the opening of the Red Sea is only about 100 m. In consequence deep water from the tropical ocean can enter the Gulf of California, come to the surface towards the north, and support a rich animal life. Basins within the Gulf follow the rule documented in the preceding paragraph of having bottom water with the relatively high temperature controlled by the depth of the containing sill.[38]

The slight movement of the deep waters of many seas caused by the shallowness of their connection with the ocean leads to the further result that the oxygen content is low and that substances lethal to animal life may accumulate. In the deep basins of the Baltic Sea, in the deep parts of the Mediterranean, especially of the Levantine and Ionian seas, and apparently also in the depths of the Red Sea, the water is poor in oxygen and rich in carbon dioxide. Animal life is therefore sparse. Thus the lack of ptychobranchiate ascidians,[25] the unusual scarcity of Hexactinellida (only two species),[36] and the small number of mussels and snails [37] in the depths of the Red Sea is striking. In the depths of the Black Sea, whose connecting straits are only 50 m. deep in the shallowest part, there is a considerable amount of hydrogen sulphide, amounting to 0.33 cc. per liter even at 180-m depth, so that from that depth to the bottom all life is absent, with the exception of anaerobic bacteria.

Furthermore, in the seas, tide movements are often very small. This is not universally true; e.g., the flood tide for the Red Sea is 1-2

m.; in the Mediterranean, on the other hand, it amounts to scarcely 0.5 m.; in the Baltic at Jasmund it is 3.6 cm. on the average, and at Memel 1 cm. The tide flat is accordingly very small in these seas, and this has its effect upon the distribution of the intertidal inhabitants; for example, shore birds are much scarcer, as they find much less food along such a coast than along a shore whose tide flat is more extensive.

Finally, the formation of species is favored by the isolation of seas in conjunction with the peculiar conditions existing within them. It is therefore to be expected that these seas should have endemic varieties and species, which become more numerous with increasing isolation. The Mediterranean and Baltic seas will be discussed below in this connection. In the Red Sea the number of endemic animal species known to 1918 was: 1 hexactinellid, 35 bivalves (24 littoral and 11 from the deeper parts), 21 snails, 4 crustaceans, together with 8 ptychobranchiate ascidians;[16] further investigation of ranges in near-by waters may decrease these numbers. The Sulu Sea in spite of its small size contains a significant number of endemic and often very distinct species, e.g., 17 endemic species of macruroid fishes, corresponding with representative species in the neighboring seas.[12] In the Caribbean Sea a characteristic deep-water fauna has developed from descending littoral species.

The Mediterranean Sea

Only a few seas have been adequately investigated as yet, but some, such as the Mediterranean and the Baltic, are among the best-studied marine areas. These may therefore be further considered at this point as examples of the peculiar animal communities in their special environment.

In the Mediterranean, primarily because of the shallowness of the Straits of Gibraltar and the low ratio of inflow to evaporation, both salinity and bottom temperatures are higher than in similar depths of the neighboring Atlantic. For these reasons the abyssal animal communities also differ from those of the connecting ocean, although otherwise there is marked similarity in the two populations.

The temperature barriers, whereby stenothermal, warmth-limited animals are prevented from entering greater depths, disappear completely. Thus the number of species of starfish that go down into the lightless depths of the Mediterranean is much greater than in the Atlantic.[22] Alciopidae, which as warm-water animals stay in the surface layers of the ocean, live at great depths in the Mediter-

ranean;[2,6] heteropod and pteropod snails, which do not ordinarily descend deeper than 300–350 m., are found below 1000 m. Appendicularians, limited in the Atlantic to the lighted layer, also descend to a depth of over 1000 m. Pyrosomas, lacking in the ocean below 400 m., have been obtained[2] down to 1200 m. at Naples; salpas, also chiefly surface animals, are at times found in masses (*Salpa maxima*) among the contents of the fishermen's bottom nets.[1]

The high temperature of the deep water makes it possible for many stenothermal animal species of warm water to survive the winter in the Mediterranean. In the Gulf of Naples, a number of fishes common in summer are not caught in the cold season, e.g., *Serranus gigas, Julis turcica.* Experiments in the Naples aquarium show that these animals do not tolerate a decrease in temperature below 12°; they become inactive, sink to the bottom, and die with further decrease in temperature.[19] Such forms can survive the winter in the warm Mediterranean depths. Thus tropical and subtropical forms, which are carried toward the Straits of Gibraltar by the southern arm of the Gulf Stream in some numbers, can survive in the Mediterranean. Such forms include the scyphozoan *Charybdea*, the tropical jellyfish of the genus *Liriope*, many siphonophores, many heteropods, the ocean sunfish *Mola mola*, the turtle *Caretta caretta*, and many others.

But the deep water of the Mediterranean does not everywhere contain sufficient oxygen to permit active animal life. Though in some places, e.g., in the northern part of the Balearic Sea, in the southern part of the Adriatic, and in the Aegean, an active descent of the surface water into the deep has been demonstrated,[8] in other parts the deep water is rich in carbon dioxide and is therefore so poor in animal life that Forbes' early investigations of this area led to the erroneous conclusion that the depths of the oceans in general were without animal life.[11]

Conditions in the western part of the Mediterranean nearer the Straits of Gibraltar and the open ocean are more favorable for animal life than those in the eastern half, and many animal groups such as starfishes, salpas, and prosobranch snails have fewer species in the eastern than in the western half. The exact cause of this eastern decrease is unknown, just as it is still an unsolved problem why many pelagic animals present in large numbers directly west of the Straits of Gilbraltar do not occur in the Mediterranean. This applies, for example, to the fishes *Argyropelecus olfersi* and *Vinciguerria sanzoi* and to a number of eel larvae, whereas the larvae of the river eel

"Leptocephalus" brevirostris pass through the Straits of Gibraltar in large numbers.[35]

Species of the most widely separated animal groups, benthic and pelagic, are known only from the Mediterranean. In this category belong, among others, two species of starfish (*Astropecten spinulosus* and *A. jonstonii*), the barnacle *Pachylasma giganteum,* 21 decapod crustaceans, 2 species of salpas, and 4 species and varieties of Appendicularia. Of fishes, the anchovies (*Engraulis encrasicholus*) contain a race distinctive of the Mediterranean; *Clupea papalina* is the mediterranean form of the northern sprat (*C. sprattus*), and the sardine (*C. pilchardus*) never attains the length of the oceanic form of this species (maximum of 18 cm. in length compared with 26 cm.).[16] These species may be considered endemic only with reservations; yet the faunae of the French and Spanish coasts of the Atlantic, as well as of the Azores and the Canary Islands, are fairly well known, so that it may be assumed that a large number of those species do not occur in the neighboring seas.

The Baltic Sea

In many respects, the Baltic Sea [3, 4, 23, 34] is just the opposite of the Mediterranean. A widespread land area sends its waters into the relatively small and shallow basin, and the great influx of water is accompanied by the smaller loss through evaporation in these latitudes. For these reasons the salt content is small, and from the Baltic relatively large quantities of water flow outward into the ocean, whereas the inflow from the ocean is much less. As the outflowing water is less dense, on account of the lower salt content, the outflow occurs on the surface, and the inflow is at deeper levels, the opposite of the Mediterranean situation. The salt content, even of the surface water, is greatest in the western Baltic near the connection with the ocean and distant from the great inflow of fresh water, and decreases toward the east until a salt content of only 2‰ and less is reached in the surface water in the Gulf of Bothnia (Fig. 78).

As a result only very euryhaline forms, brackish-water animals, and a few from fresh water live in the Baltic Sea. Pike, perch, and several other fresh-water fishes have been caught in the Strela Sound between the Island of Ruga and the mainland, and the number of fresh-water species rises in the gulfs of Finland and of Bothnia. The number of species of marine animals decreases regularly from the west toward the east; thus 55 species of decapod crustaceans are found in the Kattegat, 9 in Kiel Bay, 2 in the Baltic Sea basin, and only 1 in

the Gulf of Finland; of the annelid genera, *Nephthys* and *Nereis*, the North Sea contains at least 20 species, the western Baltic 9, the Baltic basin 5, and only 2 species extend much beyond the east coast

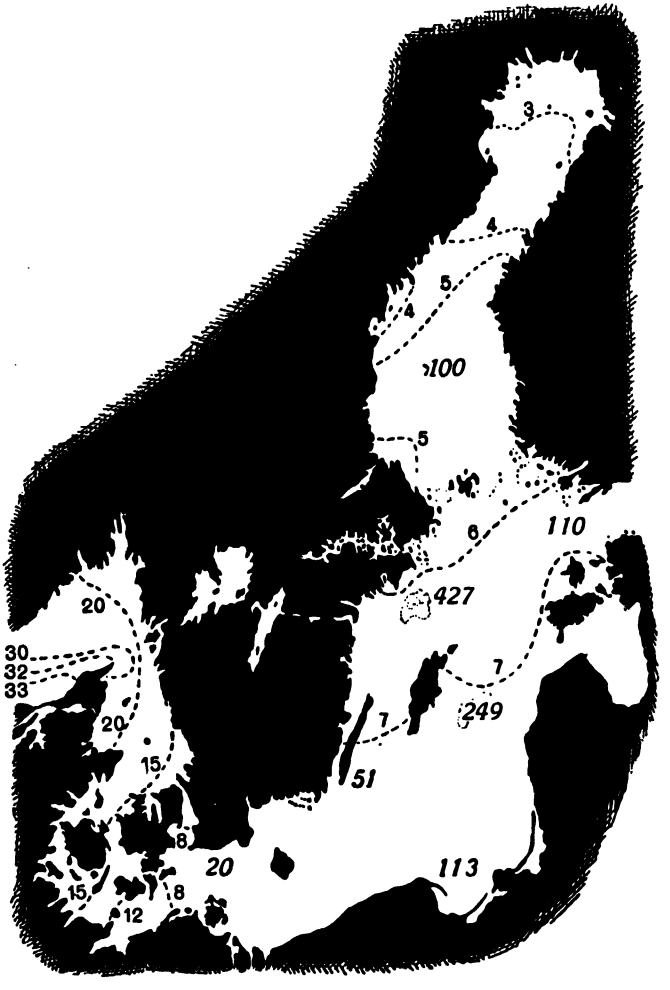


FIG. 78. Map of the Baltic Sea. The salt content per thousand in smaller vertical figures, the depth in meters in larger oblique figures. After Brandt.

of Sweden.[14] Differences also occur in the plankton. Copepod species and individuals become fewer toward the east, while the cladocerans *Podon* and *Evadne* increase; and to these may be added *Bosmina maritima* and farther to the northeast a large number of rotifers. The salt content of 3.7‰ seems to represent a limit that even eury-

haline sea animals pass with difficulty; only the barnacle *Balanus improvisus* and the bryozoan *Membranipora pilosa* extend beyond it.

Many immigrants from the North Sea are not able to propagate in the Baltic, and they restore their numbers only by means of ever-renewed reinforcements, e.g., the copepod *Paracalanus parvus.*[28] Of 11 species of marine fishes, which are common to the Gulf of Finland and the North Sea, 9 are here unfertile; only the sprat (*Clupea sprattus*) and the needlefish *Nerophis ophiodon* propagate in the Baltic. Perhaps for the same reasons that bring about their decrease in numbers

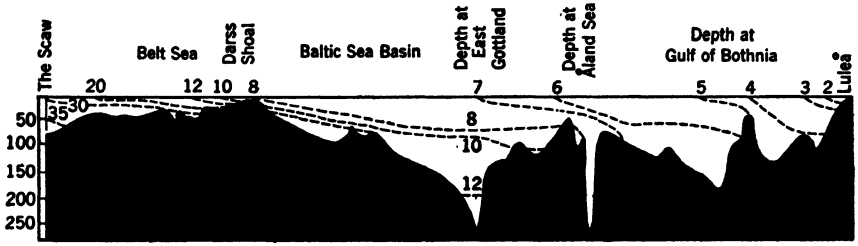


FIG. 79. Longitudinal section of the Baltic Sea, from Skagen to Luleå, with isohalines, in ‰, according to Ekman; depths in meters at the left. After Brandt.

of species, the Baltic animals decrease in size the farther east they live.

The Baltic Sea is in general a shallow sea, which increases in depth toward the east; the average depth amounts only to about 67 m. But in a few limited places (see Figs. 78 and 79) the bottom drops off to rather great depths; the most important of these depressions, located south of Stockholm, has a depth of 427 m. In these depressions, the salt content seldom goes below 12‰, but in spite of this, they contain only an impoverished fauna represented by few individuals of small size. At depths of 80 m. only 17 species of bottom forms are found, 6 species of worms, 6 of crustaceans, 4 of bivalves and 1 of bryozoans, and indeed only those that occur also in shallow water; at more than 150-m. depth 2 species of worms, *Harmothoë sarsi* and *Priapulus caudatus*, occur, and at greater depths than 230 m. all animal life is absent. The reason for this condition lies in the low oxygen content and the accumulation of carbon dioxide. The water at 0-60 m. depth is about one-third saturated with oxygen, in the deeps of East Gotland at a depth of 100 m. only one-fifth, and at 200 m. only one-fifteenth. On the other hand, while only 32 cc. of carbon dioxide per liter is present at a depth of 0-60 m., 36 cc. is present at

100 m., and 41 cc. at 200 m. Rarely, on the occasion of continuous easterly storms, the surface water recedes in the east and an undercurrent of water rich in oxygen and salt advances farther toward the east, bringing fresh supplies to the depressions. After such storms richer animal life becomes possible in these local deeps; thus, 3 species of maldanids (Annelida) were taken in the Danzig deeps in February, 1904, while only 1 species of annelid normally occurs in the western Baltic.[27]

Geologically speaking, the Baltic is still young. It has retained a number of relicts from its connection with the White Sea by means of the Ladoga and Onega seas, e.g., the starworm, *Halicryptus spinulosus*, which likewise occurs at Spitzbergen and the White Sea, but is lacking in the North Sea, the Skagerrak, and the Kattegat,[10] so also *Mysis oculata*, which is represented by *M. relicta* in the neighboring freshwater lakes, is found in the northern seas but is absent in the North Sea. It is because of this geological youth of the Baltic that the number of endemic species is small. Apart from a few races of fishes, the copepods *Pseudocalanus elongatus* and *Temora longicornis* may be mentioned as endemic.

The peculiar development of the animal life in such seas shows how obviously the composition of animal communities depends upon environmental conditions, and the study of the effects of the freshening of the waters of the eastern Baltic Sea makes a suitable transition between the consideration of marine animal communities and those of the fresh waters, which are treated in the following section.

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Part 3

The Distribution of Animals in Inland Waters, A Phase of Limnology

16. *The Environmental Factors in Inland Waters*

THE FAUNA OF INLAND WATERS DIFFERS IN MANY IMPORTANT RESPECTS from that of the ocean. Whole groups of animals, such as echinoderms, brachiopods, gephyreans, squids, and tunicates, which are plentiful in the ocean, are wholly absent in inland waters, and many others have fewer species, which are often less rich in individuals: for instance, the Coelenterata, the Nemertinea, the annelids, of which only a few species are found, and the Bryozoa. Only a few groups are more plentiful both in number of individuals and of species in inland waters than in the ocean, e.g., ciliates, Gastrotricha, and rotifers; or are essentially restricted to lakes and rivers, as are amphibians. As has been stated before (p. 43), the reason for these differences, especially the difference in number of individuals and species, is that the living conditions in inland waters vary so much from the optimum that they demand certain definite adaptive adjustments that relatively few gill-breathing types have been able to acquire.

The greatest differences between the environments represented by oceanic and inland waters relate to space and time. The ocean covers immense portions of the earth's surface and is one continuous body with only partially separated arms or seas, whereas the fresh-water lakes, rivers, and inland seas form innumerable bodies of water of every size, spread over the continents as islands are in the sea, each system more or less isolated from the rest. The ocean has probably been in existence as one body of water since the beginning of geological evolution, or at most separated into a few large divisions for comparatively short periods of time. Inland waters, on the other hand, as a rule are of comparatively short duration and appear and disappear, geologically speaking, in rapid succession.

The restriction of space becomes evident in the extraordinary variation in size of inland bodies of water. They are usually of no great extent or depth. With the exception of the Caspian Sea, which has an area of 438,000 sq. km., no lake or inland sea has an area of more than 100,000 sq. km. Only 17 lakes and seas have a surface area of more than 10,000 sq. km. (Lake Superior has 82,360 sq. km.). Most inland waters are much smaller, and we find all gradations of size down to the ponds and puddles. The depth of inland waters also varies, and, compared with the ocean, even the deepest are shallow. The average depth of the ocean is about 3795 m., while only two inland waters (Lake Baikal, 1706 m., and Lake Tanganyika, 1435 m.) have a depth of more than 1000 m., even in their deepest part. Only a few are deeper than 400 m.; the majority reach a depth of less than 100 m.; Lake Superior is about 305 m. in greatest depth. Lakes, ponds, and pools decrease in depth until they merge into marsh. The same gradation of depth is noticeable in running waters. Consequently the extent of shore line and bottom in relation to amount of water is very much greater in inland waters than it is in the ocean, and, as a result, the ratio of extent of suitable habitat for sessile forms and free-swimming forms is very different.

Salt content

The variation of the dissolved substances of inland waters is great. In the ocean, in consequence of the circulation of masses of water, the differences in the amount of dissolved material are constantly being equalized, so that its variation is always within narrow limits. Nearly all inland waters, on the other hand, have chemical constitutions of their own, depending upon their substrata and their tributary areas. In streams whose contents change rapidly and whose tributary area, compared with the waters they contain, is widespread, such differences are equalized, but are present even in such waters.

Inland waters are usually fresh waters, i.e., they contain relatively little dissolved material. The content of common salt, especially, is less than in the ocean. The water of the Rhine, for instance, contains only 0.14 part of NaCl to 1000 parts of water. Nevertheless, a good many inland waters contain a considerable amount of salt. There are salt springs whose waters, to be sure, soon become fresh when they flow into other streams; but where standing waters are fed the salt content rises, and so, aided by evaporation, salt lakes are formed. The minimum ratio for a salt lake is 0.3‰, but the ratio is often much higher, as is seen in the Aral Sea where it is 10.8‰; or in the salt

swamps of Laneuveville in Lorraine where it is 54‰; or in the Dead Sea where it is 231.3‰. In the salt seas of the steppes, where periodic rains freshen the water and long periods of evaporation during the dry season concentrate it again, the salt content changes with the seasons, and the composition of the fauna changes in consequence.

Fresh waters also vary among themselves in the content of other salts, especially of calcium and magnesium. Variability of lime content makes fresh waters very different from sea water, which contains very little calcium carbonate. We distinguish between soft waters, poor in lime, and hard waters, rich in lime. The calcium carbonate content is low in the waters of granitic or sandstone areas, high in waters flowing over dolomite or limestone. This lime content is a decisive environmental factor in animal distribution. Fresh-water sponges, Bryozoa, and the cladocèran *Holopedium gibberum,* for instance, are intolerant of excess lime. For that reason we find no Spongillidae or Bryozoa in Montenegro,[16] and in west Ireland the mountain lakes are much richer in sponges than the limy lakes;[20] *Holopedium* is most commonly found in the mountain lakes of Europe, Iceland, and America, but not in the Jura or in the limestone Alps. A wealth of lime in water is favorable for the development of snails and mussels. *Neritina,* for example, occurs in the lime-rich lakes of the Åland Islands but is not found in the inland waters of Finland [11] that are poor in lime. The smaller size of snails and mussels in Victoria Nyanza has been ascribed to the want of lime in the water.[3]

In the Highland Lake District of Wisconsin, mollusks are present even in acid water with a *p*H as low as 5.1 and a calcium content as low as 0.1 part per million. *Pisidium,* the finger-nail clam, and *Campeloma,* the gilled snail, are characteristic forms in clear lakes with soft waters that have even less dissolved carbonates than the typical bog-lakes with colored, acid waters. *Pisidium* has very thin shells when growing under such extreme conditions, while in some bog-lakes, with a *p*H of 5.1 to 6.1 and with 3.0 to 5.0 p.p.m. of dissolved carbonates, large, well-developed specimens of *Pisidium* have been taken. Mussels of the genus *Anodonta,* growing in extremely soft and acid waters, have shells so thin and poorly mineralized that when fresh and wet they can be bent through almost 20° without breaking.[15]

In the same lake region, the distribution of fresh-water sponges is, to some extent, correlated with the mineral content of the water. *Spongilla lacustris,* although found under other conditions, attains its best development in small lakes of dark color, high organic content, and rather low mineralization. In water in which the content of silicon

oxide is below 0.4 mg. per liter and which is also low in total solutes, as the mineral content decreases, *S. lacustris* shows a progressive attenuation of its spicules. If the water is sufficiently soft, the microspinal dermal spicules are lost; this is the more interesting in that these spicules have been regarded as an important species character. Similarly *Tubella pennsylvanica* shows decided variations correlated with the degree of mineralization of the water; in some cases these abrogate accepted generic criteria.[8]

Other inorganic compounds are also dissolved in great quantities in many inland waters. Borax, for instance, is present in solution in the Puga creek in Ladakh (Kashmir). Crustacea and fishes are nevertheless found there.[6] Sarasin found a lake in New Caledonia whose waters were very rich in iron salts, but in which the animal life was inhibited by this factor. Crustaceans, snails, and fishes were diminutive. In regions of alkaline flats remaining from the evaporation or drainage of formerly extensive fresh-water lakes in the American Southwest, the fishes and other life may be restricted to springs, even sometimes to warm springs, bordering the site of the former lake.[7]

Hydrogen sulphide in inland waters is just as deadly to animal life as in landlocked arms of the ocean; some Swiss lakes are unfit for animal life at depths below 13 m. because of the H_2S content of their waters. The surface animals that descend into the depths periodically or whose winter eggs sink to the bottom are at a disadvantage.

Organic content

Still other inland waters, rivers as well as lakes, are characterized by their content of organic matter. Moor and bog waters and the lakes fed by streams from such sources, and the waters in rivers flowing through extensive swampy virgin forests are especially rich in humus, which gives them a dark, blackish brown color. The waters of the Dismal Swamp in eastern North America afford an example, and the multiplication of the name "Rio Negro" on the map of South America reflects this phenomenon. High humus content makes such waters uninhabitable for many animals. The Obi River as it flows through the plains takes up so much dirty steppe and morass water that it becomes stagnant and foul, especially when frozen over, so that certain migrating salmon that are found east and west of the Obi do not enter this river, and the regional salmon (*Salmo coregonoides*) is not found in the main stream but only in the mountain tributaries.

A contamination of inland waters, especially through organic matter, often occurs near the settlements of man. The degree of con-

tamination can well be estimated by the composition of the fauna. Through the disintegration of highly complex organic compounds, the oxygen content is reduced and the hydrogen sulphide, iron sulphide, and carbonic acid content increased. In such waters only a few species of animals thrive. These are called saprocoles, and consist mostly of protozoans, especially flagellates; of Metazoa only the slime-worm *Tubifex* and the larvae of the drone fly *Eristalis* are generally present, both in great numbers. Farther down from the origin of contamination, where the albuminous substances have begun to be transformed into amino acids, etc., and oxygen is being given off by green plants, the mesosaprocoles live: very many protozoans; numerous worms and rotifers; the mussel *Sphaerium corneum;* the isopod *Asellus;* and finally a number of insect larvae. Farther down in comparatively clean water some of the oligosaprocoles, e.g., *Gammarus,* and some lower crustaceans appear, as well as a number of species of fishes. Finally, in practically pure water mayfly nymphs, stonefly nymphs, and crayfishes are found. The effects of pollution by city wastes in certain American rivers are discussed in the final chapter of this book.

Oxygen tension

The oxygen content of inland waters is also subject to much variation. The water of mountain streams is well aerated in the spray of rapids and waterfalls. In the lower reaches of rivers the amount of oxygen is less and depends upon the number of oxygen-producing plants as well as upon the amount of contamination from tributaries. In the Elbe, near Hamburg, the oxygen content fluctuates between 4 and 8.8 cc. per liter.[21] In standing waters only the relatively small, smooth surface is involved in the absorption of oxygen from the air. On the other hand, the water may be oversaturated with oxygen during the daytime because of the production of this gas by green plants, and at 18° it may contain over 9 cc. among thick *Potamogeton* or *Spirogyra* instead of 6.5 cc. per liter,[24] which is the usual amount at normal saturation at 18°. The deep water of many lakes is as rich in oxygen as the surface water, e.g., in the Alpine lakes and in the clear Eifel crater-lakes; in others, however, the deep water is poor in oxygen content, especially in shallow lakes with muddy bottoms or during the summer, in lakes with a thermocline. This is, of course, of the greatest importance for the animal life on the lake floor. The presence of salmon and lake trout (*Salmo lacustris*) is also regulated by the oxygen content of the water,[6] for they are found only in waters with a high oxygen content. Thus Lake Nantua in the French Jura

has two tributaries, one of which is much richer in oxygen than the other. The lake trout ascends only the former for spawning.

Temperature

The temperature of inland waters, like their chemical content, is rendered extremely variable by their small size. The shallower depth of many allows a rapid and intensive heating during the day but also an equally rapid cooling at night, so that there are great variations in temperature, which are more marked, other things being equal, the shallower the water. These changes are not so great as in the atmosphere, but are still much greater than in the ocean. Seasonal variations, as well as daily variations, are very great, and in extreme cases the waters may evaporate or freeze. Such conditions again naturally bring about a definite selection of fauna.

Unlike sea water, pure water is densest at 4°. This determines a condition of greatest importance for the survival of fresh-water animals during the cold season in the temperate and frigid zones. When the surface waters cool they become heavier than the warmer waters beneath them, and sink while warmer waters rise to the surface; aided by winds this overturn continues until the whole mass is cooled to 4°. Further cooling makes the water less dense, so that the surface water does not sink as it cools below 4°. Finally a covering of ice forms, in contact with which somewhat colder strata of water are found, but the temperature of the deep water remains at 4°. The ice covering, which is confined to the surface by the fact that it is less dense than water, is in itself a shelter that slows further cooling. It is because of these facts that water a few meters deep, even in the polar regions, seldom freezes to the bottom. The peculiar temperature stratification in lakes resulting from the sinking of the cooled surface waters will be discussed in more detail in Chapter 18.

Heat budgets of lakes

The amount of heat necessary to melt the ice and to raise the temperature of the water of a lake from the winter minimum to the summer maximum is called the annual heat budget.[1, 10]

Lakes of eastern United States about 10 km. in length by 2 or more km. wide and with a mean depth of about 30 m. have heat budgets (of the water itself but not of the lake as a whole) on the order of 30,000 to 40,000 gram-calories per square centimeter of the lake's surface. These lakes of approximately the latitude of Chicago tend to have a somewhat higher and more uniform heat budget than

those of Europe, and there is no evidence of an increase in the annual heat budget from latitude 40° to 60° N. For most lakes, the majority of the annual heat budget is distributed as a result of wind action.[2,10]

Light penetration

As in the ocean, many factors influence the penetration of light into fresh waters; of these the amount of suspended matter is particularly effective in excluding light. Crystal Lake, Wisconsin, with highly transparent water, has approximately the same light penetration as Puget Sound. In Wisconsin lakes, the depth at which light is reduced to 1% of that at the surface was found by Birge and Juday to vary from 1.5 to 29 m.[2]

The amount of light in inland waters is markedly influenced by their shallowness. Only a few of these waters are more than 300–400 m. deep; most of them are shallower than 30 or 40 m. But even in the deeper ones, the shallow shore region, despite its smaller surface area, is far better populated than the deeper water. This comparison is the more striking when considered in connection with similar relations in the sea. Light penetrates to the very bottom of many lakes and makes possible a rich flora rooted in the lake floor. The roots of plants make use of the mineral substances of the bottom much better than if these were merely dissolved by the standing waters above them; and the production of organic substances is accordingly increased. Besides this, vascular plants thrive in much greater abundance in fresh water than in the seas; these also are softer and are more easily accessible than land plants as food for snails and insect larvae, because they need no protection against drying and less mechanical supporting tissues; they therefore disintegrate faster after dying off, and furnish food for the detritus feeders. For these reasons the fresh waters in general are much more thickly populated with living forms than the ocean. Lohmann, in comparing the value of the catches in the nannoplankton of the tropical oceans, of the cool open ocean, of coastal waters of the Bay of Kiel, and in fresh water, got this ratio: 1:10:988:9017. A lake in Holstein produced 217.5 cc. of plankton per cubic meter of water, while in the ocean the whole mass of water under 1 sq. m. of surface area produced only 150–180 gm. of organic substance.

Multiplicity of niches

The multiplicity of the environmental conditions in inland waters is great. Every gradation in water movement is found, from foaming,

falling water, tumbling from rock to rock in the mountain torrents, to the lazily flowing streams of the plains. The standing waters, especially those of larger surface area, are often whipped into waves by the wind and beat heavily against their shores, while many ponds have placid surfaces and stagnant depths. Tides are practically absent; about 5-cm. tidal differences have been reported for Lake Michigan. Their place is taken to some extent by the seiches,* which also occur along seacoasts. Just as in the ocean, water movement has a decisive influence on living forms. There are rheocolous animals, adapted to a more or less strong current, and limnocolous, which thrive only in quiet waters.

The manifold gradations in chemical content, temperature, light, and water currents are again variously combined in the separate bodies of water. There can be no doubt that the far-reaching variation of living conditions in inland waters is primarily a result of the small size of the bodies of water as compared with the ocean. The numberless possibilities of special differentiation under the influence of the environment determine an immense wealth of species of animals, and this is further increased by very decided isolation. Standing waters are often entirely isolated from each other and, with their tributaries, often form separate systems whose contained life is connected only by passive or accidental distribution. Running waters, to be sure, are continuous over greater areas, but the individual river systems are separated from each other by watersheds. And even though they all empty into the ocean, this forms an insuperable barrier for most forms because of its salt content.

The wealth of species in the inland waters differs from that of the ocean. In the ocean there are much more numerous structural plans within which the species are invariable over wide ranges. In inland waters the number of types is limited, but within individual species an almost unlimited variation is the rule, at least among the less vagile forms, so that one might almost say, as the number of lakes, so the number of geographic forms. Variability of animals in inland waters, especially in fresh waters, may be further illustrated.

Ceratium hirundinella (Fig. 80), one of the armored flagellates, has three and four horned forms, and the size varies between the extremes of 92 μ in Lake Como and 707 μ in Lake Schwendi. List [13] found that every pond had its definite local form which is characterized by the

* A seiche (sāche) is an oscillation of water above and below mean level; it varies from a few centimeters to 1.5 m. and is usually attributed to variation in atmospheric pressure or to the action of a strong wind.

relative lengths of the horns and that there is a marked difference according to whether *Ceratium* is found in shallow (2–4 m.) or deep (4–16 m.) ponds; he proved by experiment that this depends on the direct influence of the environment. The snails and mussels vary in Germany from pond to pond and from one river system to another; similarly the lakes in Celebes have their own local forms of Melaniidae and Corbiculidae,[12] and each of the Patagonian river systems, which

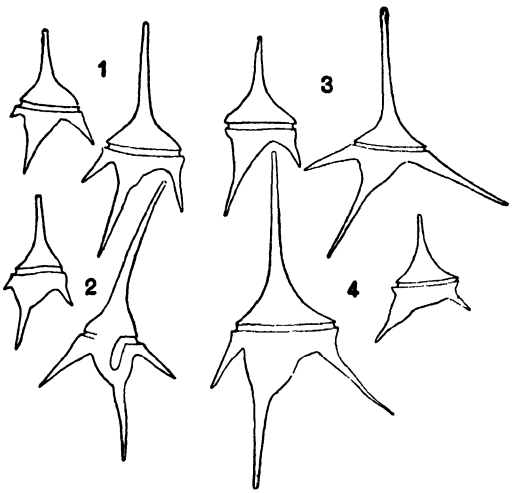


FIG. 80. *Ceratium hirundinella,* small and large forms from the same lakes in Switzerland: 1, from the Untersee; 2, from Lake Lucerne; 3, from Lake Maggiore; 4, from Lake Como. After Bachmann.

are especially effectively isolated, contains its own groups of mollusks that are distinctly different from those in adjacent rivers.[17]

The lower Crustacea give excellent examples of the endless variation of species in inland waters. The brine shrimp *Artemia salina* varies so greatly that almost every salt lake has its own race.[19] Numerous species of Cladocera of different genera are distinguished by this great variation. Among *Bosmina coregoni* the end forms are distinguished by a large number of characteristics but are united by unbroken transitional chains from various localities.[18] In the genus *Daphnia* twenty-eight forms, once described as different species, are now included in the species *D. longispina;* others are similarly variable.[22] Weber [23] reports similar local variations for the African freshwater crab *Telphusa perlata.* Just as the whitefish *Coregonus* displays peculiar characteristics from lake to lake, so the European

brown trout *Salmo fario* and the European lake trout *S. lacustris* also vary considerably, and these two are so closely connected by transitional forms that they have even been placed in one species.[4] The American black-spotted trout (west of the Great Plains) also have innumerable subspecies and local forms.[9] In Australia almost every river has its own variety of the salmonoid *Galaxias*.[14] Such examples among fishes might be greatly multiplied.

Although many inhabitants of the inland waters are subject to mutation and show exceptionally great variation within the species, the fauna of inland waters the world over maintains a marked uniformity. Species of world-wide distribution occur everywhere, along with regionally distinct species and genera of limited distribution; these are sometimes called universal, as contrasted with the regional, fresh-water fauna. The surprisingly great number of widespread species has impressed many investigators, and in this respect the fresh-water fauna stands in sharp contrast with that of the ocean as well as of the land. The explanation suggested previously (p. 102 ff.) was that the short life of a given habitat in the inland waters has conditioned the evolution of forms capable of ready transfer by accidental or incidental emigration. Local forms incapable of such transfer normally perish as their habitats change. It is sufficient merely to call attention to this matter here.

Pedonic and limnetic organisms

In the fauna of inland waters as well as in that of the ocean one can distinguish between animals of the bottom and those of the open water. It is natural for these groups to retain the names benthic and pelagic, as they are designated in the ocean; but it has become a common practice to speak of the bottom organisms of the fresh water as *pedonic* and pelagic forms as *limnetic*. Among the pedonic animals in fresh water there is also a distinction between shore forms and animals found at greater depths; practically speaking, the deep-water community begins at the border of plant growth. This level varies with the transparency of the water and usually lies between 7 m. or less and 30 m. A sunless deep stratum with a truly abyssal fauna occurs in only those few lakes whose depth is over 400 m., i.e., especially in Lake Baikal and Lake Tanganyika. The giant planarians and the non-pigmented fish (*Comephorus baikalensis*) of Lake Baikal are truly abyssal fresh-water animals. In the limnetic fauna of inland waters, we again distinguish between the drifting plankton and the

nekton, which is independent and swims without the aid of water movements. The nekton includes only vertebrates in fresh waters.

The pedonic fauna of fresh water differs from the corresponding fauna of the ocean in that sessile animals, which are so plentifully represented in the benthal of the ocean, are almost entirely absent, with the exception of several ciliates, fresh-water sponges, the fresh-water polyp *Hydra*, certain bryozoans, and a few attached insect larvae. Emigration of sessile animals into rivers against the current is probably difficult. Except certain bacteria and an aquatic glow-worm, no fresh-water luminous organisms are known.[5] The limnetic fauna, especially the fresh-water plankton, has, in common with that of the ocean, important adaptations that facilitate floating. Both the limnetic and the pedonic environments are poorer in number of species than are corresponding regions in the ocean, since so many types are completely absent in fresh water, but, although it is qualitatively poorer, quantitatively it is much richer. The almost complete absence of larvae and eggs is very noticeable in the composition of fresh-water plankton in comparison with the plankton of the ocean. Only the mussel, *Dreissena polymorpha*, which has been introduced into fresh water by navigation, has planktonic larvae; besides these there are the flagellated larvae of some Cestodes and the nauplii of many copepods. In open water, the statoblasts of many Bryozoa and the winter eggs of many rotifers and of a few cladocerans are found; the property of adhesion to the surface of the water, which these small bodies possess, gives them the advantage of being driven by the wind into the littoral region, where they find a higher temperature, which promotes development.[26] The glochidian larvae of the lake and river mussels (*Anodonta, Unio*) and the lake-floor larvae of midges (Chironomidae = Tendipedidae) are occasionally mixed with the plankton by means of the wave action of shallow waters.

The character of the fresh-water plankton is further considerably influenced by the fact that the size of its animals is much less than in the ocean. Such large forms as siphonophores, ctenophores, heteropods, pteropods, and arrowworms are not known in fresh waters. The marine animals just mentioned are mostly jelly-like; their bodies contain an extraordinary amount of water, which considerably increases their size. The absorption of large amounts of fresh water into the body of an animal is, however, impossible without damage to the organism (cf. p. 43 f.). We know of jelly-like matter in only a few cases in fresh-water animal plankters and in these only lifeless parts of the body are expanded, e.g., the mantle of the water flea

Holopedium (Fig. 81) and a few rotifers (Fig. 82). The increase of surface area by means of thread-like pseudopodia, such as serve as aids to floating in Radiolaria and Foraminifera in the ocean, though found in the Heliozoa, occurs much more rarely among fresh-water animals, perhaps because with such greatly increased sur-

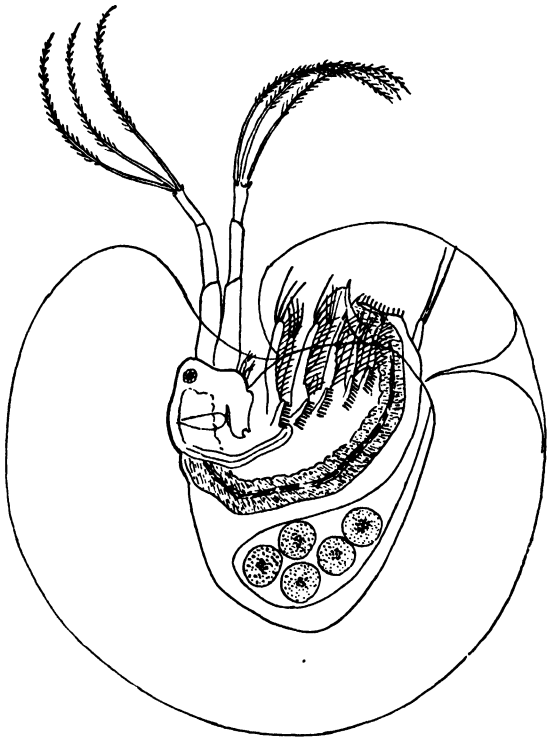


FIG. 81. *Holopedium gibberum.* × 14. After Frič and Vávra.

face area the amount of fresh water absorbed would be too great. Non-gelatinous plankton animals also reach a greater size in the ocean than in fresh water, which may be attributed to the lesser density and consequent lessened buoyancy of fresh as compared with sea water.[25] The skeletons of fresh-water plankton animals rarely contain lime. The largest animal of fresh-water plankton, the larvae of *Corethra plumicornis* (Fig. 104), which reaches a length of 15 mm., has two pairs of air-filled tracheal bladders that enable it to float. The minimum size, however, is about the same for the fresh-water plankton as for that of the ocean; there is a dwarf plankton in both regions.

Secondary inhabitants of this medium, those which have returned

from the terrestrial to the aquatic habitat, are as plentiful in fresh water as they are scarce in the ocean. They include snails, insects, arachnids, and vertebrates. The varied conditions of water movement and the necessity for getting oxygen have brought about many convergent structures, e.g., the flat, sharp-edged body shape of water beetles (Dytiscidae and Hydrophilidae) and water bugs (Naucori-

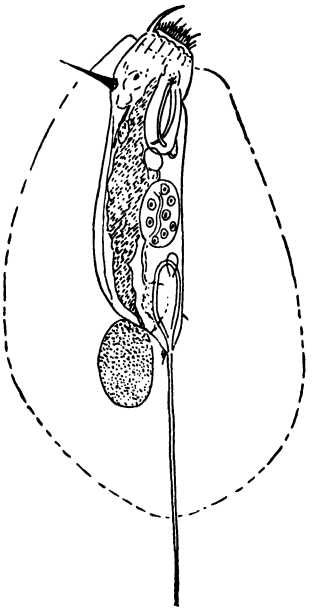


FIG. 82. *Mastigocerca setifera* in its gelatinous case. × 130. After Lauterborn.

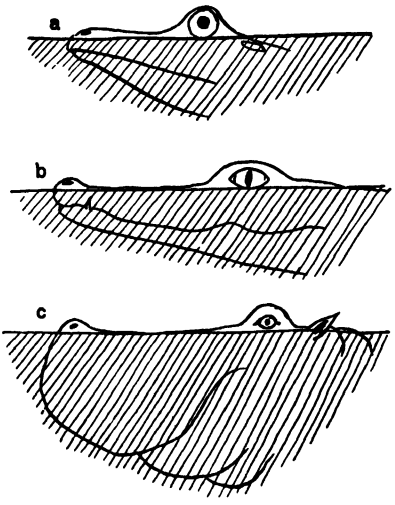


FIG. 83. Heads of a frog, a crocodile, and a hippotamus as examples of convergent adaptation to amphibian life.

dae); the swimming legs, widened by means of hairs; the lightening of the body by the carrying of air on the hairy abdominal surfaces, among beetles (*Hydrophilus*) and bugs (*Notonecta*); and the development of long breathing tubes that reach to the surface, among animals of shallow waters, e.g., some water bugs (*Nepa, Ranatra*) and the rat-tailed maggot of the hover fly (*Eristalis*). Many vertebrates are amphibious; they avoid heat, evaporation, or enemies, or some combination of these, and often find their hunting grounds in the water. They live periodically out of water; some of these have a striking similarity in that they can immerse their bodies in the water up to the nostrils and eyes (Fig. 83). The soft-shelled turtles (*Triony-*

chidae) have their nostrils situated at the end of an elongate snout, so that they compare rather with *Nepa* and *Ranatra* (with breathing tubes at the rear end of the body) than with other aquatic reptiles. One of the primary distinctions between the animal communities of fresh waters and those of the sea lies in the great proportion of such terrestrial invaders of the inland waters.

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17. *Communities in Running Waters*

INLAND WATERS MAY BE CLASSIFIED PRIMARILY INTO FLOWING, OR LOTIC, and standing, or lentic, waters. It is desirable to separate the standing waters into the fresh-water lakes and ponds proper and, on the other hand, into the salt lakes or pools, which contain in solution large amounts of such substances as sodium chloride, magnesium sulphate, and humus. It is also useful to give separate treatment to subterranean waters, whether found as ground water or in caves or wells.

There are certain regularly recurring differences between the inhabitants of running and standing waters that necessitate a separation of the two. Differences in area, movements of the water, and the differing relationships of depths and of temperatures bring about divergences, which may become extreme. These two types of water environment are united by very gradual transitions: a river of the plains in which the current is hardly noticeable (as in many of the steppe rivers of south Russia in summer), a lake through which a river flows, and an ox-bow lake through which there is a current only during floods offer examples of situations in which a difference between the faunae of running and standing waters is hardly perceptible. Furthermore, the animal communities of the wave-washed rocky eroding shores of lakes are closely similar to those of neighboring rocky rapids in streams.

Departing from common custom, we shall consider the running waters first because of their relatively long geological duration, their more extensive continuity, and their usual connection with the ocean. They furnish the routes for the active dispersal of living forms from the ocean into fresh water, which is still going on. Fishes, snails, mussels, and larger crustaceans, which are capable of considerable movement, have thus reached rivers and lakes, as have less active ani-

mals such as leeches and other annelids, turbellarians, and the lower crustaceans.

The composition of the deep-water communities of the lower Alpine lakes, for instance, makes it very probable that at least a part of their inhabitants came in at the end of the glacial period by way of the large streams flowing from the melting glaciers. Running waters thus formed a highway by which arctic animals moved into the lakes of the Alpine foothills, and perhaps, *vice versa*, some of the Alpine animals reached the Scandinavian lakes.

Chemical differences among river waters are less than those among standing waters. The mingling of waters from the various parts of a more or less large, often also geologically varied, river basin equalizes chemical variation much more than in standing waters. Even when very salty or boggy streams enter a river, the water contributed by them is as a rule negligible in comparison with that of the main stream. There is great difference in turbidity in streams, from the clear water of mountain brooks to the perpetual muddiness of such rivers as the Missouri. At flood, many streams, otherwise clear, become mud-laden torrents. The whole phenomenon of flooding, with accompanying frequently drastic changes in level, strength of current, width of stream, etc., makes another difference between lentic and lotic environments.

Rivers, furthermore, usually have no very distinct deep stratum; and even in such large rivers as the Mississippi, the Amazon, and the Congo, where the depth is great, we do not know of any special deep-water communities.

River plankton

Running waters, finally, have no plankton of their own in the sense of typical plankton animals or plankton communities found only in rivers. There is, of course, a floating fauna in rivers; this is not, however, autochthonic but has its origin in standing waters, in lakes through which the rivers flow, in ox-bow lakes connected with the rivers, and in quiet bays and back waters. The river plankton is increased by floods that flush out such places, and thus species are added to the river plankton that do not otherwise occur there; in the plankton of some rivers of south Russia, the larvae of the branchiopod *Limnetis* were found after a flood.[24] They ordinarily occur only in the transient water basins of the steppe. River plankton, consequently, is sparser than that of the lakes from which it originates. Investigations at the outlet of Lunzer Lake indicate that the stronger swimming

plankton organisms, e.g., crustaceans and even rotifers, tend to move against the current in the region of outflow and, unless the current is swift, such forms are thus enabled to move into the river in relatively small numbers.[32] The plankton communities of different rivers, however, are distinct, as are those of the lakes through which they flow. So the plankton of the upper Rhine below Lake Constance differs from that of the Aar as the plankton of Lake Constance differs from that of Lake Zürich, and the plankton of the Neva is almost identical with that of Lake Ladoga, of which it is the outlet, whereas its companion river, the Tosna, contains a wholly different plankton, which is explained by its bog origin. Evidence from a different approach supports the generalization that dissimilarity of habitat is more effective than separateness in determining distinctiveness of plankton populations. Two small lakes near Lake Huron have almost identical plankton and contribute about equally in kind, annual maxima, and mass to the population of the river. This likeness probably depends on the similarity of substrate and of drainage basins of the two closely neighboring lakes.[1]

Speed of current and short stream length are apparently the main causes for rivers not developing their own plankton. The Neva, which extends for 60 km. from its source in Lake Ladoga to the ocean, flows at a rate of 1.0 m. to 1.7 m. a second; a mass of water with its plankton, therefore, reaches salt water in 12 to 14 hours; this time is too short for any considerable multiplication, even among animals that reproduce rapidly. The water in the upper Rhine, flowing at a rate of about 2.5 m. a second, covers the distance between Basel and Mannheim in 1¼ days. The conditions become more favorable with the reduction in their gradient, which occurs in most rivers near their mouths, and in some much sooner. The river then tends to develop and maintain its own plankton. The waters of the Moskva cover only between 14 and 30 km. in 24 hours; consequently, short-lived animals that reproduce rapidly can greatly increase their numbers on their way to the ocean—rotifers, for example, whose numbers tend to be much greater than those of Crustacea in slowly flowing rivers. For the same reasons there is seldom a monotonous plankton in a river, such as would result from mass development of any one species.

In addition to the effect of their quickened run-off, rapids often serve to destroy plankton organisms. In the Mississippi River, the amount of plankton immediately below Rock Island Rapids is less than half that just above. The passage of these rapids requires about 8 hours; the cause of death is thought to be the violent impacts against

suspended sand grains or against the bottom.[10] Mats of submerged vegetation also remove plankton; a decrease of as much as 50% has been observed within 20 m. in dense aquatic vegetation.[30] *Hydropsyche* nets, if present in numbers, take a heavy toll of passing plankters, especially in shallow rapids.[20]

A peculiarity of river mouths is the piling up of the water at high tide and its mixture with salt water. Because of this, the outflow of otherwise slowly moving rivers is temporarily stopped, and the conditions resemble those in standing waters. The remarkable richness of the river plankton in such regions is no doubt connected with this fact. Thus a cubic meter of water in the Elbe above Hamburg contains a few thousand cladocerans, but below Hamburg the number rises to many millions, in the India Harbor, for example, to 11,040,000 *Bosmina longirostris*. Most important of all, forms adapted to brackish water become mingled with the water of the river mouth, and some of these increase to great numbers. The copepod *Popella guerni* is found in the Volga delta; and in the mouth of the Amazon the copepods *Weismanella* and *Pseudodiaptomus gracilis* occur. These are marine components of river plankton.

Stream subdivisions

The divisions of a flowing stream according to the amount of water, as it diminishes from mouth to source, which correspond to the popular names river, creek, brook, rivulet, spring, have little to do with the composition of its fauna. Division into lower river (with a minimum of erosion and a maximum of deposit), middle river (with a balance between erosion and deposit and a more noticeable lateral erosion), and upper river (with a maximum of deep erosion and a minimum of deposit) is also frequently inapplicable. An important factor for animal life is the velocity of the current, and, in correlation with this, the nature of the substratum, the temperature of the water, and its supply of oxygen. But the fall of a river does not increase steadily from the mouth to the source. The course of the Rhine, for instance, has three regions of very rapid current, between which there are regions of much more gradual fall. The Amazon is a stream of minimum fall through most of its course; Manaus, 1400 km. from the mouth, lies only 26 m. above sea level; the average fall in this region is 19 m. per 1000 km. In the great rapids in mid-course of many large rivers, such as the Congo or the Essequibo, there are animals with adaptive features much like those of the inhabitants of small mountain streams. The muddy Spytkowianka, a source river of the Skava, a Galician

tributary of the Vistula, contains fishes that are otherwise characteristic of the lower courses of rivers, and only farther downstream is the fall of the Skava sufficient for trout and grayling.

The gradient mainly determines the physical nature of the substratum in streams. Transportable parts of the substratum are carried along; sand and mud can be deposited only in protected quiet coves; otherwise the bottoms of rapidly running rivers are covered with coarse rock, the smaller pieces of which are constantly in motion. The slower the stream, the finer the fragments carried, until finally only very fine particles can be moved and only fine gravel is deposited; this is succeeded by sand and lastly by mud bottom. As the organic detritus is lightest and consequently the last to sink to the bottom, quantities of nutritive sediment from the whole river basin collect in the regions of the slowest current, usually near the mouth of a river. This is a determining factor for the bottom fauna. All life is crushed among constantly moving rocks; only on permanent cliffs, on especially large blocks, or in sheltered places, can animals gain a foothold in a moving water-rock environment.

The greatest amount of life in streams with rock bottoms seems to be found on or among mixed rubble rather than in association with large or with small stones.[16a] Moving ice in spring and the ice rubble that forms in falls and rapids constitute an additional destructive factor in northern and alpine waters.[16] Fine sand and mud, on the other hand, furnish an opportunity for burrowing and tunneling, and a rich food supply for detritus feeders.

The supply of oxygen is especially favorable in swiftly flowing streams with strong rapids and falls because of the immense water surface that takes up oxygen, and because of the thorough mixing. Even where the current is slow, the water is much better aerated than in standing waters containing a similarly small population of green plants.

The daily and yearly fluctuations of temperature are much smaller in rapidly flowing mountain streams, often shaded by the mountains, than in the waters of the plains, which are exposed to sunshine. The fluctuations are least in the springs that emerge from deep underground. The amount of the annual fluctuation of temperature in streams from glaciers is 0° to 1°; in high mountain springs, 1° to 6°; in lower parts of trout brooks, 15° or more; in barbel rivers perhaps about 19°; in carp rivers, about 24°.[20] Even in smaller streams with little movement, the temperature of the water is more uniform than that of the air. Stenothermal cold-limited animals, as well as eurythermal

animals, live in rapidly flowing streams, but only more or less eurythermal animals can live in streams of slow current.

The fall of a stream and its accompanying environmental factors effect a sorting out of the fauna. In general this is such that the steeper gradients demand more distinct adaptations and thus contain fewer species, mainly different from those of slack water. In the river mouth region of streams of central Europe [12] the water is always brackish near the bottom and at least occasionally near the sur-

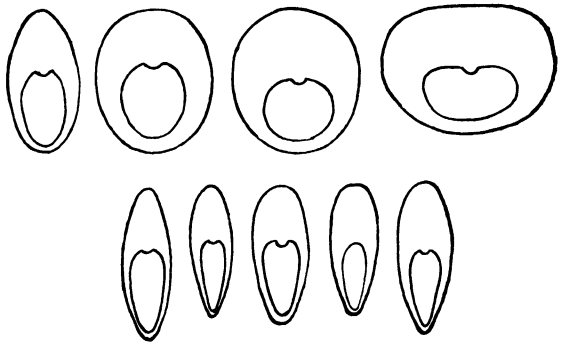


FIG. 84. Cross sections of fishes of swift streams (upper) compared with those of standing waters. Left to right, upper: trout, *Salmo fario;* European minnow, *Phoxinus;* roach, *Misgurnus;* miller's thumb, *Cottus;* lower, bream, *Abramis;* crucian carp, *Carassius;* carp, *Cyprinus carpio;* bitterling, *Rhodeus;* red-eye, *Scardinius.* After Bloch.

face; the bottom is soft, the current weak, the water muddy, warm, and deep. The characteristic fishes are smelt and stickleback, besides flounder and sturgeon in the lower regions and ruff (*Acerina*) and eel in the upper. The carp region, with similar characteristics though without a mixture of sea water, is next upstream. High tide has no effect on this region. It is characterized by weak swimmers with laterally compressed bodies (Fig. 84), unsuited for swimming in moving water because, since their muscles are weak and their bodies flat, they offer too many points of vantage for the current.* Besides these there are many fishes from the upper region of stronger currents, including the eelpout, *Lota lota,* and the miller's thumb, *Cottus gobio.* Next upstream is the barbel region with deep, moderately warm, swiftly running water that is not entirely clear, with a partly soft and partly gravelly substratum. The extremely flattened fishes are want-

* Chief among these are *Abramis brama,* and *Carassius vulgaris,* the carp, *Cyprinus carpio,* and *Rhodeus amarus,* together with *Leuciscus leuciscus* and *L. erythrophthalmus.*

ing; moderately compressed forms like the roach still occur; the characteristic fish, the barbel, *Barbus fluviatilis*, has a rounded body. A limited number of stenothermal forms also occur, such as minnows of the genus *Leuciscus*. Graylings, absent in the carp region, occur. The grayling region usually forms the transition to the uppermost, or trout, region, but may be absent. It includes larger creeks and middle-sized rivers, with rapidly moving water, as a rule, deep, moderately warm, with sandy or partly soft substratum. Besides grayling there are a number of fishes from both neighboring regions. The trout region, finally, includes brooks and smaller rivers with rocky and coarsely graveled bottoms, and clear, cool water with stronger currents. All the fishes of this region have rounded bodies (Fig. 84). The characteristic form is the trout *Salmo fario*. With an increased fall the number of accompanying fishes decreases more and more; those going farthest up are the minnow, *Phoxinus laevis*, the roach, *Cobitis barbatula*, and the miller's-thumb. Though the species differ, there is an essentially similar distribution of fishes in the Chicago region.[23]

The boundaries of these regions naturally are nowhere sharply defined; their order may even be changed according to the topography of the bottom, and a creek may be typically a trout region in the middle of its course, while its upper course may correspond to the carp region and may contain carp, tench, and pike. Wherever the classification can generally be applied, there is a decrease in number of species of fish from the mouth to the source of the river. In the Rhine, for instance, when 41 species of fishes were known in Holland, they included 22 Cyprinidae, 4 salmon, and 9 migrants from the sea.[11] In the upper Rhine, below the falls, there were 33 species, and above the falls 28, after the subtraction of 3 whitefish (*Coregonus*) confined to Lake Constance, only 25; 11 species went as high as 700 m. above sea level, 5 as high as 1100 m., and only 3 above 1900 m. (trout, minnow, miller's-thumb).[8] The distribution of fishes according to height above sea level in Colorado is similar;[7] below 1500 m. there are 44, between 1500 and 2100 m., 47; and this number decreases to 24 between 2100 and 2750 m.; only 13 species go beyond 2750, 7 of which are salmonids. Almost all those that occur above 2750 m. are also found as low as 2100, and the non-salmonids are found in the still lower regions; this gives a clear illustration of selection through severe factors of environment.*

* After considerable search, we are unable to find a more modern statement of these interesting distributional relations of fishes, either for the Rhine or for the streams of Colorado.

The physiographic history of many streams includes a transition from the swift-water and rock-bottom stage to the slow-moving, mud-bottom type as an end stage, so that the present distribution of fishes in a stream with varied types of environment from mouth to source gives us an insight into the general phenomena of ecological succession in streams.[23,33]

Many animals other than fishes are restricted by velocity of current, substratum, and temperature to certain definite regions in flowing waters. The stratifying influence of temperature is especially marked

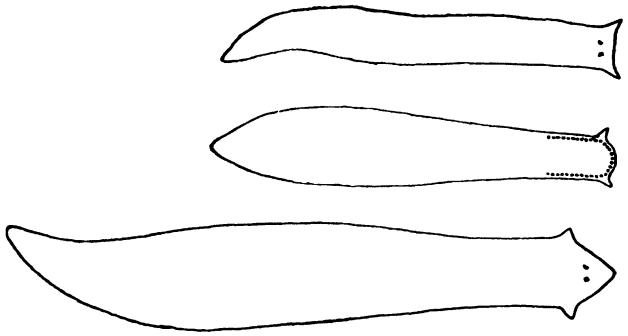


FIG. 85. The brook planarians of central Europe. Top to bottom: *Planaria alpina; Polycelis cornuta; Planaria gonocephala.* After Voigt.

among European brook planarians. The three species of flatworms characteristic of running water in Germany, *Planaria gonocephala, Polycelis cornuta,* and *Pl. alpina,* are distributed so that the first lives in the warmer waters with stony bottoms (Fig. 85), *Polycelis* further up, while *Pl. alpina* lives in the upper streams and springs. For great distances in the upper Alps and the highlands north of the Alps, *Pl. alpina* is the sole occupant. In the middle region of the highlands the regions of distribution of the three species are rather closely approximated (Fig. 86), and *Pl. alpina* is often limited entirely to the source brooks or perhaps springs at the actual source. In the warmer springs of the lower regions *Pl. alpina* and *Polycelis* are entirely missing. *Pl. alpina* breeds in the winter, and its distribution indicates that it is a relic of the glacial period and was found in all the streams of middle Europe during that time; its optimum temperature is below 10°. *Polycelis cornuta* also breeds in the winter, but its optimum temperature is several degrees higher. *Pl. gonocephala,* on the other hand, lives in warmer waters, although it can tolerate low temperatures. *P. cornuta* moved into the creeks after *Pl. alpina,* and *Pl.*

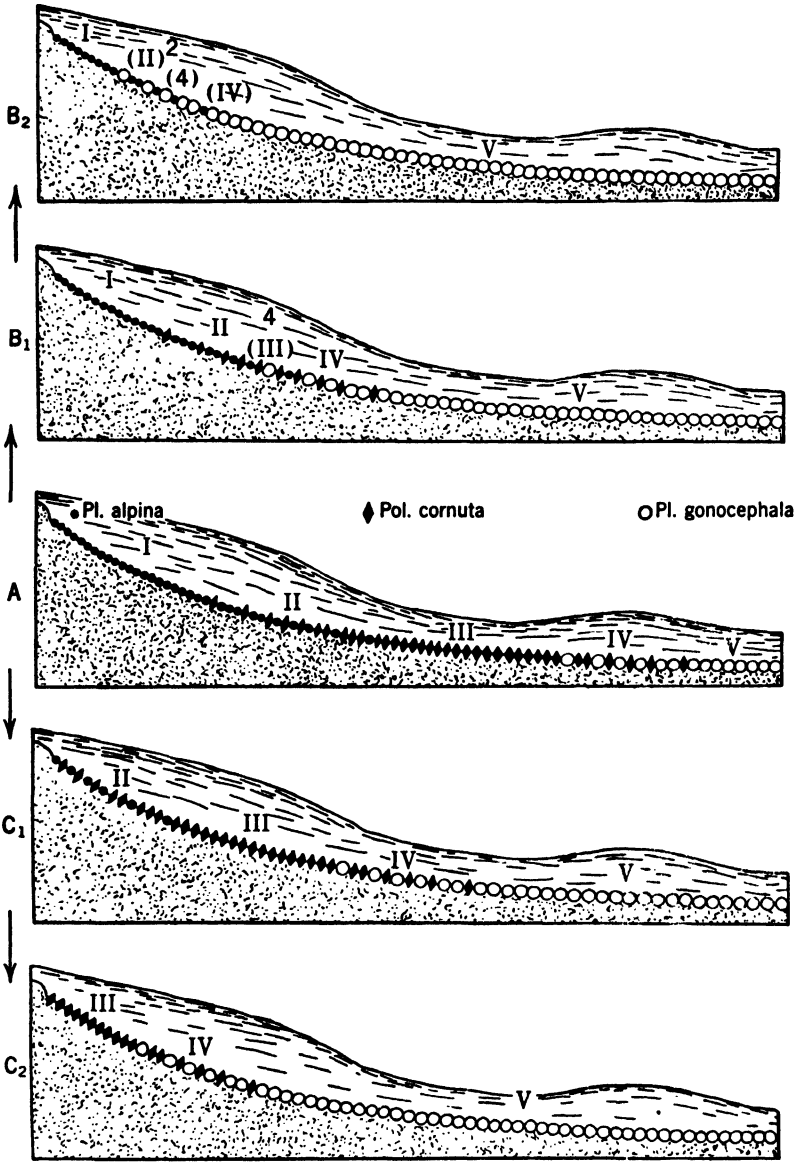
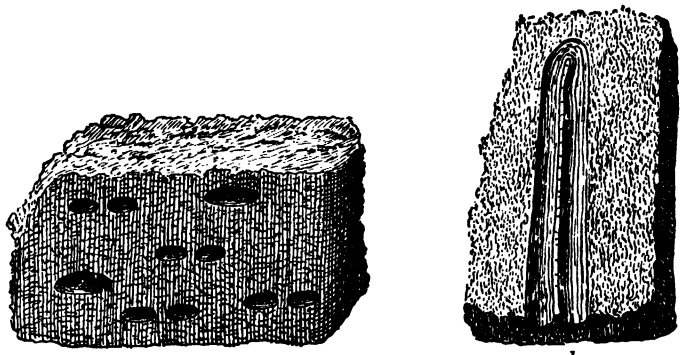


FIG. 86. Distribution of brook planarians shown on a schematic longitudinal section of a mountain stream. In *A*, under primitive conditions, *Planaria alpina* (I), *Polycelis cornuta* (III), and *Planaria gonocephala* (V) succeed each other with areas of intermixture (II and IV) between the adjacent species. This original arrangement is altered when the conditions are changed; in *B*, *Polycelis* is eliminated by the two *Planaria;* in *C*, *Planaria alpina* is replaced by *Polycelis*. After Voigt.

gonocephala followed still later. Their distribution in the brooks is determined by their competition for nourishment correlated with temperature, since each species is most efficient in its own optimum temperature.

The carp region

In the lower courses of rivers, with substrata of mud or fine sand and with slow currents, without coarse sediment in suspension, and



a *b*

FIG. 87. *a*, Piece of clay from the bank of the Marne, below the water level, riddled with the burrows of mayfly larvae (*Palingenia*); some with double, others with single openings, *b*, Longitudinal section through one of these burrows. After de Réaumur.

also in other river regions with similar conditions, the inhabitants of the bottom are to a great extent detritus feeders, like those of muddy floors of lakes and ponds. Tubificid annelids, which have their anterior ends stuck in the mud from which they extract their food, are especially plentiful. Many insect larvae also feed on detritus, e.g., the alderfly *Sialis*, the midge *Chironomus*, and several mayflies. They usually burrow in the mud, either creeping along in the surface layer (*Sialis*) or building mud tubes (*Chironomus*) or digging deeper burrows. The banks of many slowly flowing streams are riddled by the ramifying burrows of Ephemeridae (Fig. 87); they are found in such numbers that when a mass of subimagoes emerges at the same time on a sultry evening the air is filled with them as with a heavy snowstorm.[2,19,21] Mussels also occur, especially the small *Sphaerium* and *Pisidium* and the much larger *Unio* and *Anodonta*. In the Elbe below Hamburg, *Sphaerium* rivals the Tubificidae in numbers. Bryozoa also belong to the detritus feeders. These are plentiful in the Elbe and

the Bille near Hamburg, and occur in a number of beautiful forms; * they do not, however, live on the mud, but need a firmer foundation for attachment. Thus *Plumatella princeps* var. *spongiosa* overruns snail shells until they resemble small potatoes.[14] Fresh-water sponges (*Ephydatia fluvialitis*) attach themselves in like manner. Other invertebrates are somewhat less abundant than the detritus feeders.†

The large development of lower animal life on the nutritive elements of the thick layer of mud and detritus on the bottoms of slowly flowing streams affords the basic food supply for the large numbers of fishes found in the lower regions of streams. These are primarily bottom feeders such as carp, catfishes, and suckers, together with sturgeons and spoonbills, the African Mormyridae, and many others; predaceous fishes in turn are associated with the herbivores and detritus feeders. Experience in fishing shows that, the farther a fisherman lives from the mouth of a river, the greater the area of water he must have; yearly net profit per hectare (about 2.5 acres) from fishing in extraordinarily good German lakes is about one-third that in the lower Oder and one-fifth that in the lower Elbe. As a matter of course the number of migratory fishes is also largest in the lower reaches of the river. Many stop here, and those that go farther upstream must also pass through the lower river. These include principally species coming up to spawn, e.g., Salmonidae and sturgeons. The flounder (*Pleuronectes platessa*) comes up into European rivers only in search of food, and it never becomes sexually mature in fresh water. In the tropics a number of selachians also enter fresh waters, and many rays have entirely adapted themselves to life in the rivers.

The abundance of nourishment in slow streams, especially in the tropics, also attracts a number of higher vertebrates to these regions. Sirenia (*Manatus* and *Halicore*) come up the rivers (Congo, Amazon, etc.) from the ocean and feed there on water plants. Crocodiles and river turtles, otters and river dolphins (*Platanista* in the rivers of India, and *Inia* in South America) feed on the plentiful supply of fish.

Increased velocity of current and prevailing gravelly and stony bottom, which is subject to motion and consequent friction, at least at high water, conditions generally found in the middle courses of

* *Pectinatella, Lophopus, Fredericella, Paludicella, Cristatella.*

† Among snails, the gill-breathing forms such as *Viviparus fasciatus, Theodosus, Valvata,* and *Bythinia* are rather plentiful. There are the flatworm *Procotyla fluviatilis,* the leech *Herpobdella,* the water isopod *Asellus,* and others.

streams, reduce the whole group of mud inhabitants. They occur only in quiet places, in bays or on the downstream side of gravel banks; there we find tubificid worms and river mussels. Insect larvae continue to be important, but the species are different from those found on the muddy bottom of the lower river. Instead of midge larvae and the burrowing Ephemeridae, more and more of those occur that take shelter under stones; other species of Ephemeridae, the larvae of stoneflies (Perlidae), which are completely missing in the mud, a number of libellulid dragonfly nymphs, and above all a great number of caddis worms with their stone cases, are to be found in such places, as are also some small water beetles. The few freshwater, air-breathing snails living in such biotopes also cling to stones, as do *Physa* and *Ancylus fluviatilis*, and, of the gill-breathing snails, *Goniobasis* and *Viviparus*. Some of the fishes found in this part of a river are more characteristic of the barbel or the grayling region. The sparse, rapidly moving plankton has already been mentioned.

The trout region

The influence of increased velocity of current, however, becomes much more noticeable in the upper streams, the mountain rivers, or brooks.[25,28,29] There are, of course, various gradations even here; the brooks of the intermediate mountains can be divided into salmon brooks in their lower reaches, where the fall is less marked, and trout brooks in their upper regions, where the fall is considerably greater. The mechanical erosion of the current with its wild cataracts and rapids becomes most evident in the upper mountain streams.

The whole bottom is stony, usually undermining the bordering cliffs, and is covered with loose rocks and stones that are being sifted by the force of the current; the coarseness of the rubble thus varies with the elevation, and even in the trout brooks, stones the size of a fist or a head are easily carried along. Because of this movement of rubble, the settling of living forms on the bottom is very limited; for by tossing and rubbing, plants and animals are crushed and ground, and living forms can find permanent attachment only on the firm rocks and boulders that resist the force of the current. Free-swimming forms remain only in quiet places in secluded pools. Perpendicular waterfalls of considerable height block the passage of many animals, especially of fishes. Salmon overcome the barrier interposed by falls by leaping and are thus able to range into the back waters of streams inaccessible to other fishes. Many mountain fishes in the Andes and Himalayas have an adhesive organ by means of which they climb

vertical rock walls. Most swimmers, however, are excluded from mountain streams. Other animals, whose relatives swim readily in quiet waters, are stationary at this level. Of the fishes, *Cottus, Lota,* and *Nemachilus* hide under stones; the water mites have shorter legs than those in quiet waters, and the swimming hairs of the quiet-water mites are wanting on the legs of the swift-water forms; the hairs on the swimmerets of the few ostracods are also much reduced. The bottom fauna is well adapted to mountain streams. Many types have developed means of maintaining themselves in the current, e.g., sucking disks, claws, silk attachment threads, or expanded pectoral fins, which will be discussed below.

In comparison with similar conditions in the surf region of the ocean, the number of permanent sessile forms is small. The freshwater sponge *Ephydatia* and the bryozoan *Plumatella* occasionally encrust the stones on the bottom of the brooks. A few types of insects have larvae that attach themselves in swift water. Otherwise only the eggs or pupae, i.e., stages that do not need nourishment, are attached, such as the egg cocoons of flatworms and leeches and the eggs of the water mites. Little nourishment is suspended in swift water. The larvae of the black fly *Simulium* depend on the microscopic food materials brought to their fan-like feeding apparatus by the passing current; these may be present in tremendous numbers, forming a thick black blanket of writhing life on the brinks of waterfalls. The caddis worm *Hydropsyche* spins a veritable plankton net in swift water. On the other hand, the remaining inhabitants of mountain streams, aside from the small number of those that settle among the sparse vegetation of quiet places, are dependent upon effective anchorage. Their number is not large. In central Europe they include the triclad flatworms (e.g., *Planaria alpina*) and leeches (*Glossiphonia*); a number of snails (*Ancylus fluviatilis* and several small lymnaeids); a few mussels (the brook pearl mussel *Margaritifera margaritifera* and species of *Pisidium*); the water flea (*Gammarus pulex*) and the river crayfish; a variety of water mites; and, outnumbering all others in species and individuals, large numbers of insect larvae of the groups Ephemeridae, Perlidae, Trichoptera, and Diptera, besides a few Odonata and Coleoptera. The Perlidae are almost completely confined to rapidly flowing waters, many finding refuge beneath the larger stones.

Mountain brook adaptations

The devices by which inhabitants of mountain streams are able to withstand the force of the current are unusually diverse, but often

similar in forms of very different taxonomic relationships, as a result of convergent adaptation. The body tends to be flat, especially compressed at the head, often shield-shaped, the upper surface smooth, without marked protrusions. The flatworms and leeches, the snail *Ancylus* (Fig. 89*b*), water mites, and very many insect larvae, especially those of Perlidae and Ephemeridae (Fig. 88), Odonata and Coleoptera, show this adaptation. The legs of these larvae usually protrude laterally, the femurs are flattened, and the rim of the body is pressed closely to the substratum; a border of bristles often completes the attachment of the hard chitinous shield to the substratum. Most limpet-like of all are the larvae of certain beetles, such as *Psephenus,* which have a flat circular "shell" extending well beyond the appendages. The cases of caddis worms may also be shield-shaped (e.g., *Thremma,* Fig. 89*a*). They are always small in comparison with the larger cases of the inhabitants of standing waters. The shield-shaped pupa cases of the black flies (Simulidae) are also attached to the substratum, while the larvae are attached by suckers or by a silken thread. The laterally compressed bodies of amphipods enable them to slip into narrow crevices. Many pronounced rheocoles have developed a streamlined upper surface.

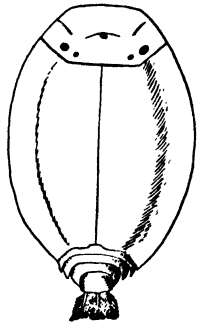


FIG. 88. Shield-shaped may-fly larva from swift streams (*Prosopistoma*). × 6. After Ulmer.

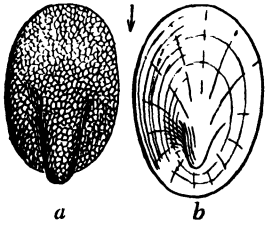


FIG. 89

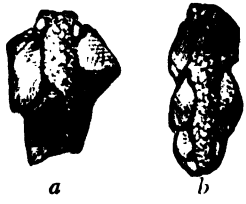


FIG. 90

FIG. 89. Convergent adaptation to swift water: *a,* larval case of caddis fly *Thremma,* after Klapalek; *b,* shell of the snail *Ancylus fluviatilis,* after Kobelt. The arrow shows the direction of flow of the water.

FIG. 90. Larval cases of the caddisflies *Goera pilosa* (*a*), and *Silo nigricornis* (*b*), from swift streams, their cases weighted laterally by stones. After Brauer.

A unique method of stabilization in running waters is the weighting down of the body. In a few species of caddis worms (*Goera, Silo,* Fig. 90) the larvae fasten larger stones to their cases, at the same time

providing for a smooth attachment to the substratum by maintaining a level undersurface of these stones and by filling in the cracks. Many fishes of mountain streams are adapted to life on the bottom by loss of the swim bladder, as in *Cottus* and the darters (Etheostominae); or there may be only a small swim bladder, surrounded by a capsule of bone, as in the Eurasian Cobitidae and the East Indian *Homaloptera.* The lungless mountain stream salamanders of North America (Pletho-

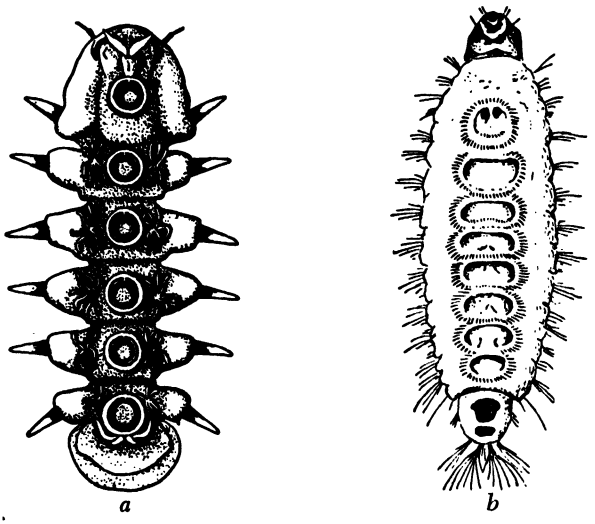


FIG. 91. Dipterous larvae from swift streams, from beneath, to show their sucking disks: left, *Liponeura brevirostris,* a blepharocerid, after Brauer; right, *Pericoma californica,* a psychodid. After Wesenberg Lund.

dontidae) apparently present a parallel adaptation, since other families of salamanders also have a few lungless mountain brook forms.[6]

Organs of attachment of the most diverse kinds are especially characteristic of the animals of this environment. The claws of the legs of all water mites and insect larvae are strongly developed. Flatworms and mayfly nymphs have strong adherent surfaces, and the snails of this habitat have these surfaces much enlarged in comparison with land snails of equal size. Leeches attach themselves by means of suction cups; the posterior end of the larva of *Melusina,* a biting gnat, bears sucking plates whose power of attachment is increased by bristles; and the flat, sole-like undersurface of the larvae of other midges of the families Blepharoceridae (Fig. 91*a*) and Psychodidae (Fig. 91*b*) bears a longitudinal row of suction disks. Many of the

mayfly nymphs have organs of attachment in the form of thickened and spiny rims on the tracheal gills, and an adhesive, disk-like thorax. The organs of attachment are especially unique in fishes and tadpoles of mountain streams; mouth, lower lip, and ventral surface, and on fishes the fins also, may be reconstructed into sucking apparatus. This may occur in very different taxonomic groups. The whole mouth of armored catfishes, which are found in great variety in South America (e.g., *Lithogenes villosus* in the rapids of rivers in Guiana, or *Placostomus*, Fig. 92), is developed into a sucker, as is the ventral surface of the cyprinid, *Gastromyzon*, in North Borneo.[3] Spines on the ventral surface are often helpful additions. The tadpoles of tropical mountain rivers and brooks with similar adaptations also belong to different groups of Salientia (Fig. 93);[9,17,31] these animals cling so tightly that they can be loosened only with great difficulty.

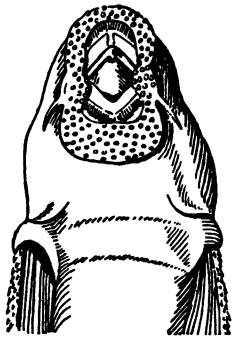


FIG. 92. Sucking mouth of the armored catfish *Placostomus* sp., from swift water, about twice natural size. After Rauther.

Finally, an attachment by means of spun fibers also occasionally may be employed in running waters. A mussel of streams in Africa and South America, *Byssanodonta*, attaches itself to the substratum by means of threads from its byssus gland, and, as in many attached mussels in the ocean, the foot is decreased in size through retrogressive development. When the spring snail, *Bythinella dunckeri*, retreats into its shell it attaches a thread to some fixed object and thus is protected against being washed away. Besides these, a few insect larvae spin threads for anchorage; larvae of caddisflies attach themselves by means of a few threads, and larvae of black flies, which need a minimum current of 0.3 m. a second, attach several threads to the substratum in order to hold fast while they change their location. Their threads are so tough that the larvae can float out into swift water without being carried away.

Mussels are buried in the quiet parts of the river bottom where it is covered with finer gravel and sand, and they are thus protected from being washed downstream. There are only a few species in the fast-flowing waters of central Europe. The brook pearl mussel, *Margaritifera margaritifera*, lives in brooks of north and middle Europe (Scandinavia, British Islands, Germany, France), which are poor in lime because they flow over granitoid rocks. In thickened old specimens, the umbo of

these mussels is often much corroded by free carbonic acid in the water. The small ubiquitous *Pisidium* is also widely distributed in mountain brooks.

The fauna of mountain brooks mainly consists of larvae of insects (Ephemeridae, Perlidae, Trichoptera, etc.), which emerge in the

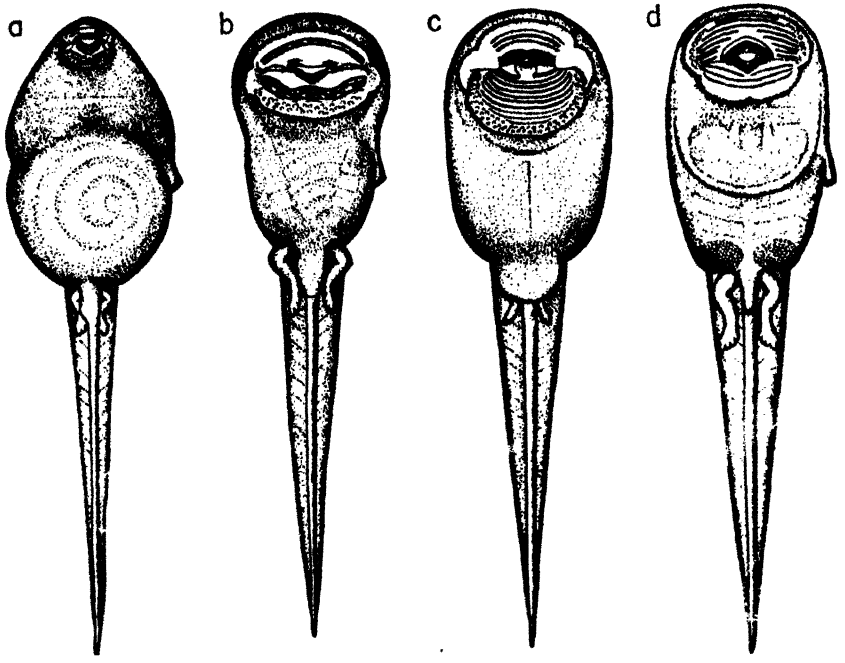


FIG. 93. Modification of tadpoles for life in mountain streams. *a, Rana pipiens* tadpole with unmodified mouthparts; mouthparts enlarged to form an effective sucker in: *b, Bufo penangensis,* Malay Peninsula; *c, Ascaphus truei,* western North America; *d, Staurois mantzorum,* west China. Original drawings by Grace L. Orton.

spring in the lower stretches, and in early summer in the higher regions. Such life histories explain the peculiar phenomenon that these brooks are most densely inhabited during the fall and winter months, have a reduced fauna in the warmer season, and do not contain developing larvae again until fall.

The zonation of the highlands, which sorts terrestrial animals and plants into different belts according to elevation, is less evident in running waters, except in progressive reduction of the fauna. Even so, in his examination of the distribution of Entomostraca of the Colorado mountains, Dodds [4] found that the species in higher altitudes

tend to be found in higher latitudes in the lower-lying plains to the east. In the regions of perpetual snow and the adjacent areas of treeless meadows little plant material reaches the brooks as food, and the algae are rather sparse at such a height. Thus the amount of animal life decreases rapidly with an increase in elevation; the number of species is reduced, and the individuals are smaller. That this fact is not simply dependent upon elevation above sea level is proved by the Aksai in the Tien Shan, which flows clear and quiet at a height of 3000 m. above sea level and there contains just as large fishes as farther down. The trout, *Salmo fario,* reaches a length of only a few inches in the mountain brooks of Switzerland and a weight of only 0.5 kg., while in larger rivers, and especially in mountain lakes, it becomes considerably larger. The average weight of all the trout caught in the Aar basin during 1913–1914, for the Aar alone was 240 gm., and for the tributaries alone only 132 gm.[27] An added reason, besides the sparseness of food, may be found in the circumstance that these stronger currents demand a much more strenuous use of the muscles of fishes in order that they may maintain position in the stream, thereby leaving a much smaller margin of food supply for growth. In regions where the conditions in headwater streams are less severe, as in central New York or in Illinois, the numbers of fishes may be two to three times as great per square meter of surface in the smaller, as compared with larger, streams. The average weight per unit is greater, however, in the larger streams.[30]

Fishes ascend to varying heights in the mountains, in the Alps perhaps to 2800 m. In the Asiatic highlands two species of fishes have been taken in a spring with a temperature of 18°–20° at a height of 4780 m. above sea level on the southern slopes of the Tang-la.[18] The fact that the genus *Nemachilus* is represented by four species in these marginal regions of fish distribution perhaps depends upon the circumstance that in these regions of very low barometric pressure the breathing of atmospheric oxygen supplements the oxygen supply. This has been proved to be true of the Cobitidae.

Fish migrations

The migratory fishes form a unique part of the composition of the faunae of inland waters. These include fishes that travel during the spawning season, either from the ocean up the rivers, like the salmon, or, more rarely, from the rivers into the ocean, like the eel. Migratory fishes going upstream include the sturgeons, numerous species of salmonoid fishes (*Salmo salar* in the North Atlantic, species of *On-*

corhynchus in the north Pacific, species of *Coregonus* in the Arctic), and several species of shad.* The migration often occurs in great masses in rivers where civilization has not too greatly altered the environment. In the Rhine near Strasbourg, 143 salmon were caught in one day in the year 1647. In the Columbia and Sacramento rivers of the Pacific coast of North America, upstream migration of salmon (*Oncorhynchus*) lasts from spring until autumn,[13] the mass of fish going up is so enormous that, instead of nets being used to catch them, large bucket-wheels are employed to scoop them out. One such wheel could catch as many as 14,000 fishes in one day.[5] The immense numbers of the whitefish *Coregonus leucichthys* and other species that come up the Obi and the Irtysch in the spring furnish opportunity for great draughts of fishes by the inhabitants of these regions. In the relatively short rivers of east Siberia, which flow to the Pacific from the Okhotsk highlands, the keta (*Oncorhynchus keta*) comes up in such great numbers to the brooks at their sources that the streams are not large enough to hold the fish; their backs protrude out of the water, they are crowded against the banks; some perish, while masses of others become the prey of birds, bears, dogs, and people. It is unlikely that any of these migrants ever return to the ocean; even those that finally spawn perish in the end from sheer exhaustion.[15]

An interesting and unexpected result of American fish tagging experiments, particularly on the Pacific coast, is found in the evidence that salmon and fishes of similar habit have a strong tendency to return to the brook in which they were spawned when they in turn are sexually mature. The mechanics of this process, whereby the fishes are able to detect significant differences to guide them in their return migration, have not yet been discovered.[22] These studies have also shown that such fishes living in a long stream are physiologically different from those of the same species from a shorter river.

In the rivers of the far north such migratory fishes make up an important part of the fauna, for many salmon remain permanently in the streams. Only two species of salmonids in the rivers of northern Siberia are entirely independent of the ocean, the grayling *Thymallus thymallus,* and a trout, *Salmo coregonoides;* besides these, seven other species inhabit these waters. It is probably this migratory habit that enables the Salmonidae, of all fresh-water fishes, to penetrate farthest to the north. Chars (*Salmo arcturus* and *S. naresi*)

* *Alosa alosa* and *A. finta* in Europe, *A. sapidissima* in North America.

ıave been caught even as far north as Grinnell Land, 82° 34′ N. latiıude. The migration of fishes from the seas to rivers is paralleled in ›ther situations by migration from lakes to rivers or from large to ;mall streams, such as the migration of redhorse and suckers in the Mississippi Valley.

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18. *Communities in Standing Inland Waters*

THE ABSENCE OF CURRENT IN STANDING WATERS ACTS IN SEVERAL WAYS TO determine the nature of the fauna. In a river the enrichment of the water with nutritive materials, which are necessary for plant life and the quantity of which greatly influences the fruitfulness of the water, is limited. All salts that have been dissolved from the ground, or have been set free by the disintegration of dead plants or animals, or have been brought in by tributaries are constantly being carried off to the sea. The most favorable conditions are found in the slowly flowing lower course of the rivers, with their decreased velocity, their increased content of dissolved substances and suspended detritus. In standing waters, however, the elements dissolved from the bottom tend to remain, and those vital elements that have already been used in developing living forms also find their way back into the water at the death of these plants or animals. Standing water may be a segregated and almost self-sufficient habitat.

The favorable character of the environment for living forms decreases wherever a river flows through a lake; Kofoid [39] states that, in lakes with outlets, the production of plankton is in direct ratio to the time required for renewal of the water; i.e., it is greatest where the renewal is slowest. The current in rivers often produces steep banks; at least at high water, the banks are scoured and their slopes increased by lateral erosion. In standing waters, on the other hand, the slope of the shores is more often gradual, and a wide border of plant growth supports a rich fauna; through the disintegration of dead plants the rest of the water is well supplied with detritus.

The fact that the plankton of open water has more favorable living conditions in standing waters than in rivers also depends on the decrease of current. An autochthonic river plankton can scarcely be said to exist; the river plankters are incessantly being carried to the

sea, where they perish and serve as nourishment and fertilizer. Aside from fishes, only such animals as are buried in the substratum, or are attached to plants or stones, or live in sheltered niches can hold their places in the current. In standing waters, on the other hand, the fauna of the open water plays an important part along with that of the substratum. Biological relations may vary decidedly in the two locations. Thus Weissensee [91] reports that the normal condition of *Anodonta* in standing water is hermaphroditic, whereas those in flowing waters are bisexual, the transference of the spermatozoa to the eggs being assisted by the current.

The factor of extent

Aside from the nature of the substratum and its richness in nutritive salts, there are differences related to the ratio of water mass to bottom area. There is relatively less bottom area per cubic meter of water in a lake than in a pond, and less in a pond than in a pool; the relationship is less favorable in deep lakes than in shallow ones. An increase in the relative amount of bottom area, especially of lighted bottom, often means an increase in the abundance of living forms.[80] In running waters, because of their generally rapid current, the smaller streams and brooks contain relatively fewer floating or free-swimming animals. Smaller bodies of standing waters, if fairly permanent, are more favorable to life than the larger.

There is every gradation of size in standing waters between Lake Superior, with 82,360 sq. km. of surface area, and ponds, pools, and puddles. The depths vary similarly. Only in very few do they exceed 1000 m., and only rarely are they more than 400 m., but from this depth there are all gradations to the shallowest puddles, and the ratio of the depth to the surface area is certainly not fixed. As was mentioned above, the ratio of the amount of water to the extent of substratum is much greater in small, shallow waters, and the amount of salts dissolved from the substratum, other things being equal, is also greater. The shallow zone is more extensive in relation to total area, and thus the total vegetation is relatively greater. A much larger part of the water is penetrated by the sun's rays; this situation favors the growth of plants. The conditions of oxygen supply are more favorable in shallow waters, for the surface area is larger here in relation to the volume than in deep waters. In Lake Constance [43] the upper lake with its 475 sq. km. of surface area and its depth of more than

200 m. is much poorer in fauna than the lower lake, which is connected with the upper and has a surface area of 63 sq. km. and an average depth much less than the maximum of 45 m. Among ponds in Holstein [5] all those rich in plankton are relatively small and shallow (not more than 7 m. deep, usually much less), and those of considerable size and of a depth reaching 25 m. or more are invariably poor in plankton. Of twenty Swedish lakes,[6,85] the smallest, with an area of 31 hectares (77 acres) had the largest amount of bottom fauna and the greatest yield of fish, 113 kg. per hectare (101 lb. per acre); the yield of the largest lakes, such as Lake Vener, with 566,800 hectares (about 1,400,000 acres), and Lake Malar, of 116,200 hectares (about 287,000 acres), is much smaller, and amounts to only 1.4 kg. and 2.7 kg. per hectare (respectively, 1.2 and 2.4 lb. per acre). Similar results are reported from lakes in Canada.[60] The relatively largest amounts of living forms are found in the small ponds (village ponds, etc.), which are richly fertilized.

Temperature relations

Temperature is of special importance for life in fresh waters. In consequence of its high degree of fluidity, the water becomes stratified according to density. As stated in Chapter 16, the density of fresh water increases with a decrease in temperature until it has reached its maximum at 4°, and then with a further lowering of temperature the water expands again and becomes lighter. The cooling of water occurs by radiation of heat from the surface; consequently the surface layers become denser and sink until they reach a layer of equal temperature, and their place is taken by the warmer masses of stagnant water, which rise to the top only to sink again when they become cooled. After long-extended cooling the whole mass of water reaches a uniform temperature of 4°. Further cooling of the surface water causes it to expand again and become lighter; this cold-water layer remains on top, and finally, when a covering of ice hinders any further giving off of heat, the cooling effect spreads but slowly to the deeper regions because of the poor thermal conductivity of water. On the other hand, when cold surface water with a temperature below 4° is warmed, the upper layers become denser as their temperature rises, and sink, and this process continues until the whole water mass has again acquired uniformity of temperature at 4°. Further warming then continues in the surface layers and penetrates the deeper water very slowly. During the season when the surface is warmer than 4° the

temperature decreases from the surface to the bottom; this is called direct stratification. When the surface is colder than 4°, the temperature rises with increasing depth; this is inverse stratification (Fig. 94).

The convection currents set up by the cooling and warming of water are of great importance in supplying the deep water with oxygen. They occur most regularly where the greatest changes of

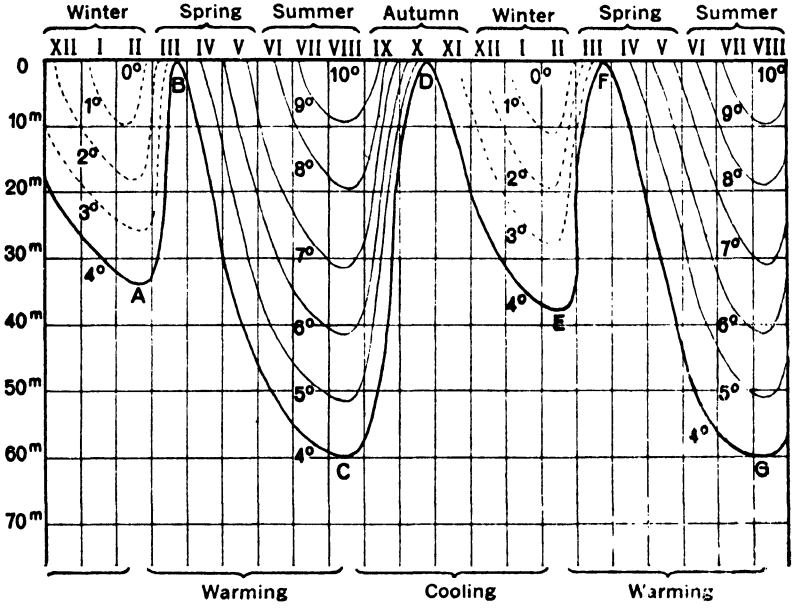


FIG. 94. Schematic representation of the temperature conditions in a body of water in the temperate zone during the course of the year. The isotherms are continuous lines when the stratification is direct, dotted when it is inverse. Spring overturn at *A–B* and *E–F*, autumn overturn at *C–D*, summer stagnation at *B–C* and *F–G*.

temperature occur, viz., in the temperate zones; they are much reduced in the polar regions, on the one hand, and in the tropical or subtropical regions on the other.

Thermal conditions in standing waters are very strongly influenced by the change of seasons in the temperate zones. At a given time in autumn all the water has a temperature of 4°; if it continues to cool at the surface, an inverse stratification sets in without creating convection currents, i.e., winter stagnation. Then warming begins, which continues up to the maximum of temperature. This results in convection currents until a uniform temperature of 4° has again been reached.

The water is now in unstable equilibrium and wave action usually produces a complete mixing of the waters of the lake, making what is called the spring overturn. Thereupon the heating of the surface water goes on from the end of April or the beginning of May (summer stagnation) until a renewed cooling again brings about equilibrium and the autumn overturn. Water at a temperature of 4° thus always fills the lower levels of the deeper basins; but twice a year it extends to the surface, in spring and fall. Between these two points the 4° isotherm describes a curve that sinks lower in the summer than in the winter and above which the water is arranged in direct stratification in summer and in inverse stratification in the winter (Fig. 94).

The change from day to night also sets up convection currents. Warming during the day in summer is followed by a cooling at night, which causes a sinking of the upper strata down to a stratum of like temperature. As a result of this an equalization of temperature among these strata occurs, so that these upper strata differ but little in temperature. Such convection currents, however, go down only to a certain depth; below this the water is warmed only by means of conduction, which acts very slowly. Consequently, below the level to which the daily convection currents extend, a rapid decrease in temperature sets in. A discontinuity layer called the thermocline (metalimnion) is formed at this level. In temperate lakes the thermocline, of course, exists only during the summer stagnation; with the beginning of autumnal circulation it sinks deeper and deeper and at last disappears.

The thermocline is defined by Birge's informal rule [14] as the depth zone in which the drop in temperature is 1° or more per meter of depth. This rule often does not apply; [92] for example, in Lake Tanganyika [8] and Lake Nyasa [9] small but fairly marked changes in temperature with depth are called thermoclines. Evidence that such less dramatic temperature changes may indicate the presence of discontinuity layers is furnished in these African lakes by accompanying changes in dissolved oxygen and in ionic content. Even when sharply developed, the thermocline tends to be more abrupt at its upper than at its lower limit. In contrast with the more definite epilimnion, two or more subdivisions have been recognized in the hypolimnion,[37] particularly in Lake Nyasa.[9] This establishes an important classification of lakes on the basis of depth. The location of the thermocline

differs in different lakes in relation to latitude and nearby topography; it also differs in the same lake as a result of changes in season and in weather, particularly as regards wind action. Its depth in different lakes is indicated in Figs. 95, 101, and 102. The thermocline may be near the surface at a depth of 1 to 3 m.,[23] or somewhat deeper,[10,35] or considerably lower, often at 60 to 80 m. or more, in Lake Tanganyika.[8] (See Chapter 19.)

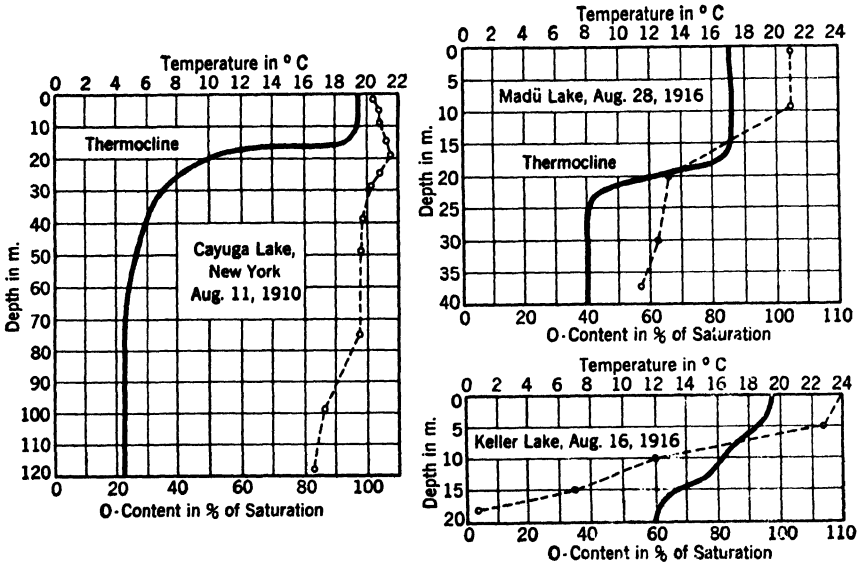


FIG. 95. Temperature curves (——), and curves of oxygen content (– – – –) in % of saturation, for Cayuga Lake, New York, Madue Lake, Pomerania, and Keller Lake in Holstein. After Thienemann.

This type of temperature stratification applies to the open water of deeper lakes. In the shore regions of such waters, and in shallow lakes, especially, if they are exposed to mixing by means of the wind, the temperature is more equally distributed through their depths; thus the greatest difference between the temperature of the surface water and of the deep water in Lake Mansfeld, 7 m. deep, is 1.5°, and in many lakes is less than 1°. Cold water is brought to the surface along the shore of Lake Michigan by off-shore winds of a few days' duration during summer.

Forel [29] has divided lakes into three types with reference to their temperature, according to whether the surface water is always warm (over 4° in tropical lakes), alternately warm and cold (temperate

lakes), or always cold (polar lakes). Stratification is always direct in tropical lakes. Polar lakes always contain cold water with a temperature lower than 4° and have inverse thermal stratification except during summer, when the temperatures of the surface and the bottom become equalized, circulation occurs, and the stratification disappears. Conditions in temperate lakes are stated above; in summer they resemble tropical lakes, in the winter polar lakes, and in spring and fall equalizing circulations appear.

Lakes of the tropical type are widely distributed throughout the tropics and subtropics. The lakes at the southern base of the Alps, such as Lake Geneva, belong to this group. Polar lakes occur in arctic regions and in high mountains near glaciers; but wherever the ratio of the surface area to the volume of water is small, i.e., in deep lakes in subpolar regions, the characteristics are those of the polar type; even Lake Baikal (51°-55° N. latitude) and Lake Telesky in the Altai belong to this group. In contrast with these, the shallow Lake Enare in Lapland, north of the Arctic Circle, becomes so warm in summer that its waters are directly stratified, so that it belongs to the temperate type. Deep lakes tend to be either polar or temperate, according to the regional climate, but Lake Tanganyika and Lake Nyasa are tropical in type as well as in location.[9] Relatively shallow lakes, on the other hand, are usually of the temperate [100] or tropical type, depending on latitude, and really shallow lakes are not deep enough to become thermally stratified.[92]

Oxygenation

The convection currents are of considerable importance in the distribution of oxygen in standing waters. It is estimated that it would take 42 years for one molecule of oxygen to be transferred by means of diffusion, without any movement of the water, from the surface to the bottom of a lake 250 m. deep (as, for instance, Lake Constance).[36] In running waters, even when the movement is slow, constant mixing takes place, which brings to the bottom water that has been oxygenated at the surface. This is not true in standing waters, though tributaries of lower temperature increase the oxygen content of deep waters in lakes of the tropical type such as Lake Como and Lake Geneva, for their water sinks below the warmer water of the surface. Where there are no such tributaries, the two periods of overturn, in spring and in fall, set the waters of temperate lakes in motion even to great depths.

During the summer the surface layers are well mixed and well supplied with oxygen, but the oxygen content of the deeper water is depleted because of consumption of oxygen in that region. In waters whose substratum is mainly composed of mineral elements the oxygen content near the bottom does not sink below 70% of saturation (Fig. 95, Lake Cayuga). Wherever the bottom is covered with ooze, which is rich in disintegrated organic material, the oxygen content, especially in shallow depths, is much reduced (Fig. 95, Lake Madue), so that often only 40%, or less, of normal saturation content is left, or, in the deepest layers just above the floor, none at all (Fig. 95, Lake Keller). The decrease of oxygen content begins at the thermocline (Fig. 95).[83] In such waters the bottom fauna is greatly influenced. In shallow lakes, in which wave action extends throughout, there is no lack of oxygen at the bottom.

Animal communities in lakes

Communities of organisms free from direct dependence on bottom or shore are called *pelagic* if in the ocean and *limnetic* if in lakes. Communities dependent on the bottom are said to belong to the *benthos* in oceans and to the *pedon* (*pedonic*) in lakes. The communities related to the shores are said to belong to the *littoral* community in both oceans and in lakes. If need is felt for further sharpening of this terminology, *littoral* may be retained for such communities along the shores of the ocean, and a new term, *paralimnic*, may be used for the corresponding community in lakes. The region would be that of the *paralimnion*. Animal communities of standing waters fall naturally into two groups—those of the deeper and more permanent lakes, on the one hand, and of the smaller, shallower, more evanescent ponds and pools on the other. There are, of course, no sharp demarcations between these groups or their corresponding waters. Our general discussion of the fauna in standing waters will be based primarily on that of lakes.

A lake may be defined as a continuously closed, stagnating mass of water found in a depression of the earth, never directly connected with the ocean (Forel), in which the shore vegetation does not extend to the greatest depth, and in which, therefore, there is a central area free from rooted plant growth. Lakes, therefore, in contrast with ponds, contain open water and have a limnetic region. In this respect conditions in a lake are more like those in the ocean; but the limnetic

region in general does not exceed the pedonic region nearly so much as the pelagial exceeds the benthal in the ocean.

The shore zone

The pedonic region is composed of a shore zone, which extends as far as the green plant growth on the lake floor, and the deep pedonic zone beneath the limnetic region. The depth to which shore vegetation extends varies in different lakes, sometimes down to about 30 m., but usually not exceeding 6 to 12 m. This depends primarily upon

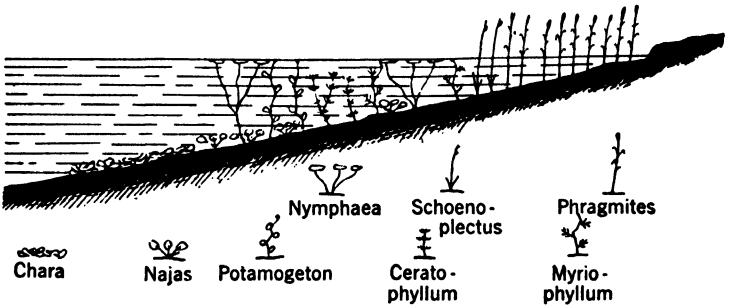


FIG. 96. Schematic diagram of one type of plant growth at the edge of a lake. After Brutschy.

the transparency of the lake water, and this is the greater when the amount of plankton present in the lake is smaller. Where the slope is gradual, the paralimnic zone is wide; where the slope is steep, as, for instance, in many places in Lake Lucerne, or in the Scottish lochs, it may be entirely absent.

The shore region contains by far the richest and most diverse fauna in lakes. It furnishes substratum for animals on its floor and on its plant forms; the plants supply shelter from enemies and protection against wave action, afford nourishment, and liberate oxygen in great quantities.

The paralimnic zone may be divided into several parts. First of all, in the shallowest waters, are found the thickly growing emergents, high stemmed grasses and reeds and growths of rushes and sedges, among which in turn grows a mass of swamp plants; then follows a strip of more strictly aquatic plants with floating leaves, such as pondweed (*Potamogeton*) and water lilies (*Nymphaea*). Finally there is a zone of submerged plants, *Elodea, Chara,* certain species of *Isoëtes,* etc. (Fig. 96). The gentler the slope of the shore, the

wider these zones are found to be. No plants can grow where waves driven by prevailing winds break strongly against the shore; there all the loose particles on the bottom are washed away and a surf shore line of gravelly or sandy beach develops, with its own peculiar sparse animal life.

The temperature factor is subject to greater change in the paralimnic zone than in other regions of lakes. Because of the closeness of the lake bottom, the water warms much more quickly than in the region of open water. This is especially noticeable on shores with southern exposure, where a temperature of 17.2° may exist under the noonday sun, whereas in the open water near the surface the temperature is only 2.5°.[98] Many insect larvae (*Corethra,** Libellulidae) congregate and undergo metamorphosis in such warmer regions. Cooling of the water likewise occurs more rapidly in the shallow shore waters, for the cooled surface waters cannot set up a circulation like that of open water. For this reason ice first forms along the shores in winter.

The breaking of waves against the shore not only kills organisms but also grinds up their excrement and remains, providing thus for the development of detritus and the occasional stirring up of these nutritive materials. This is especially advantageous to the numerous detritus feeders and furthers their increase. Fishes congregate where the bottom food supply is plentiful, and experience in fishing shows that exposed shores may furnish a richer catch of fishes than shores protected from wind.[73] A region of strong breakers, however, is fatal to most forms of life; on plantless shores where strong waves beat when the wind is high, rocks and pebbles are tossed about, and in winter, icefloes are dashed against the banks.

A harmful factor for the fauna of a littoral region is the regular variation in the water line in many lakes. This is especially true in mountain lakes where the periodic increase and decrease in size of tributaries from glaciers or melting snow cause a marked rise and fall of water level, in Lake Constance a yearly average variation of 2.2 m., with a maximum of more than 3 m. A similar condition occurs in the lakes of the plains. Even in the Great Lakes there are extensive irregular variations in lake level both from temporary seiches and over periods of years.

Only that part of the shore fauna which can resist or evade the

* = *Chaoborus.* We have preserved the familiar *Corethra* for the purposes of this book.

unfavorable conditions can live in such parts of the paralimnic zone as are dry a part of the year: animals with powers of locomotion, which retreat or advance with the water line, such as crustaceans, insects, and water mites; animals that protect themselves from desiccation by encysting, like many Protozoa; or that stand drying (threadworms, tardigrades, many rotifers and copepods); or, finally, animals of amphibian habits, such as frogs and many snails. Sessile

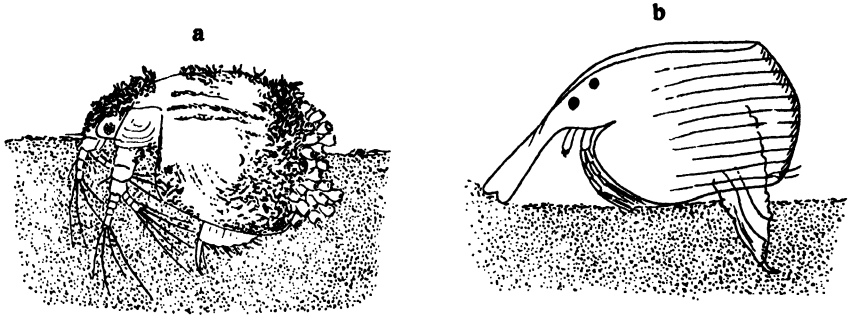


FIG. 97. Littoral mud-inhabiting cladocerans: *a, Iliocryptus sordidus; b, Rhynchotalona falcata,* digging in the mud with its rostrum. × 25. *a,* after Frič Vávra, *b,* after Herr.

or slow-moving animals, such as sponges, bryozoans, and mussels, are absent.

In the region of profuse plant growth, in and among the leaves and on the bottom, is a diverse and important group of plant and detritus feeders, with the animals that prey upon them. Protozoans, flatworms, leeches, annelids, and rotifers are abundant, being especially plentiful where the growth of *Myriophyllum* is thickest.[45] With them live a host of Entomostraca, partly in the mud (Fig. 97), partly among the leaves of plants, along with isopods and amphipods. There are numerous snails and mussels. Above all, this habitat forms the center of life for both adult and larval insects,[98] which find nourishment and resting places, as well as ladders used in climbing to the surface of the water for air; in winter the oxygen liberated by photosynthesis collects in large bubbles under the ice and can be utilized by air-breathing insects. Contrary to a condition frequently found in terrestrial insects, the aquatic insects are seldom limited to definite plants. Fresh-water sponges and occasionally many kinds of Bryozoa grow on solid objects such as reeds, submerged tree trunks, and stones.

A large number of fishes find nourishment in the region of plant growth, and especially a favorable spawning place; for this reason young fishes are plentifully represented in this region. Thus it happens that the degree of development of paralimnic plant growth may have a marked effect on the fish fauna of a lake. The Königssee (in Bavaria), without a paralimnion, produces annually 1 kg. of fish per

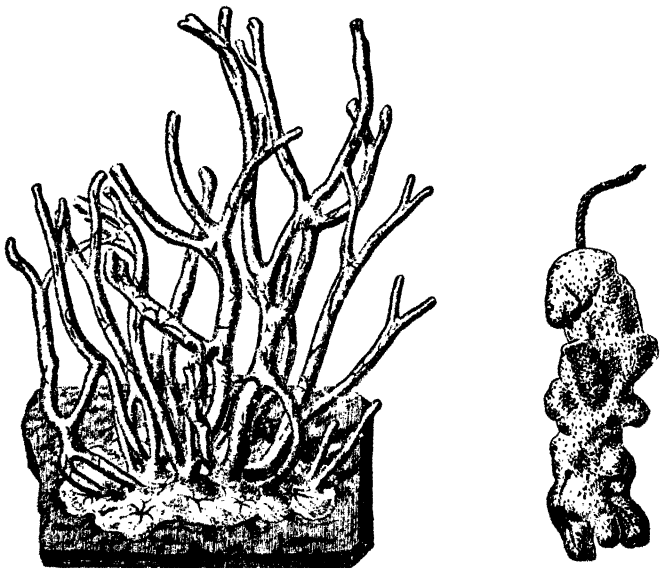


FIG. 98. *Euspongilla lacustris* from quiet water and from moving water, attached to a floating thread. After Weltner.

hectare; Lake Constance, the fertility of whose shallower water suffers from rather large variations in water level, produces 8 kg.; the Chiemsee (in Bavaria), whose shallow and wide paralimnic region is well covered with plants, produces about 20–25 kg. of fish[71] per hectare.* These relations prove to be similar in the United States.[3] It is unsafe, however, to generalize too confidently at this point.

The animal life of wave-beaten rocky shores, where no plants are found, has a faunal composition much like that of swift water in neighboring streams.[96] A close observer always finds teeming life. Fresh-water sponges grow on the stones in flat, slab-like crusts, while in quiet bays they develop into much branched stems often up to 30 cm. high (Fig. 98). Numerous flatworms hide under the stones

* 0.9, 5.3, and 18 to 22 lbs., respectively, per acre.

(*Dendrocoelum, Planaria, Polycelis*); flatly depressed leeches (*Glossiphonia, Herpobdella*) attach themselves by means of their suckers. Mayfly nymphs are also much depressed; many caddisfly larvae weigh down their cases with heavier stones. In lakes, the snail *Goniobasis,* with its wide, sucker-like foot, is widely distributed; also occasionally the shield-shaped snail, *Ancylus fluviatilis* (Fig. 89). The mussels of the plantless shores, *Anodonta* (Fig. 7*e*) and *Unio* alike, are small and convex, with relatively thick shells often considerably corroded at the umbo, in contrast with the large, thin-shelled, beautifully colored forms found in the quiet waters of bays. The *Anodonta* of Lake Constance, for instance, become 9 cm. long; those in the Waldsee in upper Württemberg, up to 19.6 cm.[49] The snails of the genus *Limnaea* change form in the moving waters of the lake shore because of the constant pull to which their shells are exposed, which in turn produces a reaction on the softer parts of the body (Fig. 99). Steep shores are poor in life.

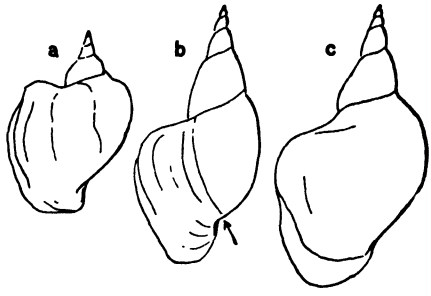


FIG. 99. *a, Limnaea stagnalis* var. *bodamica* from moving water; *b, L. stagnalis* from quiet water, normal to the arrow, beyond which the shell is weighted with cement, producing growth similar to *a* (after Voigt); *c, L. stagnalis* from a pond, the growth form produced by a strong growth of filamentous algae on the shell, which hinders its motion. × ⅔.

The deep pedon

The remainder of the lake bottom makes up the deep pedonic region. In biotic characteristics it is not sharply marked off from the communities of the paralimnion. Those parts lying nearest its borders are occasionally characterized by an abundant molluscan fauna. A truly abyssal stratum, comparable with that of the sea, into which no light rays penetrate, is lacking in most inland waters; extensive development of such a stratum is found only in Lakes Baikal, Tanganyika, Nyasa, and Posso, and in the brackish Caspian Sea.

The deeper regions of lakes have other peculiarities besides the lack of plant growth that contribute to the unique compositions of their fauna. The amount of light that penetrates into the deeper waters is much reduced. There are associated modifications of color in both

limnetic (see below) and bottom forms. The planarians, otherwise black (*Polycelis nigra, Planaria alpina*), are represented by pale yellow forms in the depths of the lakes in the Alpine foothills. Temperature is very constant in the deeper pedon as compared with that near the shore. In Lake Lucerne the temperature at depths of 30 to 200 m. is not less than 4.7° and not more than 10°; the variation at depths of 100–200 m. is only about 1°.[104] Stenothermal animals, adapted to the cold, with a few eurythermal forms, find this a favorable habitat.

There is no marked movement of water at greater depths. Because of this the floor is evenly covered with fine mud varying according to its origin, which is usually organic. The dead bodies of plants and animals living in the open water, the excrements of fishes, and the products of disintegration of shore plants sink to the bottom and form a layer of detritus, which becomes the food of innumerable pea clams (*Pisidium*), slimeworms (Tubificidae), and bloodworms (Chironomidae). These continually engulf the mud and give off small mudballs from which the largest part of the organic material has been extracted; the rest is finally disintegrated by the action of bacteria.

When more organic material sinks to the bottom than can be consumed by the deep-water fauna and the bacteria, black vile-smelling muck rich in hydrogen sulphide is produced. Peat develops where these organic elements are disinfected by the prevalence of humic acid and are thus kept from disintegrating. Bottom mud in all deep lakes comes primarily from decaying plankton; accordingly the mud of the lake bottom varies with the various compositions of the plankton, and in especially pronounced deposits one can identify different sorts, such as diatomaceous mud, cyanophyceous mud, and chitinous mud. Where rapidly flowing streams of mountains or foothills contribute masses of mineral sediment, a sterile, finely grained, more or less solid, terrigenous mud becomes deposited on the bottom, and this is inhabited by an exceedingly sparse fauna. Such sediments, sometimes excessive in amount, carry many small plankton animals with them into the deeps and bury them.

No influence of increased water pressure on the animals living on or near the bottoms of lakes has so far been demonstrated, although the evidence is not yet fully collected from lakes Baikal and Tanganyika. Great uniformity of environment prevails at the bottom of deep lakes; there is no change of temperature, scarcely any change in the amount of light, no movement of the water, and no variation of substratum. For this reason many periodicities common in the biota of shallow waters are not evident; a resting period during the winter

does not occur; the pea clam, *Pisidium,* in the deeper regions, shows no clearly marked rings of annual growth but has a uniformly developed shell.[104]

Animal life of deep water

The deep fauna of lakes consists of ubiquitous eurythermal forms and stenothermal cold-water forms, in accordance with the conditions of temperature. The largest part of the fauna is composed of rhizopods, Tubificidae, *Corethra,* chironomid larvae, the larvae of biting gnats, and the small bivalve *Pisidium.* Rhizopods occur in a rather large number of species, often in surprisingly large numbers of individuals, widely distributed, especially in the deep lakes; these consist partly of ubiquitous forms, partly also of species limited to the deeper parts of the lakes. A common characteristic of all these deep-water rhizopods is that they are larger than their relatives in shallow water. This is especially noticeable in *Cyphoderia ampulla* (measuring 200 μ in deep water, 110 μ in shallow water), a condition similar to that in some deep-sea forms (see p. 307). The fresh-water polyp *Hydra* and the sponge *Spongilla* are found in rather deep water, in the Teufelsee (in the Bohemian Forest) down to 25 m., and in Lake Madue in Pomerania down to 40 m. Of the flatworms a number of Rhabdocoela are generally characteristic of the deeper parts of lakes, e.g., *Plagiostomum lemani* (as in Lake Constance and other Alpine border lakes, or in summit lakes of the higher mountains). Where triclad flatworms occur in the deep regions they are reduced in size. The ubiquitous *Dendrocoelum lacteum* is an example, as is *Planaria alpina,* which is adapted to low temperature. Slimeworms (*Tubifex* and its relatives) are common and may be the prevailing forms; 5750 individuals of various species have been recorded from 10 liters of mud from 32 m. A few Bryozoa also grow in deep water, e.g., the widely distributed *Fredericella sultana.* Crustacea are common; ostracods, e.g., are represented by a large number of genera; of the copepods, there are species of *Canthocamptus* especially, and several species of *Cyclops.* A number of interesting cold-water isopods and amphipods live in deep water in addition to ubiquitous species in the border lakes of the Alps; the occurrence of blind forms such as *Asellus cavaticus,* and the cave amphipod, *Niphargus puteanus,* especially in the deep pedon of Alpine border lakes, is important. The slimeworms (Tubificidae) take first place in numbers in the bottom fauna, with chironomid midges next. As many as 8000 individuals of these forms may be found on a single square meter.

Most mollusks of deeper waters are not dependent upon the atmosphere for their supply of oxygen, i.e., mussels and gill-breathing snails. In Lake Ratzeburg, for instance, of pulmonates only *Limnaea ovata* and *Planorbis albus* go deeper than 3 m., in contrast with 7 gill-breathing snails, among which *Bythinia tentaculata* goes down to 12 m., and *Valvata piscinalis* var. *antiqua* to 18 m.[72] In the Alpine border lakes *Valvata* goes down even to 64 m., and *Bythinia* occurs as deep as 60 m. The tiny bivalve *Pisidium*, on the other hand, lives in depths greater than 200 m. and exhibits a great variability, which has brought about a separation into a large number of species. All mollusks of the deep pedon of lakes are stunted, even the plentiful pisidia.

In a number of Alpine border lakes, whose water contains a large supply of oxygen in the deeper parts, some pulmonates of the genus *Limnaea* have become adapted to life in the depths, as for instance in Lake Geneva.[104] They do not rise to the surface to breathe as their paralimnic relatives do, but fill their lung space with water from which they take the necessary oxygen. In Lake Geneva three forms of such *Limnaea* occur: *L. profunda, L. forelia,* and *L. abyssicola.* It has been proved that the first two are varieties of *L. ovata,* and *L. abyssicola* is a variety of *L. palustris,* for their descendants raised in an aquarium revert to the original type and again make periodic excursions to the surface for breathing. *L. ovata* and *L. palustris* are eurythermal; deep-water forms of the stenothermal warm water species *L. stagnalis* and *L. auricularia* do not exist. In lakes with a thermocline the hypolimnion typically becomes oxygen-deficient and even oxygen-free, at least in limited regions during summer stagnation. This produces a severe selection, and only facultative anaerobes such as some protozoans and chironomid larvae can survive as permanent residents.

The fauna of the deeper pedon evidently originated in the paralimnion and probably is constantly restocked from the same source. Most of the abyssal animal species also occur in shallower water. For this reason the amount and the composition of the deeper pedonic fauna depend on the type of paralimnic fauna of the lake in question. Thus the fauna of the deeper waters of Scottish lochs, like that of their paralimnion, is very sparse. Those species, however, that are found in the deeper regions but are lacking in shallow waters of the same lakes are not specifically abyssal animals; in mountain lakes they are also found in the shore zone. It may be supposed that they formerly similarly inhabited the shores of lowland lakes, and only because of a change in environmental conditions, especially because of a rise in

temperature, have they been crowded into the depths. The conditions of the lake abysses, consequently, have seldom proved productive of new species, since even the deeper regions are relatively short-lived. Special abyssal forms exist only in the very old, very deep, inland lakes such as Lake Baikal and Lake Tanganyika (see Chapter 6 and p. 410 ff.).

The limnetic fauna

The fauna of open water is especially characteristic of lakes, for it is just this constant existence of a limnetic region that distinguishes

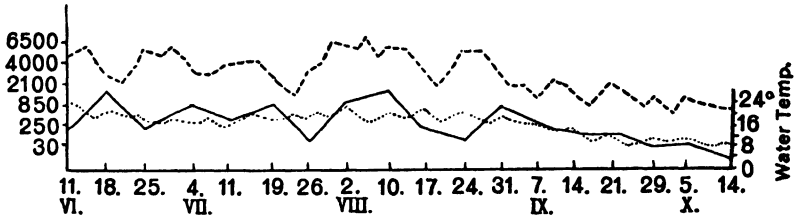


FIG. 100. Amounts of rotifers (——) and of nannoplankton (– – – –) in waters in Saxony, from June to October. Temperature curve (.....). After Dieffenbach.

them from ponds, in which small areas of open water without vegetation may exist occasionally, especially in the spring, but in which there is no continuous widespread region without plant growth. Imperceptible transitions make a sharp demarcation impossible. Although there is a pond plankton, the communities of the open waters of bodies of fresh water find their typical development in lakes.

The plankton of inland waters consists of plant and animal forms, the former furnishing the foundation for the existence of the latter. As in the ocean, some of the plankton animals are so tiny that they escape being caught with ordinary gauze nets and can be separated only by filtering or centrifuging the water. Some of these organisms, the dwarf or nannoplankton, are partly photosynthetic and partly, though to a less extent, forms that require organic food material. They are so plentiful that in Lake Lunz 160 individuals of the nannoplankton were counted to every 3 of those caught in nets, and in spite of the immense difference in size, the yearly average volume of the nannoplankton is three times as great as that of the larger plankton.[63] Many plankters are restricted partly or entirely to the nannoplankton for their food, the mass of which sometimes controls their numbers (see Fig. 100). Large plankton animals, of course, also eat diatoms

and other of the larger algae. As the development of plant elements in the plankton is limited, among other factors, by the amount of dissolved nutritive material in the water, this is indirectly also responsible for the total amount of plankton present in a body of water (cf. p. 213). This is one reason why shallow waters in general are richer in plankton than deep waters; small lakes richer than large ones; above all, why those lakes that are situated over fertile ground, over limestone, etc., or that receive other plentiful nutrient materials [5] are richer in plankton than those of a relatively sterile granitic mountain region.

Animals of open water are considerably in the minority compared with their relatives near the shore, a fact explainable by the peculiar adaptations demanded by a purely limnetic life. Of 66 phyllopods of southeastern Germany, only 11 occurred as limnetic forms; of 67 crustaceans known from Lake Balaton, only 8 were limnetic; and of 35 rotifers, only 10. Moreover, among the numerous forms of animals and plants in the plankton, only a few species are sufficiently prevalent to determine its character. Of a total of approximately 150 species of plankton organisms of the Danish lakes only a few appear in such numbers as to create a monotonous animal plankton; of animals only the species of *Diaptomus* among copepods, a number of cladocerans, and a few rotifers.[95] Besides Crustacea and rotifers, water mites furnish a number of species of limnetic forms. Only one insect, however, is truly limnetic, the so-called phantom larva, *Corethra plumicornis* (Fig. 104).

To the truly limnetic animals may be added a number of more or less irregular visitors in the open water. *Bosmina coregoni* is limnetic, whereas *Bosmina longirostris* is permanently so only in the smaller bodies of water and is only casually limnetic in true lakes.[19] The same is true of a number of other Cladocera and of a few rotifers.

The amount and composition of the plankton are very variable according to the prevalent environmental conditions in various locations, as well as in the same body of water at various depths and at various times. Very poor ponds or deep, cold lakes often contain only 5–10 cc. of animal plankton in 1 cu. m., in contrast with small fertile village ponds that may, exceptionally, contain 1500–2500 cc.[77,92] On the other hand, the amount of plankton in the Dobersdorf pond (Holstein) varies between 136 and 3977 cc. in 1 cu. m. of water, and in Lake Plon between 13 and 424 cc. during the course of one year.[6] The annual yield of plankton in the well-studied Lake Mendota (Wisconsin) is of the order of 5 tons of dry matter per acre; the mean

standing crop is approximately 200 lb. of dry stuff per acre.[15] Fresh-water plankton reaches its highest development in the temperate zones.

The plankton of neighboring water basins often shows a considerably different character, e.g., in the lakes of Switzerland and the French Jura,[103] or in the different Alpine border lakes; thus *Daphnia* and *Bosmina* are missing in Lake Brienz and their place is taken by *Diaphanosoma,* species of which occur in unusual numbers.

The transparency and coloring of the water are influenced by the amount and composition of the plankton. Very transparent blue water, like that of Lake Como, is a sign of scarcity of plankton; the richer the plankton, the more turbid and discolored the water The tint depends on the composition of the plankton, above all upon the most prevalent algae. Two different types of phytoplankton can be distinguished in temperate regions: in one of them diatoms are most common, in the other blue-green algae.[95] These two groups of algae seldom have their greatest development in the same lake or at the same time. The optimum for most fresh-water diatoms is at relatively low temperature, about 12°, whereas blue-greens thrive best in the higher summer temperatures (19° to 23°). The former are, therefore, most prevalent in the cold northern or Alpine lakes where blue-green algae, with few exceptions, are almost totally absent; in warmer, deeper lakes they occur only in spring or in late fall or at greater depths. Blue-green algae prevail in lakes of the plains. The color of the water in colder lakes, consequently, is yellowish-green (because of diatoms and *Ceratium*), in warmer lakes in spring and late fall also yellowish-green; but in summer it is a bluish-green.

Annual variations are chiefly quantitative. Plankton is less well developed in winter than in summer, but it has certainly not disappeared. Many animal forms, in fact, reach their maximum of development in winter. Thus the ratio of winter to summer plankton in Lake Constance is 1:2, in the lakes of north Germany 1:20.[6] In Lake Mendota the March minimum is almost one-fourth of the April maximum.[15] During the course of the year definite changes in the composition of plankton arise because of the fact that the breeding season of various plant and animal species occurs at different times. Perrennial plankton forms, even though not always numerous, are distinguished from periodic forms that occur only at definite seasons of the year. Those without rest periods belong to the perennial group, e.g., most copepods, many *Bosmina,* and rotifers such as *Anuraca cochlearis* and *Asplanchna priodonta.* Examples of periodic

forms are the larvae of the triangle mussel *Dreissena,* and animals with resting periods, like most rotifers, *Notholca striata,* e.g., found only in the winter, and Cladocera. In equal amounts of plankton from the same lake, the combination of species may be very different at different times.

The various depth zones of open water, moreover, also exhibit a stratification of plankton, which is determined primarily by the amount of light, the conditions of temperature, and the amount of oxygen, but partly also by movements of the water. This stratification varies with day and night and with summer and winter. In Lake Constance, the plankton forms are spread evenly to great depths in the winter, when temperature and lighting are more nearly equalized, whereas in summer the masses of the plankton extend only about 30–35 m. in depth, and during the daytime the uppermost layer of about 1 m. in thickness is poor in plankton; within this mass the individual plankters, again, stay in the layers most favorable to them (Fig. 101).[35] In Schwartzer See (in the Bohemian Forest) in the summertime, *Holopedium gibberum* (Fig. 81) and *Cyclops strenuus* are found in the upper 3 m., *Daphnia ventricosa* and *Bosmina bohemica* in deeper regions; only *Cyclops strenuus* is found in larger numbers during later months.[31] In Lake Lucerne plankton extends to a depth of 65 m. in summer, in Lake Zug to about 80 m., in Lake Geneva to 100 m.; the lower limit lies much deeper in all these lakes in winter. Figs. 101 and 102 show, furthermore, the influence of the thermocline on the distribution of the plankton, and the secondary concentration of Crustacea over the bottom layer, which is poor in oxygen. The majority of rotifers occur in a very definite order of strata in deep waters (Norway): *Conochilus* in 0 to 0.25 m.; *Notholca longispina* and *Polyarthra platyptera* in the uppermost 5 m.; *Anuraea cochlearis* seldom above 5 m., mostly below 10 m.; *Ploesoma hudsoni* rarely in the uppermost 5 m., occasionally even below 10 m., in one case as low as 25 m.; only a few individuals of *Anuraea aculeata* are found above 10 m., and the majority live at about 25 m.[45] The nannoplankton is similarly stratified. Such stratification is regularly changed by night migration, when many forms move toward the surface, and is reformed at daybreak.

A seasonal variation in body form occurs among various plankton animals, especially Cladocera, rotifers, and the flagellate *Ceratium hirundinella.* These cyclomorphic changes arise under the influence of variation in temperature, light, and nutriment. They disappear entirely in constantly warm tropical lakes as well as in the polar or al-

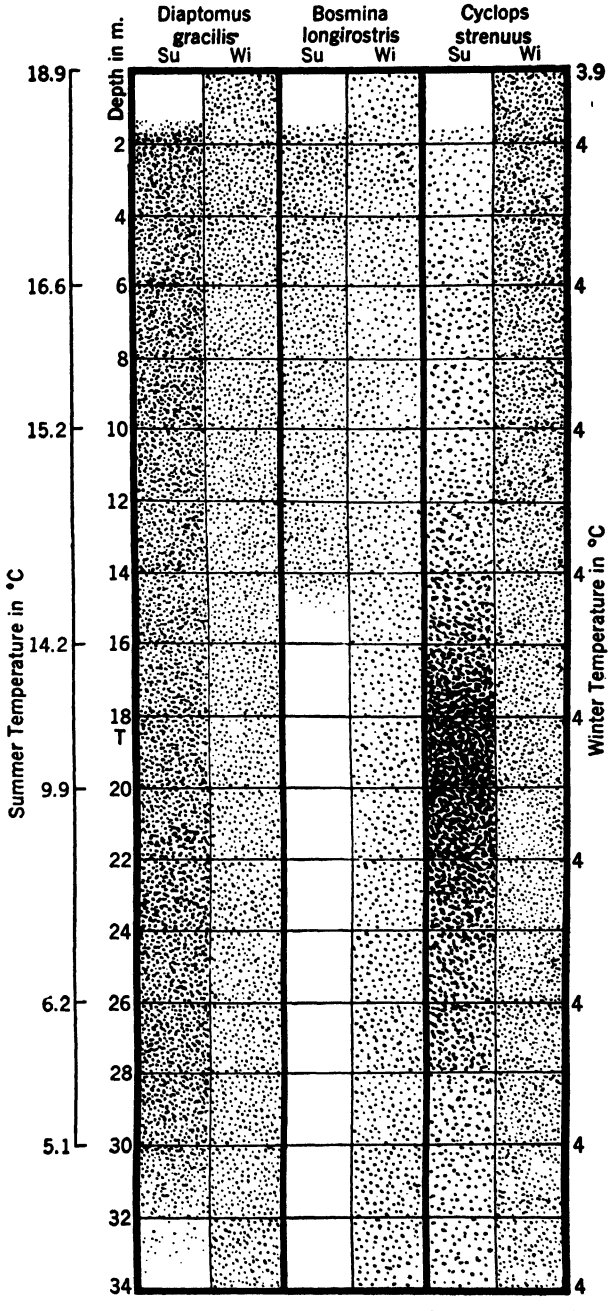


FIG. 101. Vertical distribution of *Diaptomus gracilis, Bosmina longirostris,* and *Cyclops strenuus* in Lake Constance, in summer, *Su;* and winter, *Wi.* After Hofer.

pine lakes whose temperature never rises above 12°, which appears to be a critical temperature for changes of form in these organisms.[54]

Daphnia have round heads during the cooler part of the year. Populations with pointed helmet-shaped heads are formed in some ponds and lakes when the temperature rises above the critical point of 12° to 16° in Danish waters, or 19° in Connecticut.[18] The hel-

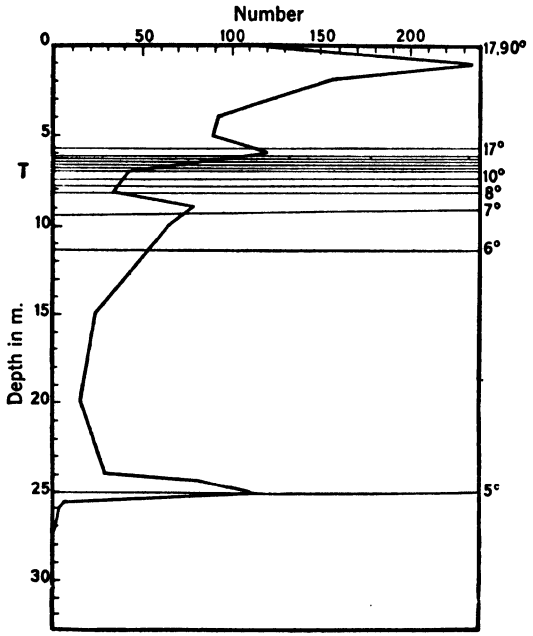


FIG. 102. Quantitative distribution of Crustacea in Lake Sakrow near Potsdam, in number of individuals per liter. Depth in meters at left, corresponding temperatures at right; *T., thermocline.* After Behrens.

meted generations again produce round-headed ones in the autumn. *Daphnia* in larger ponds tend to have larger helmets. Correlation between head form and food supply, if present, is only partial. It is possible that the helmets or spines produced by summer populations of cyclomorphic animals aid flotation in the lowered viscosity of water in summer.[22]

The character of the plankton is further changed by the cyclic appearance of males and sexual females among the Cladocera, and the development of winter eggs in ephippia, whereby the course of parthenogenetic reproduction is interrupted. At such times the surface of a lake may be covered with innumerable ephippia. The various

species differ in the appearance of bisexuality; and even the same species behave differently in different lakes. In the lakes of middle Europe dicyclic and polycyclic species are found, i.e., those with one or more appearances of males during the course of the year; farther north, and in the high mountains, on the other hand, a monocyclic condition becomes more and more prevalent. The cladoceran *Chydorus sphaericus,* for instance, generally has two sexual periods; but in the most favorable waters of central Europe it has become acyclic and consequently perennial.[90]

Bacteria

Bacteria are the smallest of the nannoplankton organisms, so small in fact that they are not collected by ordinary centrifuge methods and require special techniques for their detection. Of these, the so-called direct-count method is apparently most accurate. Employing modifications of this method, Russian workers [41] report from 500,000 to 6,000,000 bacteria per cc. in Lake Glubokoje, which probably is polluted, and Wisconsin students [11] found from 19,000 to 2,000,000 per cc. in the lakes studied. In Lake Mendota there is an August maximum and a low minimum in late winter; however, such seasonal variations do not occur in all lakes. In Indiana [76] most bacteria have been reported from the surface, the bottom, and the thermocline, but these results are not confirmed in similar lakes, and no generalization appears to be possible at present concerning the vertical distribution of bacteria in lakes. Below the thermocline, during summer stagnation, the number of aerobes decreases. In the bottom deposits of Lake Mendota, of the 100,000 bacteria per cc., about 1% are denitrifying and 0.1% are cellulose destroyers.[2]

Minute as they are, the bacteria of fresh waters form an important food source for other members of the nannoplankton and for some of the mud feeders and hence, with algae, stand at the very bottom of the food pyramid. The rapid rate of reproduction of bacteria makes their importance as food greater than is indicated by the size of the standing crop.

Lake fishes

Fishes cannot be grouped into the three life regions of lakes in the same manner as the less motile invertebrate animals, because they may range from the paralimnial to the abyssal region or from the shore line to open water.

Only minor differences exist in the composition of the fish fauna

of standing waters, as compared with that of slowly flowing waters; only the genus *Coregonus* in glaciated Europe is entirely limited to lakes; in Siberia and North America a number of species of this genus occur also in rivers and creeks.

A varied fish fauna composes a part of the great wealth of life of inland lakes. The largest yield of fish from the rivers is furnished primarily by the migratory fishes coming up out of the sea or going down to it, such as salmon, shad, and eels. The fishes of lakes, however, are autochthonic. The Lake of Fayum furnishes fish for all of Egypt, and the Caspian Sea is the large fish basin of south Russia; the number of carp near the mouth of the Atrek defies estimation or description.[89]

The fact that the smaller pedonic animals are more abundant than those of the open water, a characteristic of inland waters as compared with the ocean, also determines the haunts of fishes; the fishes of the bottom usually outnumber those of the open water. There is, however, no sharp demarcation between the shore region and the deep water. The majority of bottom fishes are found in the region of plant growth; many, however, also visit the deeper regions. The eelpout (*Lota lota*) descends to depths of 150 m. and feeds on the spawn of the salmon, and the European catfish (*Silurus glanis*) also goes to that depth. The masses of Tubificidae, *Pisidium*, and gnat larvae in the pedonic mud furnish a rich feeding ground for fishes. Careful experiments have shown how the products of the fishing industry in fresh waters depend upon the bottom fauna.[85] In the lakes of south Sweden the biomass of bottom fauna fluctuates between wide limits, between 1 kg. and 200 kg. per hectare. Lake Havgard with 93.3 kg. of bottom life per hectare produces 25.5 kg. of fish from the same area annually, while Lake Borring with 2.8 kg. of bottom life per hectare produces only 3.0 kg. of fish. The carp, for instance, become dwarfed and reach less than a third of their usual length when insufficient bottom life is present. Most predaceous fishes live in the paralimnic regions. Fishes less often have the pelagic habit in inland waters than in the ocean; this is associated with the correspondingly less-developed food supply in the limnetic region. Fish fry are typically plankton feeders; of adult fishes, the Salmonidae are especially dependent upon the plankton.

Fishes living on the lake bottom show a number of convergent adaptations in members of groups of widely different taxonomic relationships. In many of these forms the search for food in turbid water near the muddy lake floor is facilitated by means of beard-like feelers

thickly set with nerve buds. These are exhibited by the sturgeon and the sterlet, the carp from among the Cyprinidae, the Cobitidae, many catfishes, which are typically bottom dwellers, and the eelpout (*Lota*) among the Gadidae. The mouths of the sturgeon and carp and of the American suckers (Catostomidae) can be protruded for the purpose of gathering food from the bottom. The long extended snout of the African Mormyridae is of service in searching through the mud. All these fishes that feed on the bottom mud have a fine gill filter like the plankton feeders. Another characteristic common to

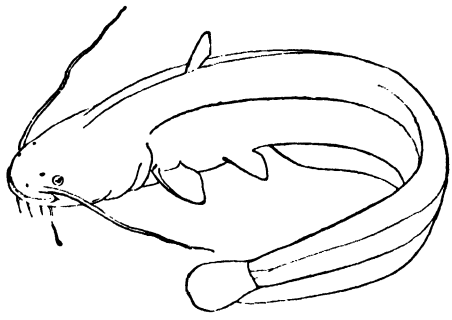


FIG. 103. Sheatfish or wels, *Silurus glanis*, a mud-inhabiting catfish of central Europe, with elongate anal fin. After Brauer.

many bottom-living fishes is the extension of the anal fin, which, with its wave-like serpentine undulations, lifts the posterior end of the fishes upward and depresses the anterior end: e.g., the European catfish (*Silurus glanis*) (Fig. 103), the eelpout, and the electric eel of South American swamps.

The depths of lakes are inhabited by certain fishes that are partly limited to deep waters, and partly also occur in shallow water; these inhabit both the pedonic and the limnetic biotopes. In the Great Lakes there is evidence of stratification of the fish fauna. Among the coregonid fishes, groups of bottom-feeding forms belong primarily to the shoal waters, others apparently are most often taken in mid-depths, and still another group of species is found chiefly in deeper waters. Similar relations hold during spawning. The lake herring and the common whitefish spawn in shoal water near the beginning of winter; *Leucichthys reighardi* and *L. hoyi* spawn in deeper water, the latter between 36 and 55 m. (in lakes Michigan and Huron) in early spring. Another group of three or more species spawn in still deeper water down to at least 110 m.[92] The siscowet, a variety of lake trout, appears to be limited to the depths in Lake Superior.[38]

Some fishes that live permanently in the deeper waters have characteristics that may be correlated with the lack of light in their habitat. Thus the pedonic charr (*Salvelinus salvelinus profundus*) of Lake Constance is pale yellowish brown and its eyes are enlarged. The peculiar fish *Comephorus baikalensis,* which lives in the abyssal region of Lake Baikal, has lost its dark pigment and is pale rose.

Lake Superior

Lake Superior is the largest body of fresh water in the world in its own right, and in addition it is in close connection with two others of the five Great Lakes of North America. Although mid-continental in position, it is only 602 ft. above sea level. As has been stated already, Lake Superior has a surface area of 82,360 sq. km.; its mean depth is 475 ft., and its maximum depth is 1008 ft. The biota of the lake has been inadequately studied; there exists a short report of work done before 1871 [78] on which the following notes are based. Of 28 dredgings, 7 revealed sand and gravel, 5 showed mud and sand, 14 showed mud and soft clay. Deeper portions of the lake have a clay and mud bottom, or mud alone. In shallow water the mud is mixed with sand, and the bottom of the most shallow parts is mainly pure sand. Water samples from the bottom are perfectly fresh. August and September temperatures below 60–80 m. were uniform at 4°, while the surface waters varied between 15 and 18°.

In shallow water near the shores the animal life varies with the character of the bottom. Deep-water communities begin at 60–80 m., and in greater depths the same pedonic species are distributed throughout. Substrata of soft clay-like mud are unfavorable to animal life except for certain worms. No invertebrate species are found peculiar to the depths, which are characterized merely by the absence of shallow-water species.

Types of lakes

Naumann [53] and Thienemann [84] have distinguished between different types of lakes in the temperate zones according to their various physical and biotic environmental factors. Thienemann distinguishes between (*a*) clear-water lakes and (*b*) brown-water lakes, whose waters are colored brown from the high humus content. Brown-water lakes will be considered below together with moorland waters. Clear-water lakes may be divided into two types: the oligotrophic type, whose water is poor in nutritive plant material and shows nearly equal distribution of oxygen during summer and winter, and whose mud

bottom contains little organic material; and the eutrophic type, which, in contrast, is rich in nutritive plant material. At sufficient depth below the thermocline in summer eutrophic lakes show a considerable reduction in oxygen content, and their mud bottom is composed of typical muck. All gradations between these two types may be found, and some limnologists recognize an intermediate type, the mesotrophic; the pronounced representatives of the two types differ considerably from each other.

The lakes of the Alps and of the Alpine foothills are examples of oligotrophic lakes; in North America the Finger Lakes of New York are of this type. Such lakes have narrow shore lines and blue to light green water, which is very transparent. The oxygen content of the deep water never goes below 70% of saturation. The consequence of the narrow width of the paralimnic region is a sparse plant growth, and the small amount of nutritive plant material makes possible only a small mass of plankton. Grass-green algae prevail in the phytoplankton; blue-green algae are of less importance. As a result of the plentiful oxygen supply, the deep waters are inhabited by many genera and abound in individuals in spite of sparse plankton production; larvae of biting gnats of the genus *Tanytarsus* are characteristic of the deep water.

Eutrophic lakes include lakes of the Baltic lake plateau and many other parts of Europe. They are plentiful in North America; the well-studied Lake Mendota in Wisconsin is an example. They are generally more shallow and therefore relatively warm in summer; they have a wide paralimnic zone, and their water is rich in nutritive plant material. The color of the water is green to yellow or blue-green. Their transparency is often much reduced. In consequence of the flat shores, plant growth is plentiful and the water contains a large amount of plankton in which the blue-green algae outnumber the grass-green; such algal coloration is of frequent occurrence. The rich bottom mud is the seat of the processes of decay, which result in a rapid decrease of the oxygen content of the deeper waters (Fig. 95).

The deeper pedonic fauna is limited to animals that do not demand a large supply of oxygen. *Chironomus* larvae and slimeworms (Tubificidae) are characteristic of the bottom, and the larvae of the gnat, *Corethra*, of the open water. The *Chironomus* larvae are the only free-living insects with haemoglobin in their blood, and it is this characteristic that enables them, as well as the Tubificidae, to utilize even the smallest quantities of oxygen; they are consequently without competition in such regions. *Corethra* larvae rise at night to the

upper water strata, which are rich in oxygen, and there renew the oxygen in their tracheal bladders, so that they can then draw on this supply. Many fishes (carp, eel, pike) are adapted to temporary life in water poor in oxygen by the fact that their haemoglobin reaches the same oxygen saturation at an oxygen pressure of 2–3 mm. as is reached by that of the trout at a pressure of 18 mm.[40] Such fishes also draw upon the oxygen stored in the swim bladder and further have adapted their feeding habits so that they oscillate between the stagnant water of the hypolimnion and the oxygenated water above. The pedonic fauna may be numerous in individuals even if it is poor in number of species.

Eutrophic lakes may represent a period of old age in oligotrophic lakes; the transformation is produced by a filling up of the lake by erosion products. When the surrounding region has been transformed into fertilized cultivated ground, the lake receives a larger mass of nutritive salts. Lake Zürich, for instance, is in such a transitional stage.

Ancient fresh-water lakes

As has been mentioned in Chapter 6, a few of the larger lakes of the world have escaped the common fate of transitoriness and have presented an opportunity for long-continued evolution of their faunae.

The fauna of Lake Baikal is extraordinary for its wealth of species representing relatively few generic types, which are for the most part endemic, as are many families. The available literature is somewhat contradictory in enumeration of species, in assigning them to higher categories, and in interpreting their zoögeographic relationships.

The great majority of groups present in the lake are dominated by endemic species. Diatoms, protozoans, and rotifers, all well represented, are the three large groups chiefly composed of non-endemic forms. Each is characterized by ease of passive transport, and all are widely distributed in the fresh waters of the world. Even so, 46, 38, and 26%, respectively, of their Baikalian forms are endemic.[18a, 87a]

The lake is notable, among other things, for the presence of a seal, *Phoca sibirica,* which also occurs in the small Lake Orion in the mountains nearby. Serological tests have confirmed the closer relation of this fresh-water seal to the Arctic species *P. hispida* rather than to that in either Lake Ladoga or the Caspian *P. caspica.* The fishes include a group of peculiar cottoids with 18 species assigned to 10 genera; representatives of many widespread Palaearctic genera are also present.

Lake Baikal contains almost 300 known species of gammarid crustaceans assigned to 30 genera. All these species are endemic except *Gammaracanthus loricatus,* the typical form of which lives along the shores of the Arctic Ocean. One subspecies lives in Baltic lakes and in the Yenesei River, another in Lake Baikal, and a third in the Caspian Sea. Only two other gammarid genera have extra-Baikalian representatives. The depth distribution in Baikal is known for 147 species of these amphipods; of the 146 pedonic forms, 8 are characteristic of the depth zone reaching from 0 to 5 m.; 29, of 5 to 50 m.; 29 more of 50 to 300 m., and 33 of the abyssal region below 300 m. Only one species is common in the plankton. It is a translucent form, which normally lives at a depth of 300 m. but has been taken at the surface at night.[21] All the known ostracods, 84% of the copepods, and all the isopods are endemic. These and other small crustaceans still are not well known.

The Baikalian mollusks are also distinctive. The common pulmonate genera of *Limnaea, Planorbis, Physa,* and *Ancylus* are represented almost entirely by endemic forms. Of the four prosobranchiate genera, *Benedictia* and *Baicalia,* representing the families Benedictiidae and Baicaliidae, are much discussed. Both families were formerly considered to be endemic, but representatives of one or the other have been found in a lake only 230 km. away and in Lake Ochrida in the Balkan Peninsula. Both have Cretaceous fossils from Transbaikalia, the region east of the lake, and one is also known from Pliocene fresh-water deposits in Hungary. The 15 recorded bivalve mollusks also are largely endemic; the widespread pelecypod genera *Sphaerium* and *Pisidium* have 5 and 9 Baikalian species, respectively.

More species of planarian worms have been recorded from Lake Baikal than are known in all Europe. Of 63 species of annelids, all polychaetes, all 5 leeches, and 93% of the oligochaetes are endemic. There are 2 species of the endemic polychaete genus *Dybowskyella,* representing a rare group in fresh water. Another polychaete worm is *Manayunkia baicalensis* of the family Sabellidae. Species of this genus live in widely separated localities in Eurasia and North America, in fresh and brackish waters, and in the marine littoral zone. Through the use of serological techniques, a definite connection has been found between Baikalian and Caspian polychaete worms, although the cross relationships are weaker than those usually found in a genus.[81,81a] Serological studies also indicate that *Baikalospongia,* one of the primitive sponge genera, is more closely related to a

Caspian sponge than to the widespread modern family of fresh-water sponges, the Spongillidae.

The wealth of species in Lake Baikal and our lack of knowledge concerning its fauna are illustrated by the fact that in the period from 1926 to 1928 over 600 species were added to the list of known inhabitants; some 725 had been known previously. More than half of the newly discovered species were new to science. Unlike that of most lakes, the animal life extends well down into the depths. An infusorian, *Spathidium,* has its maximum at 700 m. The deep-water animals in Baikal are closely related to surface forms elsewhere and not to marine animals of the deep sea, a fact that tends to confirm the geological view that the great depth of the lake is of comparatively recent origin [86] and fails to support the hypothesis of direct marine origin of the fauna as a whole. Lake Tanganyika, one of the lakes of the African Rift Valley, lies in a more open situation than the mountain-ringed Baikal. Other large lakes occur relatively nearby in east Africa. It is consequently not surprising that a number of widespread animals, such as rotifers and the bryozoan *Plumatella repens* live in Tanganyika. Along with these there exists a fauna as distinct as that of Lake Baikal.

All but one of the 22 species of ostracods are endemic. Twelve of these belong to the genus *Paracypria,* otherwise known only from Chatham Island, east of New Zealand, where the type species was described from a brackish lagoon, and from African Lake Albert, which has one of the Tanganyikan species in its fauna. Eight endemic copepods are perhaps recognizable as a subgenus of *Cypridopsis.* Of the 29 copepods the genus *Ergasilioides* is endemic. The bottom-dwelling *Schizopera* present a species flock of 8 known members in Tanganyika perhaps developed from a single ancestral stock. An equal number of species of this genus exists widely distributed in brackish coastal waters around the world in Haiti, Egypt, Hawaii, and the Chatham Islands. *Schizopera* is also known from the Caspian Sea, from a fresh-water lake in Sumatra, and from underground waters of Italy. As is usual for calanoid copepods, *Tropodiaptomus* is planktonic and is the principal zoöplankter of Lake Tanganyika.[18a, 69, 70] The fish lice, parasitic copepods of the family Argulidae, have 9 species in the lake, of which 7 are confined to it; the other African lakes usually have only a single species.[26]

The prawns, long-tailed fresh-water decapods, have 12 endemic species in Tanganyika, 11 belonging to the family Atyidae, which is characteristic of fresh waters of the western as well as the eastern

hemisphere.[20] In contrast, of two extensive neighboring African lakes, deep Nyasa and shallow Victoria, each has but a single non-endemic species. Two of the fresh-water crabs belong to the widespread African genus *Potamon;* 3 belong to the endemic *Platytelphusa.*[25]

The strong tendency towards peculiarity of the Tanganyika fauna has been well documented before reaching the outstanding mollusks and fishes that emphasize the same conclusion. The shallower shore waters are populated by *Planorbis, Limnaea, Bulimus, Viviparus,* and others comprising 19 genera with 56 forms, no less than 44 of them endemic, all closely allied to the usual African fresh-water mollusks. Another group is notable for the resemblance of its shells to marine forms (Fig. 9). These much-discussed "thalassoid" snails are quite divorced from those in rivers and other lakes of Africa. The 70 thalassoid forms, all endemic, belong to 20 genera. These live firmly attached to the rocks exposed to the force of the waves, on the bottom of the paralimnetic region, and some extend to the lower limit of oxygen distribution, at some 60 to 80 m. in summer and somewhat lower in winter. The lack of oxygen at great depths in Tanganyika prevents the development of a deep-water fauna such as occurs in Lake Baikal.[8, 9, 18a]

The whole molluskan fauna has been reviewed by Pilsbry and Bequaert,[55] who believe that the marine appearance illustrates convergence toward various marine shells in form, sculpture, or solidarity rather than being evidence of phyletic descent.

Of the 188 species of fishes recorded by Poll [56] from Lake Tanganyika and its tributary streams, 140 are regarded as endemic. There are 93 cichlid species, of which 91 are endemic, and these are so much differentiated that they are distributed among 34 endemic genera. There are two distinct monotypic genera of the siluroid family Claridae. The family Cichlidae has also undergone much differentiation in other African lakes, especially in lakes Nyasa and Victoria.

Brooks,[18a] writing in 1950, summarizes some of the relationships as follows:

> The Tanganyika fauna is intermediate between those of Nyasa and Baikal in the diversity of stocks present and the number of species by which many are represented. In the character of its affinities, too, the Tanganyika fauna falls between Baikal and Nyasa. A few of the Tanganyikan stocks belong to groups with wide distributions throughout fresh and brackish waters, but most stocks are characteristic of African freshwaters. A single species has its only known relative living in the East Indian Ocean.
>
> The bulk of the Tanganyikan fauna has been derived from African freshwater stocks which have subsequently undergone more cleavage and divergence

than have the Nyasan representatives. This divergence is evident from the many groups which are represented by endemic genera. The molluscs are most remarkable, as 25 of the 44 genera are endemic. . . . The Cichlidae, with about half as many species as in Nyasa, have 34 endemic genera against the 20 in Nyasa. . . .

Although the temperature at the bottom of Lake Tanganyika is high, standing at 23.1°, there is great thermal stability. The complete lack of top-to-bottom circulation or "turnover," even during the season of potential minimum stability, appears to be related to the lower temperature of much of the inflowing water. Being cooler, it flows down the steep sides of the lake and maintains the lower temperature of the deep-water mass. The bottom water is entirely devoid of oxygen. The chemical content of Tanganyika water is affected by the fixation of silicon by diatoms and of calcium by mollusks. The total salt content is less than in Lake Michigan, but the proportions of salts are similar to those in the sea except for the relatively large amount of carbonates, as is typical for fresh water. There is an exceptionally high potassium content. The ratio of chloride to sulphate and of calcium to magnesium resembles that found in sea water. These ionic relations may help account for the high endemicity in Tanganyika and for the notable marine aspect of many of its animals.[8]

Lake Posso in Celebes agrees with Baikal and Tanganyika in the individuality of its gastropod fauna. There are 16 endemic forms out of 21 species and subspecies. The general aspect of the fauna is decidedly ancient; the melanias, with the exception of 2 widespread forms, belong to the paleomelanias, distinguished by the structure of their radula and operculum, and an endemic genus with swollen lip is distinguished as *Tylomelania.* The wealth of the snail fauna is so great that the dead shells in places thickly cover the shore. The lakes of the Malili River system, especially Towuti, Mahalona, and Matana, also have a highly endemic fauna. They are located in the same tectonic trough with Lake Posso, and approximately a hundred miles away.[18a, 64, 65]

In Lake Lanao (Mindanao, Philippines) certain species of cyprinids have developed peculiar characters and physiognomies, although all probably evolved from a single parent stock.[34] The mollusks also are strongly endemic.

Lake Ochrida, between Jugoslavia and Albania, has been shown to have a molluskan fauna rich in endemic forms, unlike those of

most European lakes. The fauna of Lake Ochrida includes representatives of otherwise extinct Pliocene gastropods.[79]

The Caspian Sea recalls these lakes by similar deep-seated differentiation of its fauna. The Crustacean genus *Pseudocuma* has already been discussed (p. 96). Nineteen out of 26 species of snails belong to endemic genera (*Micromelania, Caspia,* etc.).[24] The clupeid fishes have 10 endemic species of the genus *Clupeonella* in the Caspian.[12] Besides these peculiar forms there are certain relicts, such as the Arctic copepod *Limnocalanus grimaldii,* which occurs also as a glacial relict in the gulfs of Finland and Bothnia,[68] and the Caspian seal *Phoca caspica.*[28b] Finally, there are also species that have entered from fresh water. The Caspian Sea does not seem to have been isolated so completely or so long as lakes Baikal and Tanganyika or the lakes of Celebes.

On account of their peculiar faunae, Baikal and Tanganyika have been thought of as marine relict lakes. It is true that in Lake Baikal certain forms suggest a marine relation; the sponge *Lubomirskia* occurs also in Bering Sea, and the polychaete *Dybowskyella* represents an otherwise marine group. A single representative of the rich gammarid crustacean fauna is a subspecies of an Arctic form, and the Baikalian seal is related to the one in the Arctic Ocean. In Lake Tanganyika, the snails with a marine appearance and the fresh-water medusa are no longer regarded as a basis for a theory of direct marine derivation (cf. Moore [50]). The faunae of these lakes mainly represent survivals of ancient fresh-water animals. However, it is difficult to account for the presence of a small minority of forms, including in Tanganyika the copepod *Schizopera* (also in Lake Nyasa) and the bryozoans *Victorella* and *Arachnoidea,* each with definite marine or brackish-water species. Brooks [18a] meets this challenge by suggesting a marine transgression from the east as indicated by marine strata from Jurassic, Cretaceous, and early Tertiary periods that possibly reached some of the former drainage system of the lake.

That Lake Baikal has never been marine is supported by the fact that all the geologic formations of the surrounding region are of fresh-water or terrestrial origin. A summary of this problem for the Baikal fauna is presented by Berg,[13] supporting the theory of non-marine origin that Brooks accepts; [18a] for the contrary theory the reader may be referred to Cockerell [21] and Verescagin.[87, 87a] Verescagin recognizes four subdivisions of the present Baikal fauna: (1) an element of uncertain origin; (2) a Siberian element; (3) a primitive fresh-water element; and (4) a marine element comprising certain

diatoms, sponges, rhabdocoels, polychaetes, bryozoans, mollusks, crustaceans, fishes, and the Baikal seal. The nearest relatives of these live either in the Indian Ocean, the Arctic Ocean, the Sea of Japan, or in the Caspian Sea and other vestiges of the ancient Tethys Sea.[86] The weight of evidence furnished by the presence of certain of these groups is open to question,[18a] and the essential problem remains whether the marine elements in these ancient lakes represent a marine derivation much more recent than called for by the evidence that all primarily fresh-water animals are ultimately of marine derivation.

Small bodies of water

Small bodies of water are distinguished from lakes by the absence of a permanent and continuous open water surface in the center; in spring parts of these waters may be free from plant growth, but with increasing warmth this open water becomes more and more reduced until only small spots remain or it is entirely gone. Paralimnic flora extends into the deepest parts of such waters. They often represent stages of old age of former eutrophic lakes. Deposits of muck fill up the lake; the plant communities of the shores penetrate farther and farther; *Chara* overruns the bottom, and mollusks and other animals follow; the open water of the surface becomes more and more restricted by *Potamogeton, Nymphaea,* and other plants. Thus ponds, pools, and marshes arise, and by further development, low and finally high prairie. The conditions of oxygen supply and temperature also change with these developments. The plant growth of the bottom produces sufficient amounts of oxygen. Processes of warming and cooling take place more rapidly because of the depth of the water, and consequently the temperature of the water fluctuates with that of the atmosphere. The great extension of the bottom area in relation to the amount of water, other things being equal, brings about an increase of the amount of material dissolved in the water. The consequent large development of the flora results in a similarly more extensive development of fauna. The animal life of the smaller water basins is much like that of larger bodies of water in number of species, but it is richer in the number of individuals. To the ponds that have their origin in the ageing of lakes may be added ox-bow lakes of rivers, and artificial ponds, because of the characteristics of their biota.

The communities of small bodies of water are not unlike those found in the paralimnic region of lakes, although they differ in many particulars. There is no room for strongly stenothermal animals; the flatworm *Planaria alpina,* for instance, occurs in the deep waters of

many lakes but not in small bodies of standing water. The relatively large extent of bottom in ponds, with its rich supply of plants and detritus, is a veritable paradise for snails and mussels. These grow to be much larger in ponds, as a rule, than in lakes. The abundant insect larvae of caddisflies, dragonflies, and mayflies belong to many different species. Many of the Crustacea of lakes are entirely missing in small water basins, e.g., *Bosmina coregoni, Sida crystallina,* and the copepods *Diaptomus gracilis* and *graciloides;* others, on the other hand, occur in both.*

There are very few, if any, of the rotifers of lake plankton not also found in the plankton of ponds.[99] The limited stretches of open water reveal a floating fauna of a different composition of species and varietal forms as compared with the open waters of lakes.[28a] In ponds one often finds forms limited in lakes to the shore region, such as the rotifer *Brachionus pala* and the cladoceran *Ceriodaphnia.* Rotifers have a noticeable mass development in ponds, especially in the uppermost stratum; in July, in Bohemian ponds, they constitute 90% of all plankton animals at the surface and 40% at 1 m.[30]

Many species of animals take on different form in smaller water basins from those shown in lakes. The rotifer *Triarthra longiseta* [102] of ponds is distinguished from the lake type by much-diminished length of the anterior bristle, and the pond type of *Anuraea cochlearis* [94] differs from that in lakes by having a brownish-yellow color and a shorter posterior bristle. Daphnias are considerably larger in smaller waters than their relatives in lakes.[88] The size of *Diaptomus laciniatus,*[19] on the other hand, increases with the size of the body of water in which it lives; it remains very small in small mountain lakes in spite of a plentiful food supply, but reaches its maximum length in larger lakes of the plains with a pronounced, though less rich, limnetic area. The pond form of the gnat larva, *Corethra plumicornis,*[97] can be distinguished from a lake form (Fig. 104); that of ponds is plumper, considerably larger, of dull coloration in contrast with the very transparent lake form, and has a larger head with a short proboscis, larger eyes, plumper tracheal bladders, and a larger tail fan.

The fact that among the daphnias of pools the males appear more often, and fertilized eggs more frequently, than among lake daphnias depends upon the greater variations of temperature in the smaller water basins or upon phenomena associated with crowding [7] or both.

* *Daphnia longispina, Scapholeberis mucronata, Polyphemus pediculus,* etc.

The animal communities of bodies of water that are not permanent—the ephemeral water basins—show marked uniformity in spite of their great variation in size and contour. These ephemeral waters usually exist periodically and disappear at more or less definite times; they are less often of entirely accidental nature. From the rain puddles and clay pits up to the widespread South African "pans," there is a complete series of gradations of such rain ponds, whose existence depends solely and directly on precipitation; with its absence they are dry for long periods of time. Aquatic animals find similar environ-

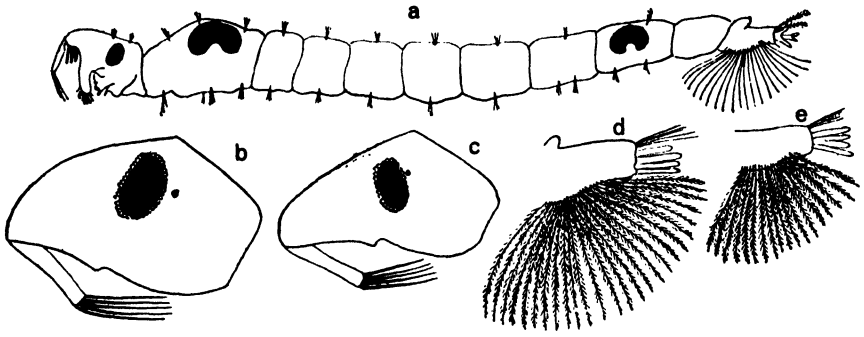


FIG. 104. *a*, Larva of *Corethra plumicornis*, with its tracheal air sacks in black; *b*, head of pond form; *c*, of lake form; *d*, anal fan of pond form, *e*, of lake form. *a*, after von Frankenberg; *b–e*, after Wesenberg-Lund.

ments in flood areas of rivers and rice fields and in the unique sinkhole lakes that periodically lose their waters entirely when they are drained through solution channels into temporarily low subterranean tributaries. Temporary water basins are especially numerous in hot regions, where there is a sharp contrast between rainy and dry seasons; but they occur also in the temperate and frigid zones. Running waters may show a similar periodicity, e.g., the wadis of Algeria, the southern tributaries of the Red Sea, or many rivers of Australia. In these rivers the water runs off quickly, and the pools and puddles that remain are similar to standing water basins.

Animals of such water basins must be able to do without water for long periods of time without perishing. A rigid selection results that accounts for the characteristics of the fauna. The poverty in species of such an animal community is shown by a comparison [44] between temporary and permanent rain-water pools; in the temporary pools 19 species of animals (2 rhizopods, 2 heliozoans, 11 ciliates) were found, in permanent water holes (over rocky substratum) more

than 88 species (15 rhizopods, 3 heliozoans, more than 12 ciliates, 22 rotifers, 13 cladocerans, 3 copepods, and 20 insect larvae). The majority are small animals, which usually live less than a year, with many generations during the course of that time. All these animals, at some stage in their life history, can do entirely without water, either as egg, larva, or adult. Another group of inhabitants of temporary water basins, of considerable size and duration of life, has the capacity to burrow in the mud and aestivate during the period of drought.

Of the short-lived inhabitants of temporary water basins, the Crustacea produce by far the most numerous forms. The survivors of the most primitive group of Crustacea, the Euphyllopoda,* are, in fact, almost entirely restricted to such temporary water basins. They have become adapted to these environmental conditions to such a degree that, so far as they are not cold-water forms, the eggs can develop only after having lain in a dry place for some time; the eggs of the cold-water Euphyllopoda must freeze before they will hatch. This group of Crustacea is best represented in those regions where steppe conditions are accompanied by frequent occurrence of such disappearing water basins, as in Africa and Australia. Seven different species of Euphyllopoda were taken from the mud of a pool in the Sudan. The number of species increases in Europe from west to east.[101] The resting eggs of these Crustacea are so enduring that they can remain dry for years without losing their ability to develop; specimens of mud from east Africa that had been dried for fourteen or fifteen years produced larvae of Euphyllopoda. This also explains the fact that these crustaceans are often absent from their usual habitat for a number of years and then suddenly appear again in great numbers in the same place. The ability to retreat into a habitat whose conditions are so severely selective has probably made it possible for these primitive phyllopods to continue to survive while their relatives succumbed in the competition with more highly evolved forms, a familiar phenomenon among relicts.

Cladocera also produce eggs that are not injured by drying, the so-called resting eggs enclosed in ephippia (Fig. 105). These eggs must be fertilized and consequently are produced only when the male forms are present; the eggs that develop parthenogenetically without fertilization have no such resistance to drying. The effectiveness of the protection rendered by the covering is shown by the fact that they pass unharmed through the alimentary canal of fishes, and even withstand formaldehyde. Rhabdocoel flatworms also occasionally

* *Branchipus, Apus, Estheria, Limnadia,* and others.

produce hard-shelled resting eggs, while vernal planarians such as *P. velata* enclose themselves, as do certain copepods, in hardened slime capsules. The fertilized eggs of rotifers are also protected by hard shells. In *Daphnia magna* and *D. pulex* resting eggs may appear shortly after the first emergence in spring,[88] and in the rotifer *Hydatina senta*, as early as the second generation. Ostracods, which are also common in small puddles, often have ridges on the ventral border of one valve and thus provide for an effective closing of the shell.

Short periods of development and great fertility are often characteristics allowing animals to live in transient waters. Many species of *Branchipus* become capable of reproducing in a week, and even the large gill-footed *Apus* is sexually mature after 14 days, at a length of 1.5 cm. Both appear in a single annual generation; but many of them lay 300–400 eggs daily for weeks,[101] and the total number of eggs produced by a female of *Tanymastix lacunae* has been estimated at 17,000.[51]

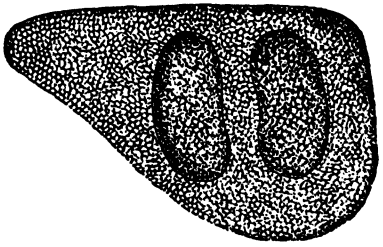


FIG. 105. Ephippium of a cladoceran, *Daphnia pulex*, enclosing two winter eggs. After Lauterborn.

Daphnia magna becomes mature in five to six days under favorable conditions of nourishment, and delivers the first brood two days later, with additional broods every three days; the number of young is increased from 12–16 at first up to 60 or more at each delivery. The rate of reproduction is often increased through parthenogenetic development; then all individuals are female and each produces young. This is true for many phyllopods and rotifers, at least in temperate regions. The descendants of any one *Daphnia magna* during one month have been estimated to be 30,000,000 individuals.[42]

Drought resistance

Finally, a number of inhabitants of small pools are so organized that they may dry up into a small particle of dust without actually dying; when the water supply is renewed they swell up again and live on. This capacity for anabiosis is found in many rotifers (*Callidina, Philodina*), bear animalcules, nematodes, and a few copepods (Harpacticidae). Many of these are limited to temporary pools, like *Philodina roseola*. Rotifers that are transported into such waters in the resting-egg stage are usually accidental, not regular, inhabitants.[52]

Another way of escaping the handicaps of drying up of temporary water basins is by burrowing or burying in the mud. This occurs regularly even among many of the smallest animals in pools, e.g., copepods and ostracods. This power explains the fact that an abundance of life can be awakened in specimens from bottoms of temporary water basins by adding water. Dried mud from the meadows of the flood area of the lower Danube produces a rather large number of animal species of the groups mentioned above (*Apus*, Cladocera, Ostracoda, bear animalcules, a number of flatworms, a nematode, as well as several annelids).[4] Many species of these groups of animals (from central Africa and Australia) have so far been studied only from such cultures.[67] These facts help to explain the extensive distribution of such forms, since they are certain to be carried on bits of mud on the feet of birds.

Some larger animals are also capable of living through temporary droughts, e.g., some insect larvae, and especially mollusks and fishes. The hardened mud surrounding them becomes an impenetrable case, which is often strengthened by a secretion of slime that prevents desiccation. Such protection is especially prevalent in the tropics. *Spatha*, a genus of mussel thriving in the temporary basins and streams of African steppes, lies buried in the mud during the period of drought. The long interruption of growth makes the annual lines of growth stand out prominently on the shell. The Pectinibranchiata are especially characterized by this habit among snails, for their operculum provides an exceptionally efficient protection against drying; *Ampullaria, Melania, Melanopsis*, and *Bythinia* thus survive the dry season in African, south Asiatic, Australian, and South American waters. It is perhaps for this reason also that in the inland waters of east Africa the Pectinibranchiata, which in 1898 had 112 species, far outnumbered the inoperculate Limnaeidae, with 46 species.[47] In the temperate zones the Limnaeidae take refuge in the mud when the water basins dry up, and thus survive. *Limnaea* and *Planorbis* survive in temporary pools; and small *Limnaea* came out of the dried-up ground of a flood region of the lower Danube on the first day after water had been added. Caddisfly larvae up to a length of 8 mm. also were found in this mud, and experiments with the larva of the dragonfly *Libellula depressa*[57] have shown that it can remain alive for 50 days or more in dry air, and therefore can live in temporary water basins.

Numerous kinds of fishes bury themselves in mud in the tropics. In Ceylon, in a very few days after the beginning of the rainy season,

the natives fish industriously in the ponds and pools which were recently dried up; [82] in Celebes, eels (*Anguilla mauritiana*) are dug out of the dried-up clay of the rice fields during the dry season.* [66] Fishes with adaptations for air-breathing, the lungfishes *Protopterus, Lepidosiren,* and *Neoceratodus* have this same habit and live in similar niches in Africa, South America, and Australia. In Europe, *Misgurnus fossilis* buries itself in the mud when the water it inhabits dries up.[75] Carp and tench (Cyprinidae) have been found in the dry bottoms of flood regions of the Danube; barbels can be dug out of the dried-up brooks in Macedonia.[28] The common mud minnows of North America (*Umbra*) survive in the mud of dried-up ponds in the same way. It has recently been observed that the eggs of a small Paraguayan fish (*Cynolebias*) can survive for five months in the muddy bottoms of dried-up water basins and can develop [1] with a renewed water supply.

Finally, in such temporary water basins many inhabitants are only casuals, such as water beetles and other water insects, frogs, and salamanders, and these move to other ponds when the water dries up. In tropical South America fishes similarly move out of waters that are drying and travel across dry land to new water basins, e.g., the catfishes *Callichthys* [74] and *Doras.*[16] The frequently temporary nature of pools and streams in the tropics also explains the fact that so many tropical frogs do not place their eggs in water but care for them until they are hatched.[17] In frogs of the genera *Dendrobates* and *Phyllobates* in tropical America, the tadpoles, 6–7 mm. in length, attach themselves by means of suckers to the backs of their parents and are thus carried from one body of water to another.[93]

The moss fauna

Convergent adaptations to frequent drying-up of a habitat niche appear most often in the animal communities of the moss on rocks, trees, walls, and roofs.[32,46,61] These moss beds may be regarded as peculiar small periodic bodies of water. While the change in them from damp to dry is usually very frequent, changes in temperature also are especially great. The opportunity for the development of active life, which is brought about in moss by a rain, is so brief at certain periods of the year that it is often too short for the animals to develop from eggs to sexually mature adults. Both eggs and adults

* The ability to survive the drought by burying themselves in mud is found among fishes of most diverse relationships; of the Symbranchia, *Symbranchus* and *Monopterus,* in the rice fields of Java; in the Siluridae, *Callichthys* in South America; and among Cyprinidae, *Discognathus* (near Aden).

of the animals of temporarily damp moss beds survive drought anabiotically. They can dry up to an element of aerial dust without losing their power to revive. A periodic sexual cycle is necessarily absent. All activity depends directly on wetting and drying of the moss environment.

The inhabitants of these periodic fresh-water biocoenoses include rhizopods, threadworms, rotifers (especially Bdelloidea of the genera *Callidina* and *Philodina*), bear animalcules (Tardigrada), and copepods (Harpacticidae). Associated with these are terrestrial animals that are not affected by the drying-up of the habitat, e.g., minute insects and mites. Most of these, with the exception of bear animalcules, which suck the juices of moss plants, are detritus feeders. Nematodes and bear animalcules may resort to the predatory habit. Some means of attachment is usually present as an adaptation to this type of habitat. This keeps the tiny animals or their eggs from being washed out of the moss during heavy rains. Tardigrada have strong claws on their feet, and occasionally long, bristle-like threads on their upper surface (Fig. 106); rotifers have cement glands in their feet, secreting a substance by which they attach themselves. The eggs of many species of Tardigrada (Fig. 107) are entirely covered with stickers and spines and are thus anchored in the moss; other species lay smooth eggs into their cast skins, which are entangled in the moss by means of the claws.

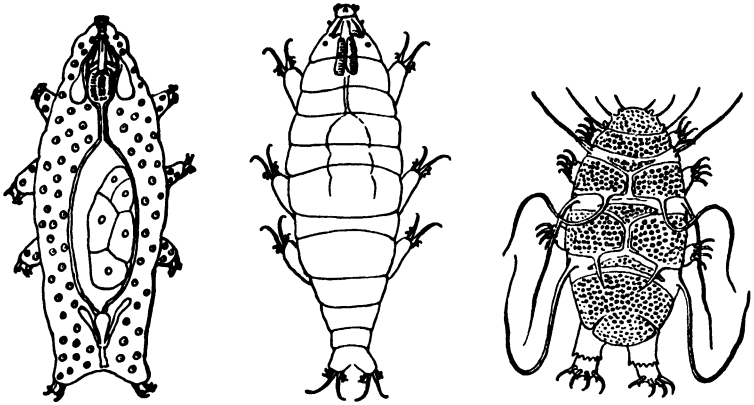


FIG. 106. Tardigrades from moss: left to right, *Macrobiotus; Milnesium; Echiniscus.* After Richters.

The variation in temperature to which moss-dwelling animals are exposed is exceedingly great in many places, since the moss is often

located in places exposed to the scorching sun's rays during the day and to extreme cooling by night. These changes can easily be endured without damage by the animal inhabitants while they are in a latent condition, for then they possess very remarkable resistance against high or low temperatures; they have been seen to revive in mosses that had been heated to a temperature of 80°, some even to 150°, or had been cooled in liquid helium to −272°.[58,59]

The moss fauna is surprising in its cosmopolitan composition. The slight weight of the dried-up animals favors their distribution by wind. Severe selection by unfavorable environmental factors pre-

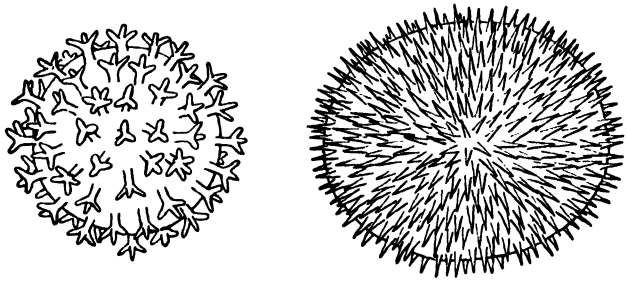


FIG. 107. Eggs of tardigrades: left, *Macrobiotus granulatus;* right, *M. coronifer.* After Richters.

vents the competition of other local animals with the moss animals. Some of these animals have a very wide horizontal and vertical distribution. Seven of twelve antarctic rotifers (Bdelloidea) have been found elsewhere. Most of the Tardigrada brought back from Antarctica were already known in Europe and in the Arctic.[33] *Milnesium tardigradum,* for instance, is known in Spitzbergen, Scandinavia, Scotland, France, Gibraltar, Germany, the Alps, Java, Himalaya, Kerguelen, New Amsterdam, and Vancouver Island.[62] The harpacticid, *Epactophanes richardi,* is likewise known in Europe, Greenland, Spitzbergen, Java, and Antarctica.[48] The number of animals, moreover, is often very large; 0.26 gm. of dry moss from Spitzbergen produced 121 tardigrades of 4 different species. There are not nearly so many in the moss beds of tropical regions.

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19. *Communities in Other Inland Waters*

Tropical fresh-water communities

THE DISCUSSION OF ANIMAL DISTRIBUTION IN FRESH WATERS HAS DEALT thus far mostly with those of the temperate zone, because these waters have been most studied. The faunae of tropical and polar fresh waters differ from those of the temperate regions in many ways.

Relatively constant high temperature throughout the year is the outstanding difference between the fresh waters of the tropics and those of other zones. Annual variations in temperature are negligible, excepting in shallow basins of standing water. The difference between the temperature at the surface and at the bottom in tropical lakes of greater depth is also much less than in temperate lakes. In Lake Nyasa, the surface temperature varies between about 29.7° [1a] and 23°+; it falls only to 22° or 22.75° at a depth of approximately 200 m. and continues almost steady to 400 m., the lowest point recorded by Beauchamp. In Lake Tanganyika, surface temperatures range between 24° and 26.5°, with the bottom temperature (1435 m. deep) at 23.1°. Both lakes have a complete absence of dissolved oxygen in the hypolimnion.[1b, 16a] The general lack of oxygen in swamps of the South American Chaco is an important biological factor.[10]

The fauna of tropical and subtropical fresh waters is more diversified than that of temperate or arctic zones, and the number of animal groups represented is larger. This is explained by the fact that stenothermal animals adapted to warm regions find their real home there, though eurythermal animals are not excluded. Many genera of snails and mussels are limited to tropical waters. A few have remained in the waters of the temperate zone as relicts of former warmer eras; thus 2 species of the snail genus *Melanopsis* are found in the warm springs of the Maremme in Tuscany and in thermal waters (32°)

in Hungary,[19] and 1 species of *Melania* occurs in the brooks and rivers of the Balkan Peninsula.

Cyclops prasinus, which is found occasionally in Germany, occurs everywhere in Africa, while *C. strenuus,* which is adapted to colder temperatures, is missing there. Dolphins, sirenians, hippopotami, and crocodiles may be mentioned as amphibious vertebrates characteristic of tropical fresh waters. The diversity of fishes in tropical waters is exceedingly great.

There are a large number of recent immigrants from the ocean in tropical fresh waters, where the transition from the ocean seems to be facilitated. Just why this should be so warrants further careful study. It is doubtful if the transition can be ascribed to temperature relations. The fact that heavy tropical rains at certain seasons of the year reduce the salt content of the surface layer of the ocean in certain regions for considerable lengths of time, affording opportunity to many marine animals for adaptation to less salty water, may be of some importance. The fresh-water snails and mussels prevalent in the Malay Archipelago, and characteristic of it, are more closely related to those in the ocean than to the characteristic fresh-water mollusks of colder regions.[25] Nowhere is so great a number of marine mollusks to be found in transition into the fresh-water habitat as in Burma and the neighboring Indian and Siamese regions.[11] Fresh-water amphipods, isopods, and crabs of the warmer zones are also often closely related to those of the ocean. The same is true to a great extent for fishes, as, e.g., in east Australia, Java, the Barbary coast, and tropical South America. Sharks and rays inhabit fresh water only in tropical and subtropical countries. The similarity of the total fresh-water fauna to marine fauna increases from the poles to the equator.[24]

In the waters of East Indian islands, Entomostraca appear in much smaller numbers than in those of Europe.[16] In Java the number of phyllopods, ostracods (6 species), and copepods is small, and in the lakes of Sumatra, though the number of individuals is great, the number of species is small.[20] In Samoa the plankton is described as being poor and dwarfed.[22] It is not surprising that cyclic morphological changes (cf. p. 404) do not occur in the region of uniform temperature; even the cyclic appearance of males among cladocerans is lacking. Decapod crustaceans, on the other hand, are much more plentiful in the fresh waters of the tropics than in temperate zones; there are 12 long-tailed and 5 short-tailed forms in Lake Tanganyika; 112 species had been reported for the Indian Archipelago in 1897, when the total known from Europe was only 7.[46] The general features of the great

tropical African lakes have been discussed in the preceding chapter.

Parthenogenetic development in Entomostraca is more and more limited toward the equator, though scarcity of males in tropical Cladocera has been reported.[7] This is not true of the phyllopods and the ostracods. Although there are species of euphyllopods in the colder regions among which males have never been found (*Limnadia lenticularis*) or are very rare, males are in the majority in the collections thus far made of African species (*Limnadia, Lepidurus, Apus,* etc.). Males are regularly present among the ostracods of tropical and subtropical Africa, in species identical with or very closely related to those in colder zones that do not produce males; for instance, *Cypridopsis newtoni,* with both sexes present in Algeria and Tunisia, is known only from females in Germany, and *Cypris puberoides* with both sexes in East Africa is represented in Germany by females only.[26,43]

Polar fresh-water communities

The low temperatures of the polar regions considerably influence the fauna of their fresh waters. The rivers are covered with ice in winter. The number of species of fishes inhabiting these rivers is low, and a considerable number are migratory. Only 45 species were known in so large a river as the Obi (a river basin of 3,000,000 sq. km.) in 1897,[25] and only 62 in all of Siberia except the Amur and Lake Baikal in 1912.[2] Of over a dozen different river fishes in the Boganida (Taymyrland, 71° N. latitude), with the exception of the eelpout, pike, stickleback, and perch, there were only salmonids, of which only 2, *Thymallus* and *Salmo coregonoides,* were permanent residents; the rest came up the river only to spawn. Similarly, polar rivers of North America do not harbor many species of fishes; 14 are reported from the Yukon and 22 from the Saskatchewan-Nelson River; the Mackenzie contains 23 species, of which 11 are Salmonidae.[32] It is the salmon that penetrate farthest to the north; even in Grinnell Land in 82° 34′ N. latitude the salmon *Salmo arcturus* and *Salmo naresi* have been caught. How resistant such polar fishes can be is shown by the Alaskan blackfish (*Dallia pectoralis*), a relative of the pike, which abounds in the rivers and tundra ponds of Alaska and eastern Siberia. It can lie frozen for weeks in baskets and revive again on being thawed out; a frozen fish swallowed by a dog was thawed out in the stomach and regurgitated alive.[41]

The standing waters of the polar regions are covered by ice to a greater extent than the rivers, and are open for only a brief period.

Thus the ice-free period in Lake Myvatn in Iceland (69° 33′ N. latitude) lasts about 5 months; in Spitzbergen (76°–80° N. latitude), in small water basins with favorable locations 2½ months, in larger waters 2 months, in unfavorable locations only 1½ months. The lakes of the antarctic Ross Island (64° S. latitude) are ice-free for only a few weeks, and some indeed do not thaw at all during the year unless the temperature is unusually high. But as soon as these lakes are free from ice, their temperature rises, thanks to the constantly shining sun, and remains fairly uniform. The fauna of such waters is poor. Only 15 species of Entomostraca (1 phyllopod, 4 cladocerans, 4 ostracods, and 6 copepods) are known in the fresh waters of Spitzbergen, 10 in Bear Island, and only 2 in Franz Josef Land.[29] Few species are capable of enduring such extreme conditions. There is a subarctic community of plankton crustaceans.* There is also a similar group of rotifers, which recurs again and again in the open water. The wide distribution of red color among northern plankton copepods is very noticeable. It is generally true that in the plankton of the northern lakes the floral component of the biota is much reduced in comparison with the faunal;[30] the plankton feeds principally on detritus.

The fact that the time of development is shortened among northern copepods is noteworthy. For *Cyclops scutifer* in northern Sweden, the time from the hatching of the nauplius larva to the appearance of eggs in egg sacs is a month, as a maximum; in middle Europe the same development requires more than 4 months;[12] similar examples are plentiful and represent a biological adaptation to cold rather than a simple physical response to temperature, which, in fact, would give exactly the opposite result. This adaptation may depend upon the influence of the extended lighting, but selection must be involved. Corresponding with the short period of life, only one generation of males appears among many *Daphnia;* they are thus monocyclic. The copepod, *Diaptomus minutus,* has only a single annual generation in Iceland. The typical cold-water forms of Euphyllopoda appear in arctic waters, especially those of the genus *Lepidurus.* They predominate in shallow lakes of melted snow and ice; they grow to an astonishing size in a few weeks. Nevertheless *L. arcturus* requires at least 1½ months from egg to egg, so that this species is absent in the coldest regions.[29] The winter eggs must freeze before they can develop.[23]

* *Holopedium gibberum, Daphnia hyalina, Bosmina obtusirostris, Bythotrephes longimanus, Diaptomus laciniatus,* and certain other species of copepods and perhaps *Heterocope.*[30]

In spite of the small number of species, life in a polar lake may be very plentiful under favorable conditions. It is extraordinarily rich in Lake Myvatn [30] in Iceland. The fine bottom mud is inhabited by immense numbers of *Chironomus* larvae, and the larvae of mosquitoes and black flies are plentiful. A large number of entomostracans, especially cladocerans, live in the pedonic region; on the other hand, because of the shallowness of the lake, there is only one species of limnetic crustacean, *Daphnia longispina.* The number of snails (limnaeids and planorbids) is very large in isolated warm springs. In correlation with this rich supply of food the lake contains large numbers of trout.

In winter the covering of ice and the masses of snow settling on it, both poor conductors of heat, form a protection against too rapid cooling. Thus even the shallow Lake Sadonach near Werchojansk in Siberia, which is only a little more than 3 m. deep in the deepest places, never freezes to the bottom, in spite of the extreme cold, and in Spitzbergen bodies of water more than 2 m. deep do not freeze solid. Moreover, many aquatic animals can bear freezing without harm. The winter eggs of crustaceans survive being frozen into the ice; rotifers also are insensitive to freezing, whether as eggs or adults. Rotifers frozen into a piece of ice 5 m. below the surface may remain unharmed for several years.[31] Nordenskjöld [28] found 22 species of mollusks * frozen in the ice, and after careful thawing nearly all the animals proved to be alive. There is, however, only one water snail, *Radix peregra,* that ranges beyond the Arctic Circle in Norway.

Alpine fresh-water communities

The lakes of the Scandinavian highlands and the lakes of high mountains [51] at a height greater than 1500 m. above sea level show a striking similarity to polar waters. These lakes are free from ice for only a short period of the year; Lake Katrak, in Torne, Lapland (776 m. above sea level), for only 2–2½ months; and lakes lying even higher up in the Sarek highlands are free from ice only for a few weeks in warm summers. Lake Partnun in Switzerland is ice-free for 5½ months, and Lüner Lake for 6 months. The temperature at the surface hardly rises above that near the bottom of the lakes in the alpine foothills. A water temperature above 10° is rare and is usually found only in very shallow water basins. The valley basins, which are not exposed to the noonday sun and are fed only by the waters from near-by ice and snow, present especially unfavorable conditions.

* *Limnaea, Planorbis, Amphipeplea, Physa, Bythinia, Valvata,* and *Pisidium.*

They differ from conditions in polar regions in that the period of illumination and of sunshine, of such importance to life, is shorter. It is perhaps for this reason that such large entomostracans as the Euphyllopoda are missing in the mountains of central Europe in contrast with those in Scandinavia.

The abundance of life in high mountains varies greatly. Open basins with plant growth and a sandy and gravelly substratum are most densely inhabited. In secluded cold glacial basins with bottoms of coarse rubble the fauna is sparse. A few species of rhizopods and tardigrades are all that are found in such waters, and they predominate even when certain rotifers, copepods, and water mites appear in addition. The cladocerans require relatively favorable conditions; some insect larvae, water beetles, and small bivalves (*Pisidium*) also appear in the sparsely populated basins.

All these animals must be cold-tolerant. They are either ubiquitous eurythermal forms (many rhizopods, tardigrades, *Galba truncatula*) or stenothermal cold-water forms (*Cyclops strenuus, Diaptomus laciniatus*). Some live actively under the winter covering of ice, while others hibernate. Many species are dwarfed, e.g., certain copepods, *Pisidium, Galba truncatula.* Reproduction occurs in midsummer or autumn, even among species that have their reproductive seasons during the winter and spring in the waters of the plains.* The number of generations is decreased; the Cladocera usually have only one generation. In favorable summers, on the other hand, their fertility is increased in comparison with that of their relatives in the plains.

The difference between the inhabitants of the limnetic and the pedonic areas, which is quite noticeable in the deeper lakes on the plains, as well as the difference in the conditions of temperature of these two biotopes,[11] is blotted out in lakes at high altitude. Animal species that are pronounced deep-water forms in the lakes of the alpine foothills and the plains live in the limnetic region in high lakes.† The composition of the plankton is rather monotonous throughout the whole region of the high Alps. Zschokke mentioned only 55 species of plankton animals: 7 protozoans, 16 rotifers, 20 cladocerans, 11 copepods, and 1 insect larva. The only ones appearing in great numbers are *Daphnia longispina* and *Cyclops strenuus* and *serrulatus;* the copepods *Diaptomus bacillifer* and *D. denticornis*

* *Hydra fusca, Planaria alpina,* and *Cyclops strenuus.*

† The typical deep-water rhizopods of the alpine border lakes such as *Difflugia mammillaris,* the unusual flatworms, *Plagiostomum lemani* and *Otomesostoma auditivum,* or the water mites, *Lebertia rufipes* and *Hygrobates albinus.*

are widespread. The limnetic forms, however, are also found near the shores, and many littoral forms mix with the plankton. The slight warming of the shore water and the absence of a luxuriant littoral flora may contribute to this fact. A number of alpine animals develop a reddish color like the arctic copepods. Red coloration is also more frequent in copepods of low altitudes and in temperate regions, if they appear in early spring when water temperatures are low.[51]

The fact that animals living in polar and alpine lakes exhibit similar trends among their many adaptations is explained in part by the influence of similar environmental factors. Another explanation, however, is needed for the fact that stenothermal cold-water animals in the alpine lakes and the far northern waters often represent the same species; the inhabitants of these regions are homologous and not merely analogous, while in the intermediate zones, in contrast with their ubiquitous companions, such stenothermal species are isolated in cold moor ponds or mountain lakes. Many * are to be considered as relicts of a fauna that retreated with the glaciers into northern or alpine waters. They disappeared in intermediate areas, except where cold springs, cold water basins, or the pedon of lakes afforded them a more or less secure refuge.

Other inland waters

Some inland waters differ markedly from the ordinary fresh-water environments. These include waters that contain in solution certain elements of organic or mineral origin in considerable amounts and hence are known as humus waters or salt waters; others may be distinguished by constant low temperature, as in mountain springs or by the high temperatures of warm springs. The fauna of cave waters characterized by the absence of light will be considered together with the rest of the cave fauna, but life in springs will be discussed in this section.

Communities associated with humus waters

Sphagnum bogs are formed over impervious clay as the last step in the transition from ponds to dry land. Sphagnum and the associated plants are intolerant of lime. Peat moors develop in noncalcareous regions with heavy precipitation, where the waters are

* Cladocera, e.g., *Chydorus piger* and *Alona intermedia;* the copepods *Diaptomus laciniatus,* and *D. bacilifer, Canthocamptus cuspidatus* and *C. zschokkei;* the water mite *Hygrobates albinus;* and *Planaria alpina.*

poor in lime and nutriment; such moors are particularly abundant in the north temperate region in Europe and North America. The water saturating the masses of peat-forming mosses and their remains is rich in humic acid, the antiseptic qualities of which prevent decay. Thus dead plants accumulate on the substratum. New generations of peat mosses continue to pile up, so that finally thick layers of undecayed plant remains, from which soluble materials have been extracted, form "peat," which may be 20 or more m. thick. In the beginning of peat formation a shallow, flat moor is formed which is still in contact with the mineral substratum from which it draws nourishment; gradually, as the layer of peat thickens, there is a transition through a "middle moor" to a "high moor," in which the connection with the substratum is finally entirely broken by the immense layers of peat.

In such moors, bodies of water are formed in various ways. Peat-bog ponds are sometimes the last stages of lakes and sometimes the results of a sinking of parts of the moor. They are usually shallow basins or even puddles. The waters laden with humus may flow out of the moor, as in many mountain lakes, like the Scottish lochs and the Teufelsee in the Bohemian Forest. Wherever peat is used as fuel by man, water gathers in the cuts and ditches. The peat itself is saturated with water that forms the habitat for a few types of animals.

These waters are characterized by low content of nutritive salts as well as by this high humus content. They are often entirely composed of rain-water more or less effectively shut off from the mineral substratum by a so-called false bottom, which may or may not occupy all the space down to the true bottom. The concentration of nutritive elements decreases upwards through the layers of peat. Thus the bottom layer contains 0.25% P_2O_5 and 4% CaO, the middle layer 0.2% and 1%, respectively, and the top layer only 0.1% and 0.5%, respectively.[33] In a liter of water from the Teufelsee there is only 0.97 mg. of lime; the total solid residue in a liter of water is 18 mg., a third of which is organic matter.[13] As far as they have been analyzed, American bog lakes are roughly similar as regards dissolved chemicals.

Bog waters are best characterized by their content of humus extracts. These consist of unchanged colloids of original plant substances, mixed with carbonaceous products of disintegration. It is these humus substances, according to their abundance, that give the characteristic yellowish-brown color to bog and swamp waters. In shallow moors a part of the humic acid is combined with lime; larger amounts of humic acid are present in the waters of high moors. At the surface, the open waters may be fairly well aerated; the deeper

waters of bogs, however, are poor in oxygen because of the amount used in processes of decay.

As a result of the poverty of the waters in nutritive and mineral salts, moors have a reduced flora, particularly as regards the higher plants, and this reduction is cumulative from the low to the high moors. The phytoplankton is also sparse and may even be wholly absent in European waters; Welch,[47] however, reports more phyto- than zoöplankton for Michigan bogs. The abundant supply of plant detritus furnishes food for countless small animals, so that the animal plankton may be rather abundant. The presence of humus, however, and the absence of lime bring about a selection so that the fauna of moors is generally poor in species, although it may contain large numbers of individuals.

The humus water fauna

Protozoans do not suffer much under the adverse peculiarities of the bog waters; rhizopods especially are represented by numerous species. Rotifers likewise do not seem to be much affected by humus substances; of 186 rotifers in Galicia, 114 are also found in the humus waters.[21] *Planaria* and leeches, on the other hand, are missing in bog ponds and from the mountain brooks draining the moors.[18,44] Hydrachnids seem, as a rule, to be absent from such waters; fishes are usually absent. Their resistance against humus elements, however, varies; it is strong in the stickleback, moderate in carp, and least in pike and trout. Together with absence of fishes there is an absence of larger mussels, *Unio* and *Anodonta,* whose larvae, as ectoparasites, are dependent upon fishes.

The scarcity of lime in moor waters handicaps the development of mollusks. They are often completely absent, as in the Blindensee in the Black Forest; [35] in other places dwarfed forms of a few species of limnaeids and planorbids are found, larger species being absent. The pearl mussel (*Margaritifera margaritifera*) is absent in the creeks of non-calcareous mountains near the mouths of even small tributaries from moor regions. The pea mussels (*Pisidium*) are least sensitive, occurring in the mud on the bottom, with *Sphaerium* in smaller numbers. In lowland moors, which have been formed by the filling up of ponds, a layer of shells is often found beneath the peat, showing that a rich snail and mussel fauna was once present.

On the other hand, the deficiency of lime in moor waters is of advantage to the peculiar limnetic cladoceran, *Holopedium gibberum* (Fig. 81), which seems to tolerate only water poor in lime and is

widely distributed in such waters. The colonial, sessile rotifers of the genus *Conochilus* are often found in association with *Holopedium.*

The zoöplankton of moor ponds is occasionally plentiful, as compared with the phytoplankton. Copepods, cladocerans, and rotifers may be found in great abundance. Larvae of the gnat *Corethra* (cf. p. 417) stay in deep water in larger basins during the day but also occur ubiquitously in the smaller ditches and puddles containing bog waters.

The adverse influence of humus extracts on aquatic life in general is clearly shown in the black water rivers of the Amazon region, the Coary, Teffe, Jurua, and Rio Negro, where mosquito larvae do not seem to thrive, so that cities like Coary and Ega are welcome places of refuge for travelers.[45]

The deeper parts of the moor waters are poor in animal life or occasionally entirely uninhabited because of the lack of sufficient oxygen. In the Scottish lochs the most prevalent inhabitants of the deeps are the larvae of Chironomidae; in addition to these there are a few *Tubifex* worms, ostracods (*Cypris*), and pea clams (*Pisidium*).[37] It is unusual to find more than 10 to 20 individuals on a square meter of bottom. The appearance of ostracods is erratic, for they occur in great numbers in high moors in the Alps and in those of the Sarek Mountains in Norway, but may be completely absent in other moors.

The temperature conditions of many moor waters are distinctive. Temperature variation is much reduced by the moss; the daily and annual variation of temperature is diminished; the minimum and maximum temperatures are transmitted very slowly to the deepest layers, so that the moor springs may be higher in temperature in winter than in summer. For this reason many moors are inhabited by stenothermal cold-water animals such as the copepod, *Canthocamptus arcticus,* together with ubiquitous eurythermal forms. These stenothermal animals are often referred to as a relict fauna of the glacial age because so many of them are found in north Scandinavian waters and in high lakes in the Alps. Though relatively little studied in America, Michigan bog lakes are known to contain all the rotifers listed by Harnish [16] for European moor lakes together with many of the same plant plankters and crustaceans.[47]

Animal communities associated with brine

Waters with strong salt content maintain the amount of salt in various ways. Springs may bring up water rich in salt from the deeper layers of the earth and either pour this into larger rivers,

where the salt content is greatly reduced by dilution, or into swamps, ponds, or lakes with no outlets, in which the concentration of the salt solution is then increased by evaporation. In arid regions, lake basins without outlet to the sea become salt by concentration, although their affluents may be normal fresh-water streams. The numerous salt-water lakes in steppes, the salt swamps of Lorraine, the Dead Sea, the Great Salt Lake in Utah, and many others arise in one or both of these ways. The Caspian Sea must at some time have been connected with the ocean. Salt lagoons may originate by the separation of salt seas from the ocean by narrow dams. These receive their salt water from the ocean, as do the salt estuaries of Odessa or the salt lakes near the mouth of the Rhone. Because of the origin of their salt content, the pools formed by the spray dashing over cliffs also belong to this group. These fill basin-like hollows in the cliffs along the shore and are supplied with salt water whenever the sea is rough.

The fauna in these salt waters varies according to their origin. Inland waters fed by salt springs are inhabited by animals related to those of fresh waters; marine forms are not definitely known from any of these. In salt ponds of marine origin, on the other hand, a large part of the inhabitants have their origin in the ocean; but with these are a number of forms derived from fresh waters, such as turbellarians and, especially, insects.

The salt content of such waters varies greatly. Thus the amount reported for Lake Aral is 10.7‰, for the Caspian Sea 13‰, for the salt ponds of Salzburg (Siebenbürgen) 88‰ to 203‰, for Great Salt Lake (Utah) 222.4‰, for the Dead Sea 231.3‰ (ZoBell lists extremes of from 227 to 330‰),[50] and for the Güsgundag (Ararat) even 368‰. Usually the salt content varies even in the same water basin, according to the weather or the season, or in even longer cycles. In spray pools along rocky coasts, quiet weather brings about an increase in concentration; storm and rain cause a decrease. In salt lakes of the steppe the rainy season lessens the salt content, and the period of drought raises it. The water level of Lake Aral has been constantly rising since 1880, and as a consequence the salt content has decreased from 12‰ to 10.7‰. Such fluctuations may influence the composition of the fauna also. In Lake Urmia (north Iran), during the period when the salt content reaches the level of that in Great Salt Lake, it contains only a few small crustaceans, but during the wet season it is abundantly inhabited by fishes that enter from its tributaries.

The influence of salt water on animals depends, on the one hand,

upon the abundance of dissolved salts and, on the other hand, upon their composition. *Daphnia* can adapt to sea water with a 10.8‰ salt content, of which 8‰ is NaCl. But in pure solutions of NaCl, *Daphnia* tolerates a concentration of only 4‰. The addition of other salts, therefore, lessens the effect of NaCl, and in such balanced salt solutions an animal may tolerate a higher total concentration than in solutions containing only one salt. One-salt solutions may be called monotonous solutions. Monotonous salt solutions, therefore, condition a monotonous fauna, whereas waters containing a variety of salts have a varied fauna until much higher concentrations are reached.[17] For higher concentrations, the number of animal species present decreases with increase in the salt content.

The inhabitants of salt waters may be divided into various groups. These include the incidentals that are widely distributed in fresh waters and occasionally or rarely are found in salt water. "Halocoles" are found regularly in waters of higher salt content but likewise occur in fresh water. As a rule they are widely distributed, often cosmopolitan animals. Finally, "halobionts" are limited to water of rather high salt content and are more or less salt-tolerant stenohaline forms. Wide distribution and abundance in favorable places are characteristic for halocoles and halobionts: the elimination of enemies and competitors is favorable to their development.



FIG. 108. Salt-water crustacean, *Artemia salina*. × 5½. After Brauer.

Even a comparatively low salt content in water clearly causes reduction of the animal life. In the Dortmund-Ems Canal, with a salt content that fluctuates between 0.3 and 2.1‰, the amount of plankton is greatly reduced in comparison with a normal stream of the plains (380 individuals against 6800 in an equal amount of water).[49] These are purely fresh-water animals except the hydroid, *Cordylophora lacustris*, which inhabits brackish waters. Even at a salt content of 25‰ a plentiful fauna is present in which the incidentals are by far in the majority. The higher the salt content and the greater the fluctuations, the fewer the incidental forms; at 100‰ salt content incidental species are entirely missing, and only halocole and halobiontic species are found. If the salt content rises beyond 100‰ the halocoles also disappear more and more, and specifically salt animals are the only ones found; in addition to the brine shrimp *Artemia*

(Fig. 108) these include the larvae of Diptera, especially of the genus *Ephydra* (Fig. 109). In a concentration of 120–160‰ the fauna is very poor in number of species, but the number of individuals of *Artemia* and of *Ephydra* larvae is not diminished. These are often present in countless numbers; myriads of *Artemia* give the water a reddish color, and the number of *Ephydra* may be so vast in certain Californian salt swamps as to give a brown color to the water. Great Salt Lake in Utah supports an immense number of *Artemia fertilis*, *Ephydra* larvae of 3 species, and a corixid bug. Adult *Ephydra* flies settle on the surface in dense swarms. The waters contain also a considerable number of protozoans, including an *Amoeba*, and of algae, including 2 species of diatoms, 2 of chlamydomonas, and 1 species of blue-green algae.[1] The lack of animal life in the Dead Sea, with a salt content above 231‰ as compared with 222.4‰ in Great Salt Lake, cannot be attributed to the slightly greater salinity. This is more obvious since in Lake Bulack, near the Caspian Sea, in water with a concentration of salt of 285‰, there are *Monas dunalii*, *Chironomus* larvae, and 1 species each of annelids, copepods, and rotifers.[40] Numerous bacteria and several diverse species of algae live in the Dead Sea.[50]

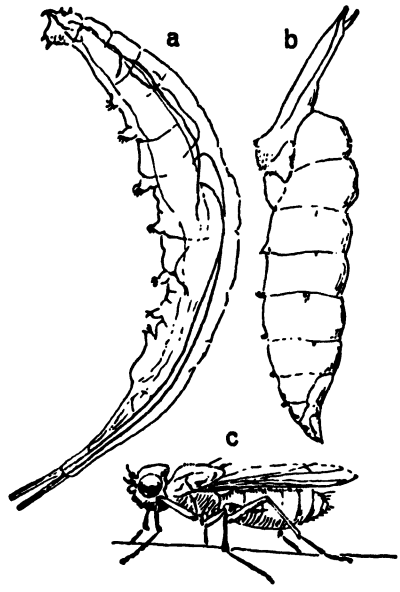


FIG. 109. Salt-water fly *Ephydra macellaria*; *a*, larva; *b*, pupa; *c*, adult. × 6. After Steuer.

Coelenterates, sponges, planarians, eels, Bryozoa, and, of the Crustacea, the cladocerans, are entirely missing in the salt waters of higher concentration. The larvae of mayflies and stoneflies and usually of caddisflies are absent. Of mollusks of temperate zones only *Radix ovata* occurs in water with slightly increased salt content. Amphibians are almost entirely absent; *Rana ridibunda* and *Bufo viridis* are found in pools in Algeria where waters have a low salt content.[48] Of fishes, the stickleback is insensitive toward low salt content and tolerates concentrations up to 60–70‰, and carp are also to a limited degree salt-tolerant.

Protozoa take first place among animals of highly concentrated salt waters. In the salt estuaries of Odessa their species number 7 to 10 times as many as those of metazoan species.[9] Rotifers are also numerous. Of crustaceans, the brine-shrimp *Artemia* is a salt-water inhabitant of world-wide distribution and usually occurs in great numbers. Resting stages, in all these forms, survive periods of increased concentration; thus the Protozoa have cysts, and the rotifers and *Artemia* have hard-shelled winter eggs. The winter eggs of the brine shrimp,

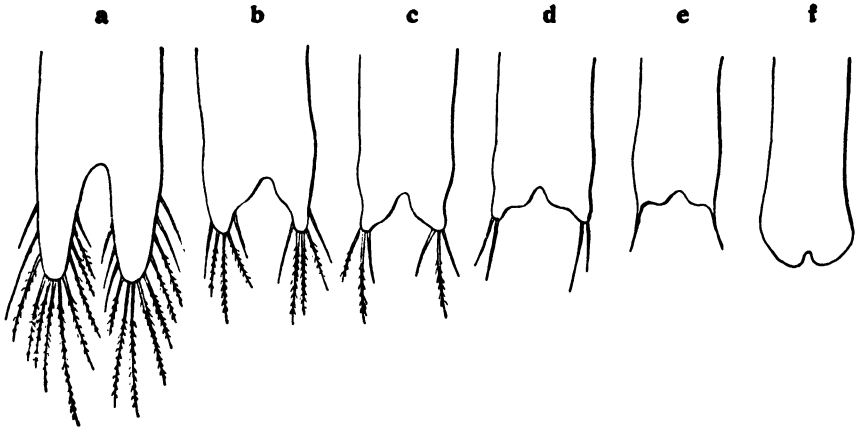


FIG. 110. Caudal fork of *Artemia salina* from waters of varying salt content near Odessa: *a*, from water of 8°; *b*, 14°; *c* and *d*, 18°; *e*, 23.5°; and *f*, 25° Baumé. After Schmankewitsch.

like those of other Euphyllopoda, are very resistant; they may develop even after a period of 8 years of drought.[27]

Artemia is very variable in its appearance; every habitat has its own form, distinguished by color, size, location and number of setae, form of the posterior end, etc. A large number of these differences are correlated with salt content;[14,34,36,39] since this is constantly changing, reliable information concerning these phenomena can be obtained only by breeding experiments under controlled conditions. With an increase of salt content the animals become smaller, the length of the narrow post-abdomen in comparison with the abdomen increases, the furca (tail fork) becomes shorter and is set with fewer hairs (Fig. 110).

The appearance of males also varies with the habitat; in many places there are only females, in others both sexes are constantly present. One copepod, *Diaptomus salinus,* is also resistant to fluctuations of

salt concentration; this species is rare in fresh water, but may be abundant in salt lakes such as Lake Aral.

Insects and insect larvae are the most numerous of metazoans. A number of genera and species of hydrophilid water beetles and their larvae occur in salt waters, *Ochthebius* and *Enochrus,* for example. The power of resistance of many dipterous larvae is exceptionally great; larvae of *Culex, Stratiomys, Trichocladius halophilus* (up to 60‰), and, above all, various species of *Ephydra,* are plentiful in salt waters. The thick, impenetrable chitinous armor of these insect larvae seems to be an effective protection against damage by osmosis in salt water. The larvae of *Ephydra* are not at all affected by a 160‰ salt content, and even withstand 222.4‰ found in Great Salt Lake. These larvae are also resistant to other substances, such as formaldehyde and alcohol. The inability of salt-tolerant insects such as *Ephydra* to invade the sea when they have dense populations in highly saline lakes provides one of the puzzles of animal distribution.

Animal communities of springs with low temperatures

The animal life of springs is peculiar in several respects. The waters of springs are usually uniform in temperature, and, except in thermal springs, they generally have the average temperature of the ground from which they flow. If the springs arise from deep strata or emerge in a forest, the maximum temperature is low and the range of temperatures small. In the low mountains of central Europe the temperature of spring water seldom rises above 13°, and the greatest range of temperature is 12° but may be as little as 0.8°. Stenothermal cold-water animals, therefore, find a favorable habitat in such springs. On the other hand, the springs communicate freely with subterranean waters, and thus animals often appear in them that ordinarily live in the waters of crevices and in caves.

Springs may be classified into torrent springs and pool springs.[5] The former emerge from the ground in a rushing stream and their water flows immediately away, frequently with more or less steep rapids or falls; their environmental characteristics are similar to those of mountain brooks. Pool springs, on the other hand, usually emerge in a more or less perpendicularly rising stream, and the water fills a basin before it flows away; their characteristics and the composition of their fauna are more like those of the pools of alpine streams. The fauna of torrent springs is on the whole more individual than that of pool springs.

In central Europe *Planaria alpina,* with its temperature optimum at 6–8°, is the characteristic species of stenothermal cold-water animals of springs (cf. p. 369). Besides these there are a number of water mites and, as exclusive inhabitants of springs, the small gill-breathing snails of the genus *Bythinella* whose optimum temperature is 8°, maximum 12°, and minimum 3°.*,6

The subterranean origin of many inhabitants of springs is especially noticeable among fishes found in the springs and artesian wells of the Sahara; [3] these belong to 6 different genera. These fishes seem capable of living periodically in subterranean basins with which the springs are in communication; because of this they are often numerous in very small springs and sometimes appear suddenly at the mouths of newly drilled wells. In some springs there are no living forms other than the fishes, and these are so underfed that they may attack bathers.

The fauna of springs is everywhere sparse because of the small amount of available nutritive material; the forms represented are small and insignificant, and if they have a rather wide distribution, e.g., *Gammarus pulex* or *Radix ovata,* the individuals in springs are smaller than others of their species. Besides the scarcity of food materials, space limitation itself may be a determining factor in producing this size relation.

Animal communities of warm waters [19]

Increased water temperature, like increased salt content, hinders development of animal life. Algae can grow in water up to 80° and bacteria up to 88° C.,[8a] but the maximum limit for protozoans is somewhat above 50° and for Metazoa almost the same. Protozoa of hot water basins are primarily the shelled rhizopods † and ciliates such as *Cyclidium glaucoma.* Dwarf specimens of the ciliate *Nassula elegans* (27 μ, elsewhere up to 200 μ) and a few *Amoeba limax* (12–15 μ in diameter) are found at 50–52°, and the rhizopod *Hyalodiscus* lives at

* Representatives of an otherwise subterranean fauna in surface springs in central Europe include the flatworms *Dendrocoelum infernale* and *Planaria vitta,* the annelid *Haplotaxis gordioides,* the cave isopod *Asellus cavaticus,* and the cave amphipod *Niphargus puteanus;* and of the snails the species of *Lartetia* in numerous local varieties, these being often found only as empty shells in the Jura and Muschelkalk regions.[15] To these are added the ordinary inhabitants of creeks such as the snail *Ancylus fluviatilis,* the amphipod *Gammarus pulex,* and many insect larvae. There are also a number of ubiquitous forms such as varieties of the small bivalve *Pisidium* (on muddy substratum) and snails, *Galba truncatula, Radix ovata,* and *Bulimulus tentaculata.*

† *Centropyxis aculeata, Difflugia, Trinema,* and *Quadrula.*

a temperature of 54°. Few metazoans endure so high a water temperature. The ephydrid fly *Scatella thermarum* of hot springs in Iceland does not occur at temperatures above about 50°.[42] Of rotifers, which are more numerous than other metazoans in very warm waters, *Philodina roseola* shows the greatest power of resistance. A number of mollusk species are also able to live in fairly warm water; *Radix peregra,* a very adaptable form, occurs in the thermal waters of the Pyrenees up to a temperature of 45°; *Pseudamnicola aponensis* also tolerates 45° in the warm waters of Abbano in the Euganean Hills of north Italy, but its optimum range is from 32° to 36°. Species of *Melanopsis,* which are otherwise limited to warmer regions (Spain, north Africa), have found refuge in Hungarian and Italian warm waters. The small annelid *Aeolosoma quaternarium* has been found in a number of Italian warm springs up to 40°. A few crustaceans such as *Palaemonetes varians* are present as dwarf forms in Abbano, and a few ostracods also occur in thermal waters. Water beetles are relatively most plentiful; 8 species, some in large numbers of individuals, occur in the thermal waters of Valdieri and Vinadio in northern Italy. Brues [8] reports that in the hot springs of the western United States a population of 51 species at 32.5° falls steadily to one of only 2 species at 45.5°. Saussure found eels in the basins of Aix at 46°, and the minnow, *Leuciscus thermalis,* is said to live even at 50° in the springs of Trincomaly. It is noticeable that the fauna of thermal waters in general is made up of the same groups of animals as that of the salt waters.

Brues reports that at only one place in the world has it been possible to follow the changes in composition of the thermal fauna over a considerable range in water from a single source. This has been done at the springs of Meskhoutine, or Hammam Meskhoutine, in northern Africa.[38] These springs are of very large size, yielding between 400 and 500 gallons of water per minute, or about 100,000 liters per hour at a high temperature between 78° and 95°. Descending the stream arising from these springs to where the water has cooled to 60°, one finds dark green algae but no animal life. At 51° the crustacean *Cypris balnearia* first appears. At 45° this *Cypris* becomes very abundant, and frogs jump into the water when disturbed but do not remain there voluntarily. At 44° *Cypris* is still abundant, while the fresh-water crab *Telphusa fluviatilis* and tadpoles of *Rana esculenta* appear. Adult frogs are numerous and are readily made to enter the water, where they remain for extended periods. At 43° *Cypris* becomes scarce; annelids of the genus *Näis* appear, and frogs and

their tadpoles remain abundant. At 39° the *Cypris* has disappeared and occurs only between 43° and 51°.[4] Below this temperature the fauna gradually becomes normal.

Cypris balnearia is restricted to a definite range of temperatures above 40°. To this may be added also the acarine genus *Thermacarus* with 2 species, one from eastern Asia and another from the western United States, both found only in hot springs; they represent the only known species of a genus that constitutes a distinct family of hydracarine mites.[4]

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Part 4

The Distribution of Land Animals

20. *Ecological Factors of the Land and Their Effect on Animals*

THE CHARACTERISTICS OF TERRESTRIAL ANIMALS THAT CONTRAST WITH those of aquatic are principally associated with the chemical and physical properties of the atmosphere. We have already discussed (p. 34) how these properties determine the selection of those animal groups that live out of the water. Certain basic questions require further elaboration. The reader is referred also to the more detailed discussion of environmental factors in *The Principles of Animal Ecology.*[1]

Local differences in the chemical composition of the atmosphere are almost entirely unknown except in the vicinity of volcanoes and as they are occasioned by the industries of man. Just as the lack of an effective barrier in the oceans makes possible a constant mixing of the waters and thus causes a certain uniformity in its chemical condition that contrasts with the diversity of the chemical conditions of the widely separated inland waters, so in the atmosphere a quick and thorough mixing of the much more easily diffusible gases takes place to an even greater degree. In a few isolated and restricted natural areas the admixture of such gases as sulphur dioxide, hydrogen sulphide, and carbon dioxide (cf. p. 23), with the air, under natural conditions, makes life impossible.[58, 116]

The physical differences in the atmosphere are expressed in the climate: in humidity, temperature, pressure, and in the movement of the air, according to their periodic and non-periodic fluctuations during the course of the year. Temperature variations and currents are much more evident in the air than in the water, and the moisture content of the air varies greatly. Hence temporal and local variations in the physical conditions of the air are much greater than those of the water, especially those of the sea, and accordingly the environ-

mental complex under which terrestrial animals live is decidedly more varied.

Humidity

The humidity of the air is conditioned by evaporation, the amount of which is dependent upon the area of exposed water surfaces, upon rainfall, and upon the nearness of mountains, which cause a condensation of water vapor. Sea winds bring damp air; continental winds are dry. The higher the moisture content of the air, other things being equal, the more suitable it is for the development of animal life; it requires fewer adaptations on the part of primitive air-inhabitants derived from aquatic ancestors.

The separation of animals into those adapted to moist conditions and those adapted to drought (hygric * and xeric animals) has been mentioned (p. 57). Hygric animals include all air-inhabiting animals with insufficient protection against drying, such as land planarians, terrestrial leeches, earthworms, land isopods, snails, and amphibians; xeric air-dwelling animals, adapted to aridity, are specially protected against desiccation, as, for example, most insects, spiders, reptiles, birds and mammals. Nevertheless, the above examples are not without exceptions. Desert isopods, derived from the generally hygric land isopods, are found in arid regions, and many snails live exclusively on dry southern slopes, as *Zebrina detrita* and the species of *Xerophila*. Many reptiles, especially lizards, give off remarkably little water vapor, whereas various species of crocodiles and *Python molurus* vaporize an abundant amount. Indeed, though cattle in general give up much water and are therefore hygric, there are cattle in the arid Lower Californian peninsula that drink only every two days or even only once every week.[60]

We can carry the above classification still farther, in that we may distinguish between the euryhygric and stenohygric animals, those that endure more or less variation and those that are harmed by the greater fluctuations of humidity. To the euryhygric group belong many insects, such as cerambycid beetles, flies, dragonflies, and many birds and mammals. The roe deer, *Capreolus capreolus*, for example, occurs in the swampy lowlands of the Danube as well as in the dry valleys of the Swabian Alb. One may also designate as euryhygric the terrestrial leeches *Xerobdella lecomtei* or the genus *Armadillidium*, of the land isopods, or various common toads that live in regions

* "Hygric" is here preferred to "hydric" in order to restrict the latter term to amphibious animals.

of low humidity but are not limited to them. Stenohygric animals may be hygric or xeric. Land planarians, many snails (*Succinea*), mayflies, mosquitoes, the buffalo (*Bubalus*), and the hippopotamus can endure only slight reduction in humidity; on the contrary, other snails, like *Zebrina detrita* or *Xerophila*, are limited to dry regions, and the camel is injured by a vapor pressure of more than 11–12 mm. and soon succumbs.[92] Hygric animals are most often stenohygric; xeric animals are much less narrowly limited. Between the two extremes a median group of so-called mesic animals may be recognized, which may be euryhygric or stenohygric. These thrive best under moderate conditions and may be killed by extended exposure to dry or moist extremes.

High humidity excludes animals adapted to arid conditions in far fewer instances than does the reverse condition. Gadow deduces from the study of the distribution of reptiles in Central America that it is easier for the xeric northern genera and even species to extend their ranges to the south and to adapt themselves to a more uniformly warm and decidedly damp region with a luxuriant vegetation than for the hygric southern animals to range to the north.[46] Regions with uniformly warmer and damper air, like the Amazon region, the rainforests of the Congo, or the island of Ceylon, have a rich plant life and support an abundance of animals. Such regions, like islands and coastal regions, are especially suitable for animals adapted to humid conditions; land planarians thrive on the Malayan islands; the species of land snails of the West Indian Islands are easily as many as are found in all the rest of America from Alaska to Tierra del Fuego; and the Philippines are richer in terrestrial snails than the Indian and Indo-Chinese peninsulas together.[107]

Animal life of arid regions is sparse, corresponding to the scanty development of plant life and the severity of selection. In dry regions the snails have unusually thick shells, as in *Zebrina detrita*, or protect themselves by a thick mucus, as in *Arianta empiricorum*. Clausilian snails, abundant in hot, dry, calcareous mountains, close the mouth of the shell by means of an operculum; some species, however, that inhabit the seacoasts or misty altitudes have a weaker operculum or none at all; *Alopia maxima*, for example, has no operculum on the peaks of the Muguria Mountains in Transylvania; 200 m. lower the same species occurs with a well-developed operculum.[81] The isopod, *Porcellio scaber*, ranges in Germany to the limit of the coast climate, with its high humidity, and also occurs abundantly on dry,

sandy soils; in the interior, however, it is found only in damp places, under stones and underbrush or in cellars.[28]

The humidity of the air seems also to have an effect on the coloration of animals, in that darker colors tend to appear with greater humidity; but this is not applicable to all animal species nor to all degrees of humidity. Crickets, *Gryllus campestris*, reared in a moist environment with a relative humidity of 60–80%, produced deep black specimens.[110] Keeping various species of birds in a more moisture-

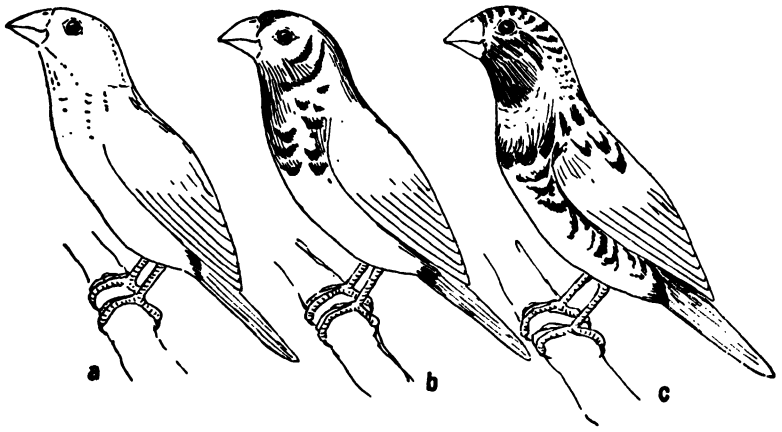


FIG. 111. *a*, Australian weaver-finch *Munia flaviprymna*, a desert inhabitant; *b*, the same after three years' residence in a humid climate; *c*, *Munia castaneïthorax*, not a desert form. After Seth-Smith.

saturated air leads to a darkening of the plumage. The experimentally darkened thrush, *Hylocichla mustelina*, and the Inca pigeon, *Scardafella inca*, approach subspecies that are found in regions with a moist climate.[9] The weaver finch, *Munia flaviprymna*, from the Australian desert, after a captivity of three years in the damp climate of England, assumed a coloration of its plumage that shows agreement with the related but not desert-dwelling species, *M. castaneïthorax*, in color pattern as well as in the deeper tinge (Fig. 111).[139]

Observation corroborates these experiments. Mountain and northern butterflies display much darker scales; however, this may be related rather to temperature or to the higher intensity of solar radiation than to humidity. The darkening of the red slug *Arianta empiricorum* is said to parallel the degree of humidity; in the same manner certain snails, *Helix arbustorum* and *Succinea pfeifferi*, are darker than usual in damp habitats.[93] On the other hand, an abundance of

moisture seems to favor the preservation of albinistic snails. The common frog *Rana temporaria* and the mountain lizards *Lacerta vivipara* are also said to be darker in a more humid environment. The song sparrow is paler in the arid parts of the United States and more melanistic in the wet Puget Sound country than it is in the mesic regions of the eastern states. This reaction is widespread among mammals, without being, however, a universal phenomenon. Thus the water-inhabiting subspecies of the field mouse *Microtus terrestris* are generally darker colored than the garden-inhabiting form. North American moles of the genus *Scapanus* (and less clearly *Scalopus*) are quite black in regions of abundant precipitation (west Washington and Oregon) and become lighter with greater aridity; thus in northern California they are brown, in southern California silvery.[148] The forest lemming inhabiting damp pine forests is darker than its relatives. Similar color gradations have been observed in the serval.[97] In general, birds and mammals living in cool dry climates are lighter in color—have less melanin pigment—than races of the same species living in humid warm climates. This is Gloger's Rule, which also holds among insects with certain modifications.[34] The effects of temperature on animal coloration confuse the picture of the relations with humidity. Rensch [119] found only one exception to Gloger's Rule in a survey of sixteen species of nuthatches and titmice.

A heavier rainfall may decidedly affect the faunistic characteristics. The fact that butterflies are not found in Iceland, while they are present in very much colder lands, may be associated with the rainy summer of this island, which interferes with flight and therefore with copulation.[137]

Temperature

The evaporating power of the air may be the primary factor upon which the organization of the entire terrestrial fauna depends. Once protection against desiccation has been acquired, however, the effect of temperature upon the distribution of land animals appears to be as powerful and is usually more evident. Although the 20-inch isohyet, which approximates the hundredth meridian of west longitude in the United States, is a well-marked line of distribution that does not coincide with physiographic features of the landscape,[96] the temperature boundaries that limit the distribution of an animal species are many and often much more distinct than those associated with variations in humidity. Humboldt states that isotherms, especially of equal winter temperatures (isocheims), manifest themselves as boundaries

that certain plants and animals seldom cross in the direction of the poles or in the direction of the peaks of snow-covered mountains. The elk (*Alces alces*), for example, lives almost 10° farther north on the Scandinavian peninsula than in the interior of Siberia, where the lines of equal winter temperatures become so strikingly concave.[71] The northern boundary of the regular range of the migratory locust *Pachytylus migratorius* coincides with the June isotherm of 20° C.[85] and the southern boundary of the Arctic butterfly *Colias palaeno* follows the January isotherm of −1° or −2°.

Land animals in their turn may be stenothermal or eurythermal, and stenothermal animals may be limited to high, low, or intermediate temperatures.

All classes of terrestrial animals are represented among stenothermal warmth-limited animals, which live primarily in the tropics. In the temperate zones such animals are confined to exceptionally warm places, to warm islands or to protected southern slopes. In Germany the region around Freiburg is a focus of animals with Mediterranean affinities.* The Orthoptera are important stenothermal warmth-limited insects. If the earth is divided into cool, warm, and hot regions, the relative number of species of the Blattidae plus the Mantidae in each of these regions is respectively 1:4:18, that of the walking sticks (Phasmidae), 1:1.5:35. The butterfly family Syntomidae has a similar distribution proportion of 1:3:63.[54]

The true home of buprestid beetles is the tropical region, and in our latitudes they appear in numbers only at midday in summer. Among arachnids, scorpions are especially stenothermal, warmth-limited animals; whip scorpions (Pedipalpi) are confined entirely to the tropics. The reptiles form another division of the animal kingdom composed of such stenothermal animals. Their numbers diminish rapidly in the direction of the poles. There are 82 species in southern Europe, 22 in Central Europe, and only 6 in northern Europe. Germany, with an area of 540,000 sq. km. has 13 species; Java, with 132,000 sq. km., has 122. The warmer the climate, the larger the reptiles become and the more active they are. The wall lizards (*Lacerta muralis*) of the Mediterranean region reach a much larger size than those in Germany, and the southern green lizards (*L. viridis*) may be double the length of the northern.[36] The greater activity of the reptiles of warm zones is reflected in the more rapid locomotion

* The centipede (*Scutigera coleoptrata*), the praying mantis (*Mantis religiosa*), the snail (*Ericia elegans*), and the green lizards (*Lacerta viridis*).

of the lizards, which may even run upright on their hind legs, notably the American *Crotaphytus* and *Basiliscus* (Fig. 112) and the Australian *Chlamydosaurus.*[127,141]

Stenothermal cold-limited animals also occur, but in smaller numbers. Snails of the genus *Vitrina* may be seen crawling about among the melting snows; individuals of this genus have been found at an altitude of 3000 m. in the Alps, while in the tropics they are con-

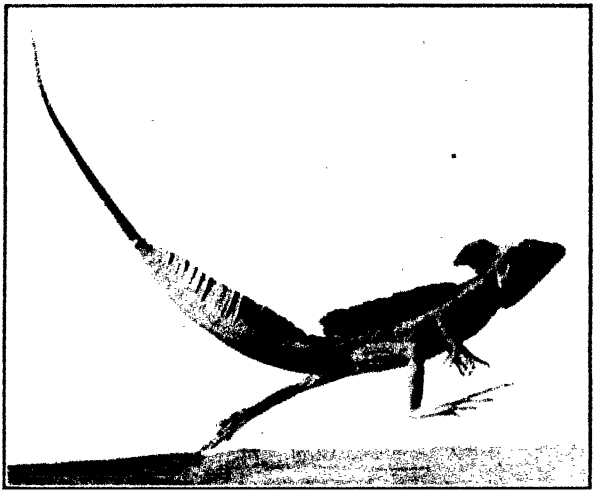


FIG. 112. The Central American iguanid lizard *Basiliscus* running bipedally. (Strobilite photograph by Arthur A. Allen, Cornell University, courtesy of Richard C. Snyder.)

fined to the highest mountain peaks, such as the Kilimanjaro, Ruwenzori, and Cameroon mountains. The helicid land snails *Cylindrus obtusus* and the enid *Mastus reversalis,* which normally live in the Austrian and Transylvanian Alps above the tree line, cannot be brought alive into the lowlands by collectors.

The number of eurythermal animals is much greater among terrestrial than among aquatic animals, as would be expected from the greater temperature variations in the air. In this group belong many insects, especially those with complete metamorphosis, for example the Diptera with short antennae, and many butterflies, as the white butterflies *Pieris* and the painted lady, *Vanessa cardui,* whose world-wide distribution shows their independence of temperature. Collembola, e.g., the glacier flea, *Isotoma saltans,* are also eurythermal. Of the Amphibia, the toad (*Bufo bufo*) is especially eurythermal; this species is distributed from 65° N. latitude to north Africa, and ascends

in the Alps to an altitude of 2200 m. above sea level. In North America *Bufo terrestris* ranges from Hudson Bay to Florida.

Homoiothermy

The homoiothermal * or so-called warm-blooded animals occupy a unique position. Physiologically they are plainly stenothermal, because their vital parts are not exposed to air temperatures, but to their own internal medium, in which an optimal temperature of 37° to 44° (according to the species) is maintained with but slight variations. With the exception of hibernating animals, the body temperature variations are normally not more than about 4° C. The pigeons (*Columba*) have a variation of 1.44°, the Adelie penguin of Antarctica 2.8° (37.4°–40.2°), goats (*Capra*) 0.25°, rhesus monkeys up to 3.8°; in the camel, temperature variations may attain a maximum of 4.4°, which is very exceptional.[159] Only the most primitive mammals, the monotremes, have greater body temperature variation; in *Echidna* it amounts to 7.5° (26.5°–34°). Nervous regulation is necessary to maintain a constant body temperature; cooling causes a reflex increase of the oxidative processes in the body and consequently a greater production of heat; in rabbits the entire store of glycogen can be caused to disappear by cooling. The body temperature of the arctic ptarmigan, 43.3°, may be as much as 80° above that of its environment. The maintenance of a relatively high internal temperature frees animals from the numbing influence of low temperatures. The external temperature becomes dangerous for a homoiothermal animal only when it begins to affect the internal temperature permanently.

The methods of internal temperature regulation depend upon whether the external temperature is lower, approximately equal to, or higher than the body temperature. In the first case reduction of heat radiation is required, with increase of heat production; in the last case, the regulative processes are reversed.

Heat radiation through the surface is diminished by thermal insulation. The poorest conductor of heat and hence the most effective insulator is non-circulating air. The "warming" effect of the feathery and hairy coats of birds and mammals results from the encircling layer of confined air immediately about the body. In birds the coverts

* The terms ectothermy and endothermy, for poikilothermy and homoiothermy, respectively, have been introduced in a series of papers on the temperatures of cold-blooded animals by Raymond C. Cowles [24a] and C. M. Bogert,[15a] who point out that both the vernacular "cold-blooded" and "warm-blooded" and the technical "poikilothermal" and "homoiothermal" have misleading connotations.

or contour feathers cover air-retaining down; in mammals the bristly outer hairs close over the inner woolly hairs and lie thickly upon them, attracted by the opposite electrical charge of the lower layers.[42] Birds have in addition an inner air envelope in the form of air chambers. In both birds and mammals, the poor heat-conducting qualities of the subcutaneous fat add further insulation.

Birds are superior to mammals in cold resistance; they do not have richly vascular exposed structures such as ears and tail; their lower legs and feet are tendinous and their bills are non-vascular and horny and thus give up little heat. Through the application of the wings to the body and by other protective devices already mentioned, they possess exceptional means of retaining warmth; further, their body temperature is higher than that of mammals. For these reasons it is not surprising that they endure the cold of winter even better than do mammals. The smallest mammal fully exposed to the winter temperatures of north Germany is the hare; all the smaller and many larger mammals, mice, shrews, moles, squirrels, martens, foxes, etc., retreat to earth or holes in trees or to well-lined nests. Small birds like the wren and titmouse do not need such protection.

The thickness of hair and feather coats is definitely related to environmental conditions. Among birds, the fliers that rise to the higher and colder air strata have a thicker plumage than those remaining close to the ground in the same climate; in the birds of prey, the raven, and the passerine birds, feathers compose 10–13% of the body weight, in gallinaceous birds, pigeons, and web-footed birds, only 7–9%.[102] In cold climates the hair and feather coats are thicker than in warmer climates. Reindeer and Tibetan antelope, which are exposed to cold winds, have a rough, coarse-haired, thick pelage, whose bristly hairs are so thick and matted together that the strongest blizzard cannot blow them apart. The most valuable furs come from the coldest regions. The thickness and consequently the value of fox or skunk fur is graded according to its origin. The Manchurian tiger (*Felis tigris amurensis*) has a very thick, shaggy coat in contrast with the Bengal or Sunda tiger. On the other hand, homoiothermal animals that dispense with these heat retainers entirely or in part are present only in the tropics. Such forms include the hairless dog, the Somali rodent *Heterocephalus philippsi* (Fig. 113), the sparsely haired buffalo, and the monkeys with bare faces, hands, and rumps. These clines in fur and hair illustrate what Rensch calls the hair rule.[120] Birds with featherless necks are more numerous in warmer regions.

Subcutaneous fat is especially abundant in aquatic homoiothermal animals, notably in penguins, seals, and whales. In the seal, 50 kg. of a body weight of 115 kg. is hide and fat. Such fat is common among terrestrial animals, especially in cold regions and in the winter; this is notably true of reindeer, red deer, musk oxen, wild hogs, bears, badgers, and skunks. The effectiveness of fat as a thermal insulator is evidenced by the fact that a seal causes no visible melting after remaining for hours upon an ice floe, and that a dead walrus has a high body temperature even after 12 hours in ice-cold water. In many animals that store fat in warm climates, the fat is localized, as in the



FIG. 113. *Heterocephalus philippsi*, × ¾. After Thomas.

fatty humps of camels and zebus or the fat tails and rumps of Mediterranean sheep.

The Bergmann Rule

Under identical conditions all homoiothermal animals give off equal amounts of heat per unit of surface.[140] Two dogs with body weights of 20 kg. and 3.2 kg. each were found to have surfaces of 7500 and 2423 sq. cm., respectively; for each kilogram there are 375 sq. cm. of surface in the large one, 757 sq. cm. in the smaller one; the heat production for 1 kg. of mass amounted to 45 calories for the large dog, 88 calories for the small one, per unit of time, which agrees closely with the corresponding value of the surfaces.[126] Thus a decrease of surface is of advantage for the maintenance of the body heat in a cold environment.

Whether mammal or bird, a homoiothermal animal under otherwise similar conditions has an advantage when its body surface is proportionately small. In otherwise similar bodies, the larger one has the smaller surface in proportion to mass, since volume and mass increase as the cube of the linear dimensions and surface only as the square. A more considerable body size therefore serves to reduce the heat radiation. With this basic fact in view, it is significant that among homoiothermal animals the same species attains a greater body size

in colder regions than in the warmer ones and that in closely related species the larger ones inhabit the colder climates. This is in direct contrast with the latitudinal size relations of poikilothermal animals, such as reptiles and amphibians, which are smaller in colder regions. This principle has been called the "Bergmann Rule" after its discoverer; [13] it is a phenomenon of animal geography of great importance.

A general agreement with the Bergmann Rule may be seen in the geographical distribution of the species of penguins:

Species	Body Length, mm.	Weight, kg.	Distribution
Aptenodytes forsteri	1000–1200	34.4	Antarctic continent, certainly the farthest south of all its relatives, exceptionally up to 61° northward.
A. patagonica	900–1000	♂17.2 ♀15.2	South to 55° (Macquarie Islands).
Pygoscelis papua	750–800	—	South to 60° 30′ (Paulet and Dundee Islands), mostly between 47° and 45°.[a]
P. adeliae	700–750	—	South to 66°. Most northerly breeding places South Orkney Islands.[b]
P. antarctica	700–750	—	South to 64° 30′ (Seymour Islands), north to 52° S. latitude.
Eudyptes chrysolophus	700	—	South to 61° (South Orkney Islands), north to 46° 30′.
E. crestatus	500–650	—	South to 55° (Tierra del Fuego), north to 37° (Tristan da Cunha).
Spheniscus magellanicus	700	—	South to 52° (Falkland Islands).[c]
S. demersus	550	5–6	South to 34° 30′ (Cape of Good Hope), north to 17° (Great Fish Bay).
Eudyptula minor	480	—	South to 46° (New Zealand).
Spheniscus humboldti	—	4–5	West coast of South America.
S. mendiculus	490	—	Galapagos Islands.

[a] More stationary than *P. adeliae*, in the antarctic region even during the winter.
[b] Distinctly migratory; goes northward for breeding.
[c] Breeds in caves.

The footnotes offer an explanation for the apparent exceptions. A giant form of the puffin, *Fratercula arctica naumanni* (wing length 175–195 mm.), lives in Spitzbergen and north Greenland; these birds are smaller on Bear Island, on the Norwegian coast, in Iceland, and in south Greenland (wing length 158–177 mm.); and still smaller (wing length 155–166 mm.) on the Channel Islands and Helgoland, while a dwarfed form (wing length 135–145 mm.) winters in Mal-

lorca.[57] The horned larks of North America exhibit a graduated series of subspecies; those from Hudson Bay have a wing length of 111.5 mm., those from Kansas and Nebraska measure 105.8 mm., those from Nevada, 102.9 mm., the coast inhabitants of Lower California, 99.1 mm., and finally those of Santa Barbara Island near California have a wing length of 97.1 mm.[121] These data partially illustrate Rensch's Rule concerning wing shape in birds. Concisely stated, this rule holds that within the same polymorphic birds, species of forms from cooler climates have relatively narrower and more pointed wings in comparison with the broader shorter wings characteristic of warmer regions.[120] Hummingbirds that live in the greater altitudes of the Andes have a minimum body length of 45 mm., and the largest species, *Patagona gigas,* goes far to the south; a very small species, one of the smallest of birds, *Chaetocercus bombus,* with a body length of 28–28.5 mm., inhabits the tropical zone in Ecuador and northern Peru, just south of the equator. When the same species inhabits different climates, the individuals tend to attain the largest size in the coolest regions; thus *Chlorostilbon aureoventris* in Paraguay and north Argentina is larger than in southeastern Brazil and is smallest in central Brazil. Countless other examples may be found in the literature.[4, 15, 55, 56, 57, 61, 82, 90, 145]

Mammals verify the theory; the larger mammals of central Europe increase in size toward the northeast and decrease in size toward the southwest, as is shown by the roe deer, fox, wolf, and wild boar. The skull length of the wild boar varies as follows: from Southern Spain 324 mm., from northern Spain 353 mm., from the Pyrenees to Germany 380–410 mm., from White Russia 465 mm.,[108] and from east Siberia 560 mm. The average basal length of the skull of the alpine hare (*Lepus timidus*) varies similarly: in Ireland it is 73 mm., in Scotland 70 mm., in Scandinavia 73.2 mm., in north Scandinavia and Russia 77.8 mm., on the main island of Japan 80 mm., in northern Siberia 87.5 mm.[12] The mole rat *Spalax* exhibits: (1) small forms from Tripoli, Egypt, Palestine, and Syria; (2) medium-sized forms from Asia Minor, Transcaucasia, Balkan Peninsula, Dobruja, and Hungary; (3) large forms from Galicia, Bucovina, southern Russia, Cis-Caucasia, and from the Kirghiz Steppes.[65] The pocket gopher, *Geomys bursarius,* of North America north of 46° N. latitude attains a total length of 296 mm., between the latitudes of 40° and 46° only 284 mm., and south of 40°, 256 mm.[111] The length of the skull in the American mole *Scalops aquaticus,* in millimeters, averages as follows: those of Florida, 30.8; of North Carolina, 31.8; of Virginia, 33.4;

of Maryland, 34.1; of Pennsylvania, 34.9; of New York, 35.3; and of Connecticut, 35.5.[148] The Virginia deer (*Odocoileus*) of North America becomes progressively smaller towards the south; a dwarf form (*O. mexicanus*) is found in South America.[66]

Exceptions to the Bergmann Rule are encountered, but when one recalls the many other means of reducing radiation and the many other factors that may regulate body size, the small number of such exceptions is astonishing. There are various mammalian exceptions; the woodland caribou of North America is larger than its relative of the Barren Grounds, and the Spitzbergen reindeer is smaller than that of Lapland.[123] Ritchie [122] points out that the red deer from Norway are smaller than those from Sweden, and these in turn are smaller than those from central Europe. There are exceptions among the birds, especially among migrants, which are not exposed to the winter cold in their breeding habitat. An exception is also found in the capercaillie *Tetrao urogallus*, which is smaller in Siberia than in Germany. Burrowing mammals may form exceptions, since they, like migratory birds, can withdraw from the winter cold. For example, *Microtus pennsylvanicus* is larger in Pennsylvania than in Labrador. Raccoons decrease in size northward. Allen claims that the decrease in size corresponds with the transition into the less suitable climate. The hot climate of the tropics is certainly the normal one for kingfishers and orioles, and in spite of this the Bergmann Principle can be applied to them, since they are larger in cooler regions: the wing length of the kingfisher *Alcedo athis bengalensis* of India, the Malay Peninsula, and the Sunda Islands ranges from 68 to 71 mm., of *A. a. pallida* of northern Africa and Palestine 74–75 mm., of *A. a. corsicana* 75–77 mm., and of *A. a. ispida* of Germany 77–81 mm.; and similarly *Oriolus oriolus kundoo* from India, Kashmir, and Afghanistan has a wing length of only 140–142 mm. as compared with 149–158 mm. of *O. o. oriolus* in Europe.[57]

Laboratory experiments yield similar results. White mice became larger than the stock animals when reared in a temperature of about 6.1° C., and smaller when reared at a temperature of 26.3° C.[146] Chickens two months old grew more rapidly during four months' continuous exposure to 6° than did comparable ones maintained at ordinary room temperature.[2] A direct effect, therefore, seems to be involved.

It naturally follows from the Bergmann Rule that in neighboring regions with distinct climatic differences and with related animal populations, differences in size become noticeable simultaneously in

many homoiothermal animals. Thus, the faunae of southeast Australia and Tasmania show great similarity in composition; but the mean temperature, which amounts to +16° on the south coast of Australia, sinks to +11° in Tasmania; a large number of mammals and birds attain a significantly larger size in Tasmania than in Australia: [142] the duckbill and spiny anteater are larger than on the mainland, and the Tasmanian giant kangaroo *Macropus giganteus fuliginosus* somewhat exceeds that of the continent in size. The same relation applies quite generally to birds; reference may be made to *Corvus coronoides,*[145] and also to the Tasmanian species *Gymnorhina organicum,* which is larger than the vicarious Australian species *G. tibicen.*[11] Corresponding comparisons apply to the north and south islands of New Zealand. The north island has an essentially warmer climate, with an average yearly temperature of +16.6° in Auckland; on the southern island, with mountains rising to an elevation of 3500 m., the average yearly temperature is only 10.4°, even at Dunedin on the seacoast; the same or corresponding species are larger on the southern island than on the northern island. This is true of the modern *Apteryx* as well as of the extinct Moas,[104] of the parrots of the genus *Nestor,* and of an entire series of other birds.*

In closing the discussion of the Bergmann Rule it is interesting to note another type of exception: while cold Alaska is a center for maximum size of many species of birds and mammals, warm Somaliland is a similar center for minimum size of its homoiothermal animals as compared with the same species in African territory nearer the equator.

In keeping with this general rule we find that mammals of cold climates have their heat-radiating surfaces decreased by a reduction in size of the ear and tail, by a shortening of the neck and legs, in general by a more compact form. This has been referred to as Allen's Rule.[4, 118] Mammals with such a great surface as the bats are mainly inhabitants of the warm regions. The flying foxes (Megachiroptera) belong entirely to the tropics. Of the 16 families of Microchiroptera, 9 are confined entirely to the tropics, 4 are tropical and subtropical in distribution, and only 3 extend into the temperate zones; and even of these the large family of Vespertilionidae has only 10 of its 33 genera in the temperate latitudes.[114] The ears of the hare become shorter towards the north: the African rabbits are slender and have strikingly

* Representative forms from the genera *Glaucopis, Turnagra, Petroeca, Miro,* and *Sphenoeacus.*[72]

long ears: in contrast, the varying hare of the Old World (*Lepus timidus*) has much shorter ears than the field hare (*Lepus europaeus*) or the alpine hare (*L. varronis*). The same picture presents itself in North America. Jackrabbits of the subgenus *Macrotolagus*, in the southwestern United States, have ears that measure almost a third of the body length; in the common jackrabbit (*L. campestris*), from Kansas to Canada, the ears are as long as the head; among the varying hares (*L. americanus*), which extend southward as far as 40°–45° N. latitude, the ears are shorter, and are still shorter among the arctic hares (*L. arcticus*). The size difference of the ears of the desert fox (*Megalotis zerda*), of the European fox (*Vulpes vulpes*) and of the polar fox (*Alopex lagopus*) is shown in Fig. 114. Figure 115 exhibits

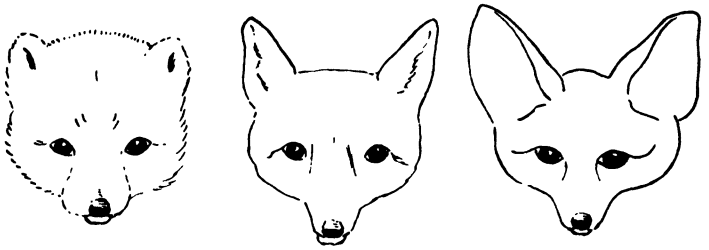


FIG. 114. Head of arctic fox *Alopex lagopus, a;* red fox *Vulpes vulpes, b;* and desert fox *Megalotis zerda, c.*

the extreme difference in the surface development and body form that may be found in antelopes from cold and warm climates. Similar differences appear in *Gazella picticauda*, of the Himalayas at an elevation of 4000–5000 m. above sea level, and *G. bennetti*, inhabiting the plains of north and central India; with approximately equal length, the mountain animal has shorter legs, ears, and tail.[14]

The body appendages of many mammals are lengthened by the direct action of various factors. Mice reared at higher temperatures develop relatively longer ears and feet, and chickens reared so have longer tarsi and tails. The growth of lop-ears of rabbits is favored by leaving the animals in hutches with a temperature of 15°. Heart size can also be increased experimentally by exposing pullets at two months of age to 6° for four months, while appropriate control chickens are kept at 21° to 24.5°.[2] Such considerations make it possible that the body proportions just discussed are, at least in part, a direct consequence of the temperatures to which animals are exposed in nature. The degree to which body size and appendage length have become genetically fixed is no doubt variable.

Heat given off by radiation must be restored by an increase of metabolism. The reduction of food into small bits by the gizzard of birds or by the teeth of mammals accelerates the digestion of foodstuffs and thereby makes possible greater intake of food; this forms the basis for the increased body temperature. An increase of the body temperature, in turn, causes the acceleration of digestion, and this

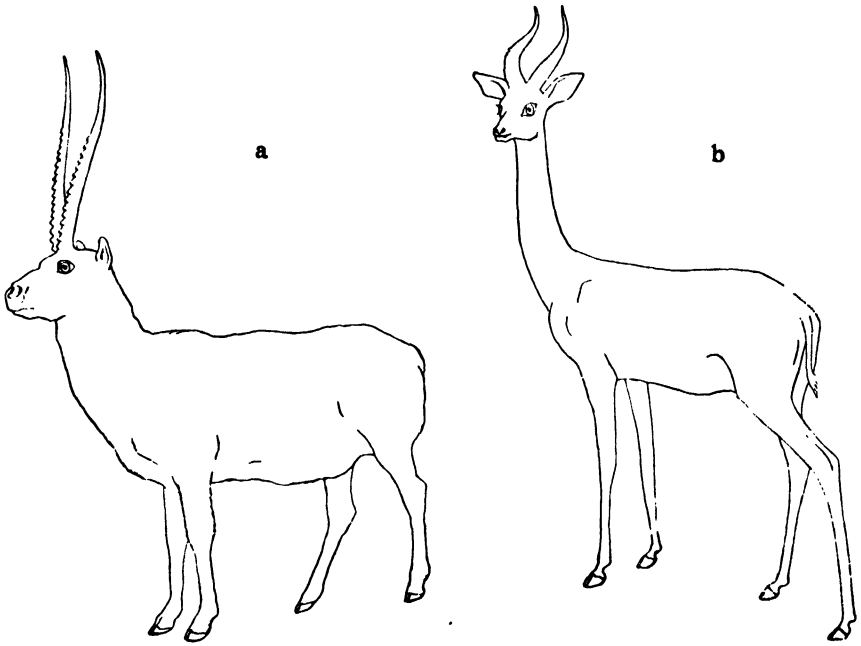


FIG. 115. Antelope from Tibet, *Pantholops hodgsoni, a;* and Waller's gazelle *Lithocranius walleri* from Somaliland, *b;* After *Brehms Tierleben.*

permits further and more abundant food intake. This cycle proceeds until the optimum body temperature is reached.[35] More heat must be produced by metabolism at lower external temperatures; a canary, at rest in twilight, produces 319 calories per kilogram per hour at 22.3°; at 14° it produces 992 calories.[89] In times of food shortage, stored materials such as fat and glycogen must be "burned." In small animals, however, the radiation of heat may become so great at lower temperatures that, in spite of continuous food ingestion, they cannot furnish sufficient oxidizable material for the maintenance of their body temperature. Lapicque [89] found by comparing three birds of different size, the domestic pigeon (body weight 390 gm.), the small pigeon *Geopelia striata* (weight 48 gm.), and the tiny weaver finch

Estrilda astrild (7.5 gm.), that the heat radiation calculated per kilogram results in a series of 144, 344, and 1020 calories, and the daily food requirements, similarly calculated, amount to 48, 132, and 390 gm. In *Estrilda,* two-thirds of the ingested food is used in heat production; with a reduction of temperature to 15°, the shortness of winter days does not afford sufficient time for an adequate food intake for the tiny animal; in spite of continuous eating it becomes thin and dies of hunger; on the other hand, at a temperature of 30°–35°, it thrives and is active. If the feeding time is increased about two or three hours by artificial illumination, it can endure a temperature of 14° and even of 13°.[49] A certain minimum size is essential for homoiothermal animals in order that they may subsist in cold regions; warm-blooded animals of the size of hummingbirds can leave the tropics only during the warm summer.

Increasing metabolism, however, inflicts increased demands upon the heart, for an increased circulation is correlated with increased food and oxygen consumption and with increased excretion of metabolic products. Through size adjustment, the heart can adapt itself within certain limits to these greater demands. Thus, weight of the heart of the sparrow *Passer montanus* in Leningrad is 15.74‰ of the body weight, in northern Germany 14.0‰, in southern Germany 13.1‰. A similar relation holds for the squirrels *Sciurus,* whose relative heart weight increases from 5‰ in the middle Neckar region to 5.9‰ in the Black Forest, 6.2‰ in East Prussia, and 6.5‰ in the Brocken region. The tundra birds that migrate to Germany in the winter all have a greater relative heart weight than their nearest relatives of similar size living in these regions; these values for the rough-legged hawk *Buteo lagopus* in comparison with the common hawk *Buteo buteo* are as 8.35‰ to 7.1‰; and many similar relationships could be cited.[63]

Other temperature relations

The surface temperature of the desert soil may reach 60° in parts of Palestine;[21] readings of 78°–84° have been obtained in other desert regions and of 65° on the exposed sandy surface of the Indiana dunes near Chicago. It is unlikely that surface temperature of soil ever exceeds 93.3°.[77] Nymphs of two species of *Mantis* and adult grasshoppers have been observed moving about where the surface soil temperature was 50.8°, and thermopyle tests showed the internal temperature of the insects was approximately that of the surrounding

air. Such high temperatures are found only during the day, and even then only on the surface exposed to the full rays of the sun.[21]

Many tropical animals quickly perish when they are exposed for some time to the unabated effect of the tropical sun. A simple method used by collectors for killing large crocodiles quickly without injury consists in exposing them for a time to the full rays of the sun; elaborate experiments with alligators have been made to bring this phenomenon into possible relation with the extinction of the dinosaurs.[23] In the Zoölogical Garden of Antwerp a number of ostriches died because they could not obtain shade.[133] Such effects have usually been ascribed to increased temperatures, but more recent work indicates that light may have lethal effects for other reasons. At any rate, tropical and desert animals in general are forced to seek shade. For homoiothermal animals, the avoidance of overheating is especially difficult, since their own body temperature lies very close to the lethal condition, and every active movement immediately gives rise to an increase in the temperature, which becomes dangerous if cooling does not occur.[25] Sunstroke in man is a somewhat inadequately understood phenomenon, especially as to its varying degree of incidence in different tropical regions.*

Body cooling is frequently attained by retiring to water, as is illustrated by the habits of water buffalo, water buck, rhinoceros, elephant, and especially by the hippopotamus. In Australia during the hot season, rabbits may be seen at the edge of water holes with only their heads above water.[65] The elephant showers itself with water. During great heat many animals seek the shade of trees or caves where they fall asleep and avoid continuous movement. Skin capillaries have reflex dilation and so promote the radiation of heat at high temperatures. The ears of rabbits and elephants, the hairless tail of the rat, and the hanging tongue of the dog, all serve as heat regulators.

A most effective means of reducing body temperature consists in the evaporation of water, which possesses a high latent heat of evaporation; each gram of water that evaporates takes from the body more than 500 calories. The chief means of water evaporation is by breathing. The accelerated breathing of many animals when greatly heated is often accompanied by opening of the mouth and more rarely by extension of the tongue. Cold-blooded animals also utilize this means of cooling; it has been observed for lizards that their temperature may

* The fear of mid-day sunlight on the part of white-skinned residents of the tropics may be carried to a ridiculous extreme. The pith or cork helmet so much worn in Africa and India has never become the vogue in the American tropics.

rise from 17° to 38° within 30 minutes on exposure to the sun; at a body temperature of 39° the rate of respiration rises suddenly from 70–80 to 180–360 per minute, and the lizard opens its mouth. A special characteristic of many mammals is the possession of a large number of sweat glands in the skin, as in ungulates, bats, and primates; others have only limited numbers of such glands, especially on the ball of the foot. With many species, as in the horse and man, the sweat glands are so modified that they secrete large amounts of water and thus serve to diminish body temperatures.[130] As the air approaches saturation, water evaporates more slowly, and this means of cooling fails.

Despite the inner stenothermal condition of homoiothermal animals, one ought not to infer that they are all eurythermal in relation to external conditions, and therefore endure wide fluctuations of temperature. This is, however, frequently true; the wheatear (*Saxicola*) that lives in Greenland as well as on the hot Spanish plains, the two-humped camel that must endure temperature ranges of −37° to +38° [92] in the Gobi Desert, the tiger whose distribution extends from the Sunda Islands to the Amur River, and the puma, ranging from Canada to Patagonia, are examples of marked eurythermy. The homoiothermal animals are to a certain degree independent of one of the chief factors of climate, the temperature, and investigators like Wallace and Heilprin, who based their conclusions concerning the factors causing animal distribution primarily upon studies on birds and mammals, naturally concluded that climate is not closely correlated with animal distribution.

The means for controlling body temperature are quite differently developed in different animals, so that all gradations of temperature limitations are found in the mammals and birds as well as in the poikilothermal forms. Vultures, buffaloes, giraffes, dwarf musk deer, hippopotami, and the anthropoid apes are examples of stenothermal warmth-limited animals. Polar and alpine animals tend to be stenothermal cold-limited forms. The principle of Bergmann applies only to homoiothermal animals. Poikilothermal animals generally attain larger size in warmer climates. This applies to insects [143] (with the exception of the arctic bumblebees, cf. Chapter 25), tree frogs, toads, and reptiles among land animals. The regularity involved has been regarded as the inverse of the Bergmann Rule, to which, however, it bears no relation.

Temperature also has an effect on the coloring of animals, as may be gathered from the appearance of seasonal dimorphism of butterflies and certain other insects. This influence is by no means uni-

form; the heat may cause dark coloring, as in *Polyommatus phlaeas,* or bright coloring, as in the species of *Papilio.* Final decision concerning the factors that produce color varieties in the various climates can be arrived at only by experimentation, because of the complexity of the intermixture of hereditary and environmental conditions and because of the variety of effects produced by different combinations of climatic factors. Such experiments have been made most extensively upon butterflies. Through the effect of raised or lowered temperatures upon the pupae, directly after pupation, wing colors have been produced in many central European butterflies that resemble the colors of the southern or northern populations of the species. Thus, the effect of high temperatures on *Polyommatus phlaeas* was the production of dark specimens like the variety *eleus* that occurs at Naples; the second generation of German swallowtails, *Papilio machaon,* can be so altered by increased temperature as to resemble the Syrian form of this species; exposing the small butterfly *Vanessa urticae* to higher temperature produces a form similar to *ichnusae,* which lives in Sardinia; and exposure to low temperature produces the form *polaris,* found in Lapland. The Apollo butterfly *Parnassius apollo* changes to the dusky mountain form *brittingeri* through the effect of cold.

By comparing the colors of related birds from different climates, one may arrive at an analysis of the effects of temperature.[48] The pigments of feathers (melanin and lipochrome) may be distinguished by their reaction to different temperatures. Melanins (black, brown to clay-yellow pigments) undergo an increase at higher temperatures and a reduction at lower temperatures, just as they are affected by increased and decreased humidity. The yellow lipochromes (zoöxanthines) are somewhat increased by heat and diminished by extreme cold; the reds (zoöerythrins) are not affected by heat. The dependence of colors on external conditions may explain the fact that non-migratory birds tend to develop geographical forms more generally than do the migratory types. Migratory birds, in fact, are the more uniform the shorter the time they spend in their nesting ground, that is, the more pronounced their migratory nature. Thus, among the birds listed by Hartert there are on the average 9.6 geographical forms for every species of permanent residence, 6.1 for every migrating species arriving as early as March, 3.1 for those arriving in April, and 2.0 of such forms for species arriving as late as May. Many other environmental factors besides temperature, such as humidity, light, and food, must of course be taken into consideration.

Light

Light has a much stronger effect upon terrestrial than upon aquatic animals, since in water the intensity of the light rays diminishes rapidly with depth, and the coloration of animals appears to be closely related to light intensity. Cave dwellers are almost always colorless; but *Proteus*, even if exposed only to weak daylight in an aquarium, rapidly becomes dark brown, whereas this does not occur among genetically determined albinos, like the albinistic axolotl. That the internal organs are protected by the pigmentation of the skin from the influence of strong light, especially from the chemically active short-wave rays, is shown by a series of observations on the domesticated animals. Mottled cattle, fed on buckwheat, when allowed to graze freely in the direct sunlight, develop a skin rash on the white spots, a disease that increases to the point of desquamation of those skin regions, fever, and symptoms of cerebral irritation, finally ending in death. White mice get along well on buckwheat in a dark room, but in the bright light they quickly die. Materials derived from buckwheat apparently act as a sensitizer [59] of protoplasm to the short-wave rays. Buckwheat is a common winter food for man in the United States, but is avoided in summer. In Florida, white domestic pigs die if they eat *Lachnanthes* growing in the pastures, but black ones are immune to its effect.[31] Decomposition in blood and the formation of haematoporphyrin through the action of tropical sunlight may be the reason for the difficulty with which the blond races of mankind establish permanent colonies in the tropics. The protection that the skin pigment provides against the penetration of rays into the inner parts of the body is often further strengthened, as for example, in man, by pigmentation of the sheaths of the central nervous system; the pigment in the pia mater of brunette Europeans and brown Egyptians is in fact more abundant than in that of the black races, as for example, the Sudan negroes.[153] Sun-dwelling geckos, such as *Lygodactylus picturatus*, have a black pigmented peritoneum, while in those with the nocturnal habit, like *Hemidactylus turcicus*, it is unpigmented.[136] Life in direct sunlight is made possible only by certain protective adaptations; amphibians and reptiles that often sun themselves (*Hyla, Lacerta*) have some protection against the penetration of radiation into the body.[87] Desert reptiles retreat into shade or beneath the ground to avoid excessive sunlight and accompanying heat.

Pressure and air currents

Atmospheric pressure and its fluctuations are of significance only for the animals of high mountains, and will be discussed in Chapter 24.

The drying effect of strong air currents on animals produces a distinctive selection pressure, eliminating soft-bodied forms or driving them into sheltered niches. Flying animals—insects, birds, and bats—may be more directly affected. Off-shore winds deliver millions of coastal insects to the sea, as attested by the windrows of their bodies at the strand line when the wind is on-shore. The absence from the Frisian Islands of the butterflies *Pieris*, *Hipparchia*, and *Vanessa* and the flies *Eristalis*, *Anthrax*, and *Empis*, all of which occur on the neighboring coast, is explainable as the result of wind elimination.[83]

In regions where strong winds prevail, flying animals may survive by increase of their powers of flight or by the contrary means of loss of the capacity for flight. On the treeless and stormy Faeroes the starling *Sturnus vulgaris*, a permanent resident, has longer and stronger wings and a longer tail than its relatives elsewhere.[57] Butterflies copulate in the air, and this habit causes them to be more dependent on wind conditions than other insects; hence only the sturdy and strong-flying butterflies are found on such islands as the Marshalls.[137] Nineteen of the most beautiful butterfly genera at Ega on the Amazon River, with about a hundred species, are not present farther downstream in reach of the sea winds.[7] Most striking, however, is the frequent occurrence in stormy regions of insects with more or less degenerate wings. On the subantarctic islands, as on Kerguelen, Crozet, South Georgia, and Auckland, where calm days are the exception, the majority of insects have reduced wings or no wings at all (cf. Chapter 26). The causal relations are not simple, and wingless insects also occur in continental regions without extreme winds.[29]

On the other hand, many birds make great use of both vertical and horizontal air currents in their flight. The effect of rising air currents may be observed on steep coasts during sea winds, which strike the slope and are deflected upwards; there one may regularly see gulls and other sea birds soaring without beating their wings. Areas where low barometric pressure is almost stationary, as, for example, along the east coast of the Adriatic or over the Tyrrhenian Sea, are characterized by ascending air currents. Ascending currents also originate by solar irradiation in places where areas with different heat capacity lie in close approximation; thus forests warm up or cool off

more slowly than grasslands or fields; water and land have a similar relation. As a consequence the air rises over the grassland or shore by day and over the forest or water by night. Vultures, which are essentially gliders, usually wait for the development of "thermals" before beginning their daily foraging (Hickey, J. J., personal comm.). Vertical air currents are present especially on seacoasts and in river



FIG. 116. The three principal migration routes of European birds: -·-·- the west coast route; ..... the Italo-Spanish route; and ---- the Adriatic-Tunisian route. After Lucanus.

valleys. It is not improbable that for this very reason such stretches are used as the migratory routes of birds, since they present narrow channels in the ocean of air in which such upward currents are an effective aid in their flight.[33] Large groups of birds of various species travel these routes independently (Figs. 116, 117); in the Old World such routes lie along the coasts of Scandinavia, of the Baltic and North seas, of Spain, Italy, the Balkan Peninsula, and Syria, or they follow the Rhine, Vistula, Danube, or Nile; in North America, the Mississippi, the long Appalachian ridges, and both coasts are important migration lanes.[94] The problem of migratory routes thus becomes, in part, a meteorological one.

The petrels (order *Tubinares*) are associated in their distribution with regions of almost continuous air movement. The albatrosses and

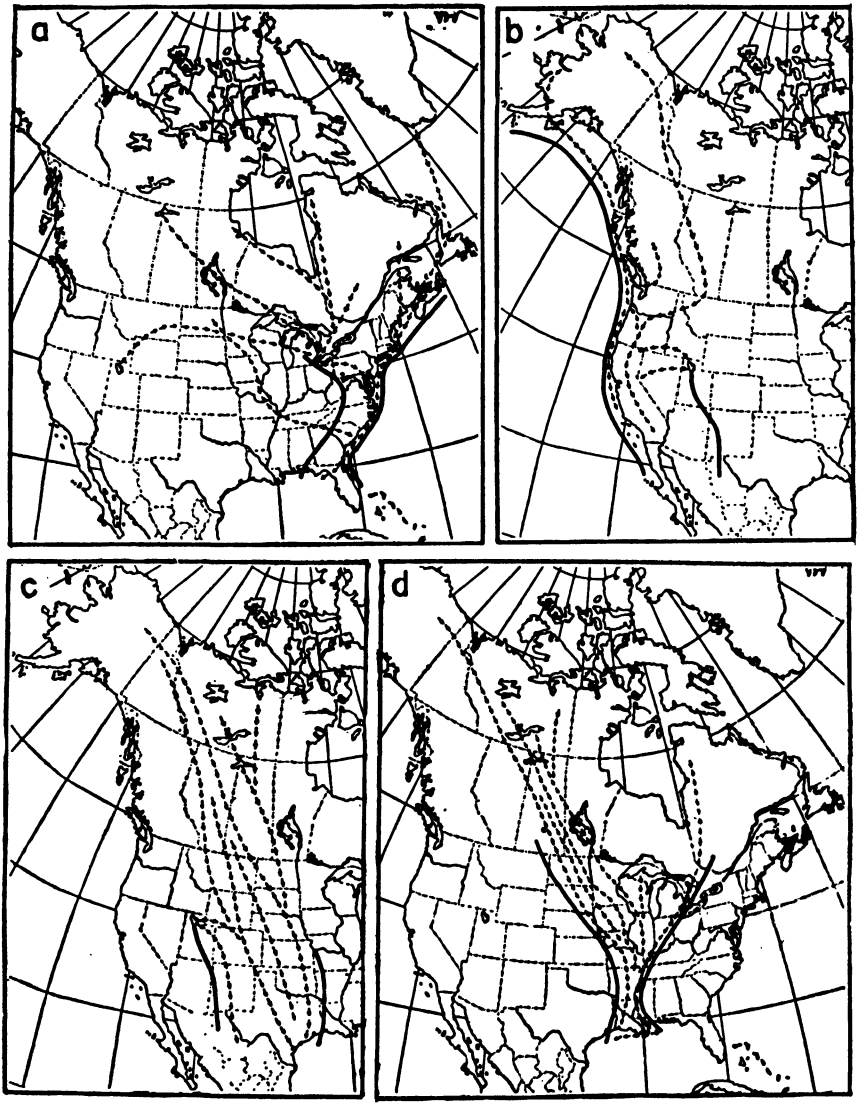


FIG. 117. Four principal migration routes of waterfowl in North America, with tributary routes. *a*, Atlantic flyway; *b*, Pacific flyway; *c*, central flyway; *d*, Mississippi flyway. (From Lincoln.)

the fulmar make use even of horizontally blowing winds deflected from the rising and falling waves. In calm weather they may be seen resting on the smooth sea.

Environmental periodicities

The climate is rarely uniform in any given place. The succession of day and night produces a periodic change in light and darkness, in warming and cooling, and in relative humidity. This has a fundamental effect on animal life. Animals that are directed by their sense of smell, like many insects (for example, the large moths among the Lepidoptera, the lamellicorns among beetles) and many mammals, are independent of the light and can obtain their food by night as well as by day, but animals dependent upon their eyes for orientation, like the dragonflies among the insects, and most birds, are forced to rest upon the arrival of darkness. The varying length of the day according to season and geographical position is also an important influence.

Differences in day and night temperatures are often great. In a large part of the tropics, the amplitude of the daily temperature variation is about 6° and is greater than the mean monthly variation, which often amounts to only 2°, so that it has been aptly said that night is the winter of the tropics. In the Sahara, however, and in the Sonoran desert, the temperature difference between 3 P.M. and 3 A.M. may amount to more than 50°. The greater humidity at night, evidenced by the dew, makes it possible for many stenohygric animals adapted to humid air to exist in regions where the daytime conditions are intolerable. Snails that have withdrawn into shells by day come out at night; the Spanish gather snails for food at night by lantern light in places where no snails can be found during the day. Earthworms also are nocturnal.

Many stenohygric insects, like mosquitoes or stoneflies, fly only by night and after rain, since at these times the danger of desiccation is slight. Likewise salamanders, toads, common frogs, and other amphibians wander about principally at night. Thus, the periodic variation of conditions occasioned by the rotation of the earth makes it possible for many animals to frequent certain regions that are unfavorable and hostile for a portion of the day. Finally, the change of light and dark plays a rôle in the struggle for existence, in so far as it permits many animals to exist beside one another, since some rest at the time when others are active, so that the competition between them is reduced.

On the greater part of the earth's surface there is still another cycle in addition to this short period, namely that of the annual seasons. However, there are places where such differences in the weather do not occur, so that one may speak of regions where temperature, humidity, and sunlight are essentially the same on one day as on another. In such regions the concepts of weather and climate coincide.[5] Most of these places lie between the tropics of Cancer and Capricorn in America, Africa, India, and Malaysia. There are a few places elsewhere without pronounced periodic cycles, such as Tasmania, the evergreen forests of Chile and New Zealand, and various island archipelagos. In such regions plants grow equally well throughout the entire year, the forest is always green, there is no drying of the vegetation, and the animal population is not involved in seasonal changes; just as in the Cuban caves fishes breed throughout the entire year [39] and in the grottos of Carinthia insects reproduce continually,[128] so tadpoles may be found throughout the year in Tasmania,[40] and there, as in the tropics, the course of life goes on without interruption. Of land habitats, aside from caves, the most nearly uniform are the dark interiors of tropical rain-forests, where, rain aside, short-term changes in weather are entirely or almost entirely absent and even diurnal changes are minimized.

The tropical environment

Associated with the absence of seasonal periodicity, most tropical localities approach optimal environmental conditions, high temperatures and humidities, much light, and a great quantity of food. The poikilothermal animals are particularly favored by conditions that approach those obtaining in the bodies of homoiothermal animals. Heat radiation of the latter is low, and the food requirements are correspondingly less; those of man, for example, are about 20% less in the tropics than in Germany.[88] The utilization of vegetable food by invertebrates is much greater than in the temperate climates; in particular, the Orthoptera and the termites play a far greater rôle. From this fact arises a series of peculiarities that distinguishes the animal life of the tropics from that of the temperate and cold zones. Poikilothermal animals are in general larger, and, as in the tropical ocean, there is an immense number of species.

The average weight of the tropical insects is decidedly greater than that of insects of the temperate and cold belts. The largest forms of most orders of insects occur in the tropics; this is just as true in the phylogenetically old groups (locustids, dragonflies, Fulgoridae) as in

the groups of latest origin (acridids, butterflies, and lamellicorns);[53] the large insects occurring in the cold regions are always small in comparison with the tropical forms and are mostly relicts of a warmer period.* Myriapods may become 28 cm. long (*Spirotreptes seychellarum*); among the scorpions, tropical forms, such as *Pandinus imperator*, attain a length of more than 17 cm., and the Javan bird-catching spider (*Selenocosmia javanensis*) becomes 9 cm. long. The land snails in the tropics are also of a much greater weight than those in temperate climates. The shell of *Achatina schweinfurthi* from Africa becomes 171 mm. high, that of *Bulimus garcia-moreni* from Ecuador measures 147 mm. in height and 85 mm. in width, and the animal lays eggs 51 by 35 mm., as large as those of a hen; many helicids, like *Helicostyla lampas* of the Moluccas and *Pleurodonta gigantea* of the Antilles, also attain a large size; tropical species of the limacid genus *Vaginulus* may be 20 cm. long when extended. It should be noted, however, that *Strophocheilus popelairianus* of the high Andes has a shell as much as 163 mm. in height and 104 mm. in width. Amphibia thrive better in the tropics than elsewhere; the largest frog, *Rana goliath*, with a body length of 250 mm., lives in South Cameroon. Reptiles are nowhere as large as in the tropics. The crocodiles are at home there; the giant tortoises are confined to the tropics; large iguanas and boas live in tropical America, and monitors and pythons in Asia and Africa grow to gigantic size.

The above does not apply to the homoiothermal animals; they bear optimal conditions within themselves, and universally live in a physiologically tropical climate. As shown in the discussion of the Bergmann Rule, they can attain large sizes in the temperate zones. It is true that the largest living bird, the ostrich (*Struthio*), is at present an inhabitant of the tropics and subtropics; but in relatively recent times its range extended through Central Asia to Mongolia. The powerful moas of New Zealand, which surpassed the ostrich in size, lived in temperate climates, and other birds of great size, the condor, the American rhea, the large penguins (*Aptenodytes*), and the extinct great auk, are or were inhabitants of cooler or cold climates. The elephant is the largest land mammal now living, but the mammoth that lived even in arctic regions in the post-glacial period was approximately as large.

Much has been written about the beautiful coloration of tropical animals, but the hypothesis that this phenomenon may be caused by

* *Mantis, Locusta, Lucanus, Saturnia.*

climatic conditions remains to be proved. The tropical genera of birds are striking to us both because of individual brilliancy of color and variety of color pattern, but the proportion of brilliant forms in the whole fauna remains approximately the same as in temperate regions, since the number of dull-colored forms in the tropics is likewise increased [152] (see also Chapter 26). The notion that there are no good singers among the singing birds in the tropics is emphatically contradicted by many travelers (Wallace, Darwin, Bates, Sarasin, and others); but the warbling of the birds is not limited so much to a definite and relatively brief period as in our latitudes.

Especially striking is the tremendous wealth of animal life as well as of plant life in tropical regions. The warmth hastens the course of life activities according to simple physicochemical laws, and therewith sexual maturity; the generations follow each other much faster, in an unbroken series. This again presents additional opportunity for variation and mutation, and therewith for evolutionary differentiation.

The shortening of the developmental period of tropical animals in comparison with northern animals is particularly striking in insects. The butterfly *Danaus chrysippus*, which has only one generation per year in the northern parts of its range, has in the Philippines one generation after another and requires only about 23 days for its development. The pupal stage of the hawk moths *Chaerocampa oldenlandiae* lasts for 18–21 days on Bohol Island in the Philippines, 24–25 days at Manila, and 8 months in Sydney.[138] Whereas the mason bee *Chalicodoma muraria* requires two years for a generation in northern Europe, *Polistes*, in Java, requires a pupal stage of only 12 days; [91,124] the larva of the mason bee in southern Germany hatches in about 14 days, and an additional period of 4 weeks elapses before it is ready to spin; in Eritrea, the hatching of *Eumenes* occurs in 2 days, and pupation follows after an additional 5–6 days.[82] The entire development of the beetle *Crioceris subpolita* is completed in 25–31 days in Java, whereas in Germany the asparagus beetle (*Crioceris asparagi*) requires a whole year between generations. A more rapid sequence of generations is also observed in mammals. In New Zealand the red deer brings forth young a year earlier than in Germany.[147] Other animals show similar relations. This great hastening of development insures rapid succession of birth, growth, propagation and death. If an insect has a length of generation of 30 days in the tropics, and lays, let us say, 100 eggs, the descendants of one pair, assuming that all of the progeny live to propagate in like manner, may amount

to 488 trillion individuals at the close of the year, as against 5000 individuals from two generations per year in temperate latitudes.

Some figures will help elucidate the abundance of species native to the tropics. In Cooke's comprehensive account of the Mollusca (1895) 727 species of land snails are listed from the Philippines; in Japan, 1½ times larger, there are only 193; Cuba has 614 species of land mollusks, Jamaica 463, and in contrast, Tasmania, about 6 times as large as Jamaica, has only 80, while all Scandinavia has only 148 species.[24] The superiority of the tropics in number of species of insects is especially noticeable. If we compare the number of species of certain larger groups occurring in the tropics and subtropics with the number in other regions, as of 1913, we find: [54]

	Tropical and Subtropical	Non-tropical
Locustids	2726	1120
Acridids	2811	1842
Dragonflies	2096	921
Pentatomids	3675	1560

In this connection, it should be remembered that the species of the temperate zones are much better known. Bates, one of the great naturalists of the Darwinian era, knew of 4560 species of butterflies in 272 genera in South America, at a time when 716 species were known from the entire Palearctic Region. Within the radius of an hour's walk at Pará (now Belem) Bates collected 700 species of butterflies,[7] whereas all Europe has about 400 species. Many insect groups do not exhibit such a preponderance of tropical species. Thus bees, gall insects, mayflies, and caddisflies are fewer in the tropics than in higher latitudes.

Ants are especially characteristic of the insect life of the tropics, and the termites are still more so. In 1913 we knew 2888 formicid species from the tropics, from the temperate zones only 1055.[54] The termites are confined mainly to the tropics. Ants and termites have a powerful influence not only on the rest of the insect world but also on the biota as a whole; even man may be helpless against them. The highly developed method of rearing the broods, together with the protective nest structures that are situated everywhere, above and under the earth in the most varied types and sizes, may well offer the explanation for their overwhelming numbers of individuals; the ability of ants to thrive on the most diverse food, and of termites to feed on wood or other parts of plants, gives them an advantage over

other animals; both are protected also by soldier castes. The hosts of ants may explain the fact that other predatory and carrion insects, like the carabids, the staphylinids, and necrophorids, are reduced in numbers, as reported from all parts of the tropics by various observers.[7,30] Wherever the armies of the predatory driver or army ants arrive (*Dorylus* in Africa and India, *Eciton* in tropical America), there arise an energetic flight and a great massacre; Vosseler [151] estimated that such an ant colony collected 1,600,000 insects from a single field in 10 days. These ants are also dangerous to larger animals, if for any reason they are unable to escape.

The enormous numbers of ants and termites occurring in the tropics has led large animals of varied origin to live on these small insects; indeed, some animals confine their diet entirely to them and are especially equipped with powerful claws and long sticky tongues, with which they open and plunder their nests. Whereas woodpeckers are the only birds known as ant eaters in temperate zones, there is a host of ant predators in the tropics. The mammals include the species of *Myrmecophaga* and the armadillos in South America, aardvarks (*Orycteropus*), pangolins, and a correspondingly adapted carnivore, the earth wolf (*Proteles cristatus*), in Africa, and *Myrmecobius* together with certain other marsupials in Australia. Insect-eating birds support themselves mostly upon the swarming sexual forms and destroy them so thoroughly that only a small fraction of the swarming individuals remains. There are also birds that pick up the insects flushed by the ant armies on the march. Many frogs and toads also live on the ants and termites; some have become exclusive termite-eaters, such as the toad *Rhinophrynus dorsalis* in Mexico.[46] Dragonflies prey upon the flying sexual forms, and a number of ant species, especially among the large ponerines, have become exclusive eaters of termites.[43]

A distinct superiority of the tropical fauna in number of species is shown by the air-breathing vertebrates. The uniformly humid tropical forests afford an excellent habitat for amphibians. The caecilians are confined to the tropics, and frogs are much more abundant than in the temperate belts. All Europe has only 20 species of frogs and toads (exclusive of subspecies), while British Guiana with only one-thirty-seventh as great an area has more than 50. The fact that salamanders are almost entirely confined to the north temperate regions is a conspicuous exception to the usual rule. Only a single genus, *Oedipus*, reaches the tropics in Central America.

Reptiles have their true home in the tropics. Thirty-one species of snakes [112] (again exclusive of subspecies) are found in Europe; there

are 38 in Trinidad, which is less than one-two thousandth as large. The increase of snakes from south to north in Australia is about as follows: Tasmania has 3 species of snakes; Victoria, 22; New South Wales, 42; and Queensland, 70. Birds are also much more abundant in the tropics than elsewhere. North America north of the Rio Grande has 1420 species and subspecies of birds,[6] many of which are migratory; New Guinea, with an area less than a twentieth as large had 1501 known forms in 1941, only 79 of which are migrants.[109] Tropical areas are especially rich in birds such as flycatchers that capture exclusively flying prey. Among mammals, apes, and lemurs, and edentates occur principally in the tropics; of bats, the fruit-eaters are entirely confined to it. Insect-eating bats occur in much greater number of species; the number of individuals of bats is also very great, and in Java, for example, may equal the numbers of birds.[86]

With such an abundance of species, it is clear that the struggle for existence between animals is extraordinarily intense, in contrast with the lessened struggle with inanimate nature. In the tropics the adaptation of these animals for this struggle is therefore unusually stressed. Here we find the number of poisonous animals and the virulence of their venom increasing toward the tropics. Scorpions and centipedes, which are more abundant in the tropics, are also more venomous there. Repulsiveness to taste and smell occur more often in tropical than in the temperate belts; and for this reason, together with great intensification of the competitive struggle among animals, mimicry, protective coloration, and protective form are widely distributed. The phasmids and mantids and the leaf butterflies are mainly tropical.

The small number of individuals characteristic of many tropical species is in some contrast to the great number of species by which the tropical fauna is distinguished. Beebe [10] reported from Venezuela that he seldom found many individuals of a species. There was always present an ever-changing panorama; except when the birds were just nesting, he could never be certain of seeing the same species twice, although he was sure that new forms would be added to the list every day. Nevertheless, the exceptions to this impression of wealth of species correlated with small populations of each are so many as to cast doubt on any generalization as to tropical life in this respect. The vast abundance of individuals of termites, ants, and, among vertebrates, of certain riparian forms like caimans (*Caiman sclerops*) or basilisk lizards is familiar. Fewness of individuals may be an illusion resulting from the abundance of cover. Of the snakes reported by Dunn [37] from mass collecting in Panama, it appears that the rela-

tive numbers of individuals of abundant and rare species may be not unlike the same relation in a temperate region.

It is difficult to give a satisfactory explanation for the small numbers of individuals of so many species. It has repeatedly been stated that number of species and number of individuals are in inverse proportion. Among plants it may happen that only a single specimen of a species of tree can be found in a large area of tropical forest. Many plant-eating animals, however, are specialists; caterpillars, longicorn beetles, and others restricted to such species of plants are therefore isolated with the host-plant individuals.

The lack of a definite periodicity in tropical climates has important further effects on animal life. In plants the development of leaves, blossoms, and fruits is not associated with a definite season as in the temperate zones. The number of species of trees blooming throughout the year especially is larger, and the time during which blossoming specimens of a species may be found is, in general, longer in the tropics than in places where the seasons display very great temperature variations; the phenomenon of repeated blossoming at short intervals, though occurring in the temperate zones almost as an anomaly, is a normal and ordinary occurrence among many tropical plants.[132] Only under such conditions could plant-eating animals develop that are dependent upon blossoms or upon pulpy fruits through the year.

The nectar- or pollen-eating birds are wholly confined to the tropical and subtropical regions. The Nectarinidae in Africa, Madagascar, and the Indian region, the brush-tongued parrots and honey-eaters of the Australian region and the hummingbirds of the New World are the principal groups. The hummingbirds of South and Central America have representatives that advance into the temperate belts as summer residents but remain there only a short time. The tongue of all these nectar-feeding birds is long, extensible, and brush-like, or rolled up like a tube, in adaptation to the sucking of nectar. These birds are the means of pollination of many of the blossoms they visit, and, just as many flowers possess special contrivances that attract pollinating insects, so in the tropics many flowers are adapted to the visits of birds by size, provision of special resting places, rigid and solid formation of pistils and stamens, and abundant honey production. About 84% of such bird-attracting flowers are orange-red, scarlet, cinnabar, carmine, or purple in color.[154] In like manner birds and mammals that are dependent essentially upon pulpy fruits have their principal distribution in the tropics, where such fruits may be obtained during

the entire year; this is true of many parrots, plantain-eaters (Musophagidae), toucans, and other birds, and of many monkeys.

The distribution of the reproduction period over the entire year is usual among tropical animals in uniform climates. In temperate zones the breeding period of almost all the invertebrates and most of the vertebrates is in the warm seasons of spring and summer, and there are usually only one or at most two generations a year. Tropical insects, on the other hand, have many generations each year. In the Philippines, for example, eggs, caterpillars, and butterflies of *Papilio pamnon* are found simultaneously throughout the year;[138] in Java the lamellicorn beetles, *Lachnosterna, Anomala,* and *Exopholis,* likewise are present in all stages of development at all times. In Ascension, Dahl found the few spiders and insects both present in all stages.[27] This is also corroborated by the fact that the oft-described nocturnal tropical concert, the thousand-voiced chorus of the males of many species of grasshoppers and crickets, to which frogs also add their calls, lasts throughout the year. However, it is not the same individuals that sing; the concert remains, but the musicians change. The limitation of certain insect colonies to one season, as in our bumblebees and wasps, is not paralleled in the tropics. In Java,[86] as in Brazil,[73] perennial wasp colonies with persistent nests avoid too great an increase in population by swarming, like honeybees in our latitudes.

In many vertebrates the breeding habit is not associated with a special season. The larvae of the toad, *Bufo melanostictus,* for example, and apparently those of many other frogs and toads, are found in Batavia throughout the year.[79] The nesting of some birds is also independent of the season. In Cuba one may find eggs of the finch *Euethia cepida* and of the hummingbird *Riccordia ricordi,* as well as their young, in any month.[103] The booby (*Sula*) and the noddy (*Anous*) breed continuously on the St. Paul Rock in the Atlantic, near the equator. Pregnant females of many, but not all, mammals may be found at all times of the year. These include a number of South American monkeys,[135] the pigs in the Malay archipelago,[150] many of the African antelopes, and the marsh deer and sloth of South America. On the Galapagos Islands the breeding activities of the fur seals (*Arctocephalus*) are continuous.[78]

The tropics are without periodicity of seasons with reference to temperature. Daily cycles are much more uniform than in higher latitudes; year in and year out the day is approximately 12 hours long, while with progression into higher latitudes the length of day

increases in the spring and decreases in the fall. This is important for the birds, which are essentially diurnal animals and are directed principally by their eyes in their search for food. Since the three or four hottest hours of midday are deducted from the 12-hour day, there remain only 8 or 9 hours for the search for food. This is enough for the birds so long as they have only themselves to provide for, but the time becomes short when they must also provide food for their young. It is different in temperate regions. The farther toward the pole, the longer the day becomes; at such latitudes there is twice as much time and more at the disposal of the day-feeding birds. This is one of the advantages that birds obtain when they leave the tropics for their summer breeding grounds nearer the poles.[17,47] The longer feeding hours make possible the production of a greater number of eggs and the maintenance of a larger brood. That better nourishment results in greater egg-laying follows from the observation that, in mouse years, marsh owls (*Asio flammeus*) and barn owls (*Tyto alba*) lay 6 to 10 or more eggs instead of only 3 to 5.[75] There is also experimental evidence for this fact. American chicken breeders have established that a greater number of eggs are produced with artificial illumination of the chicken coops until 9 P.M., and the result is associated, at least in part, with the accompanying increase in food consumption; on the average, every hen laid 16 more eggs per year than the control animals that were kept without such lighting.[100] This may help account for the fact that birds of the tropics lay relatively few eggs, rarely more than three. In British Guiana[135] birds of prey, parrots, pigeons, plovers, toucans, and many sparrows lay but two eggs even when related birds lay more eggs in temperate regions.[38,57] Hickey has summarized American data for birds in southern Wisconsin for comparison with Whitehead's data for 53 Bornean birds[155] as follows:

Number of Eggs	Southern Wisconsin,* Number of Species	Borneo, Number of Species
1	0	5
2	5	33
3	12	10
4	40	5
5	35	5
6 or more	21	5

* Hickey, personal comm.

Hibernation and aestivation

In contrast with the relatively uniform climatic conditions of the rainy tropics, one finds in many tropical regions an alternation of wet and dry seasons. This alternation has effects somewhat analogous to the alternation of warm and cold seasons characteristic of the higher latitudes. The differences in the two contrasting seasons are not equally great everywhere. In most of tropical America, rainy and dry seasons are not so sharply distinguished as in India or Africa. Likewise, there are all sorts of gradations between summer and winter. Proximity to the ocean diminishes the temperature difference, affording cooling in the summer and warming in the winter. The difference between the extremes is accordingly less in coastal regions than in the interior of large continents, where the summer is exceedingly hot and the winter is very cold. Localities with an oceanic climate and those with continental climate may have the same average annual temperature and nevertheless offer entirely different living conditions, because of the differences in extremes.

The rainy season and summer exemplify at times the optimum, the dry period and winter the pessimum. Under the effect of unfavorable conditions, animal life declines extraordinarily; but in their effect there is an indication that the deficiency in humidity is more injurious than the lack of heat. Many animals supply their own heat more readily than their own water. Homoiothermal animals can endure winter hardships so long as they find nourishment in sufficient amounts; extreme dryness is injurious to them. In other respects, however, winter and the dry season are very similar in their effects, and are often compared with each other; both result in marked reduction in plant and animal activity. As soon as the inhibiting factors are removed, a tremendous awakening occurs. The long-restrained activities of life are again resumed simultaneously in many forms. The majority of animals begin to propagate at once. The spring concerts of male insects, of frogs, and of songbirds, raised against the background of vegetation awakened to new life, form an abrupt contrast to the desolation just passed.

The increasing length of the summer day in the higher latitudes permits an increased rate of plant growth, which affects all animal life, at least indirectly. We have already seen how profoundly the increase in feeding time affects birds. Similarly, insects such as the bumblebee utilize the entire day in searching for food and in the arctic regions discontinue work for only a short time about midnight.

Survival through the unfavorable period, be it the dry season or the frost of winter, is the problem that faces the animal population of regions with changing seasons. Certain adaptations become necessary, and these must be the more complete, the longer the adverse season lasts and the greater the extremes of aridity or cold. Hence the number of species that live in such regions decreases, as the living conditions approach the pessimum.

The great majority of invertebrates, the poikilothermal vertebrates, and also many mammals, fall into a sleep-like, inactive condition in protected places during the unfavorable season. Such inactivity is referred to as aestivation if caused by dryness, and hibernation if caused by cold.

Aestivation is common among snails and may last tolerably long even in mid-latitudes during a summer drought; in snails of hot climates with extended dry seasons, the aestivating period can be prolonged for years at a time without killing the animal. A quiescent period of six years' duration has been noted in *Micrarionta veatchii* of southern California; [158] *Helix* (*Eremina*) *desertorum* from the border of the African desert came to life in the British Museum after five years; ampullarids, after one to two years.[106] Land planarians and land leeches of warmer regions spend the dry season buried in the ground. Insects and spiders may aestivate in the steppes; for example, the bumblebees in Corsica and Sardinia,[113] or the solpugid *Galeodes* in the Transcaspian steppe.[64] Amphibians withdraw into crevices and holes in the ground and lie there in a death-like sleep. Of reptiles, crocodiles, turtles, and snakes aestivate; even many lizards, as in the Sudan, crawl away and hide during the driest period. Crocodiles bury themselves in the mud through the dry period. Aestivation is also known among the mammals. The aardvark of the African steppes aestivates,[131] and so, in Madagascar, do the peculiar insectivores *Centetes* and *Ericulus* and the lemurs *Chirogale milii* and *Microcebus*.[80] Birds certainly do not ordinarily hibernate; it was long believed that various migratory species like swallows and chimney swifts that make a sudden appearance in spring had spent the winter beneath the mud in ponds, but the winter ranges of these species have now become known. It is the more remarkable to have a circumstantial account of hibernation in the poorwill (*Phalaenoptilus nuttallii*) in California.[76]

Hibernation in the winter corresponds to aestivation in the dry season. Earthworms crawl deeper into the ground and discontinue their activities. Many insects and spiders overwinter in the egg stage, and thus are less susceptible to the injurious effect of the cold; many

other insects survive the unfavorable period as pupae. Many overwinter as larvae and imagoes hidden away in cracks and holes in the earth, under pieces of bark, and in hollow trees. Snails bury themselves under the covering material on the ground or bore into available fissures and crevices. Some amphibians hibernate at the bottom of bodies of waters; others bury themselves in the mud or in dry earth. Similarly, reptiles of temperate regions creep into suitable places, sometimes in mixed groups. Many mammals also sink into a state of sleep in some frost-free hiding place, in holes in the ground, or in hollow trees, during which their rate of metabolism is much lowered; the frequency of the heartbeat and breathing is greatly decreased, and the temperature of the body falls as low as 1° and averages about 1° above that of the environment.[52] Bats, marmots, and dormice survive the winter without ingestion of food, living entirely upon the stored-up supplies in the body. Some carnivores undergo a kind of pseudo-hibernation, as is especially reported of bears and skunks. These animals do not become fully torpid like a marmot, and may not hibernate at all if food is to be found. There may well be a gradient in this habit from north to south in North American bears. The capacity for suspension of activity with cold is not common to all mammals.

In general, only homoiothermal land animals can be active during winter. Even these require a sufficient food supply and a means of protection against excessive radiation of heat. Most of the north temperate mammals, even those that do not hibernate, have hiding places for the winter into which they can withdraw when they are not occupied in the search for food. These recesses are mostly holes in the ground (moles, mice, hamsters, rabbits, foxes), at times the hollows of trees (martens, raccoons), less frequently warm, lined nests, such as squirrels make for themselves. Only the larger mammals can brave the winter cold without such protection, the deer, wolf, lynx, wild boar, with the hare as the smallest, but these normally retire to sheltered niches. Birds are better able to endure the cold of winter unprotected; they have such excellent heat insulation that they require nothing more than shelter from the winds. Even so, the ptarmigan in the far north[84] and the capercaillie and black cock in Siberia,[18] the bobwhite and others, dig shelter holes in the snow.

The heat-retaining devices are furthermore reinforced for the winter. In autumn, the mammals acquire their winter fur, thicker than the summer coat, and at the beginning of the warm season this is again lost; among birds the coat of feathers becomes thicker during the

fall molt. In addition to this, especially among the herbivores, a thick layer of fat is deposited as a result of good nourishment during the summer and fall. It is significant that among the animals of the cold zone the fat is softer and less easily hardened than that of the inhabitants of the warm regions. These masses of fat also serve as food during the lean period of the winter, and the animals become thin toward spring. It has been shown, however, that the subcutaneous fat stored by male reindeer and caribou is entirely used up in the autumn breeding season.[74]

Scarcity of food is a greater peril to homoiothermal animals than is cold. Small birds such as titmice and kinglets with their relatively high food requirement can find sufficient food only by continuous search throughout the short winter days (compare Lapicque's experiment on *Estrilda*, p. 469); if the day is shortened because of cloudiness many of them starve. Certain birds and mammals of the temperate and cold zones gather supplies for the winter during the favorable period. The titmice and the nuthatch (*Sitta*) [115] gather seeds; the Old World jays (*Garrulus*) hide hazelnuts and acorns in the cracks of trees and under leaves for later use. The only wild bird of the temperate zone reliably reported as breeding at all seasons is the barn owl (Hickey, personal comm., per Irving Kassoy's observations in New York City). Mammals are especially given to storing provisions. Hamsters (*Cricetus*), chipmunks (*Tamias*), and ground squirrels (*Citellus*) collect grain and other food in subterranean chambers, the hamster at times up to 25 kg.; dormice and squirrels collect nuts, and voles (*Microtus terrestris*) gather roots into their nests as winter food. Such vegetable materials keep well if stored in a dried condition. The arctic fox even manages to store meat by placing ptarmigan or similar booty in crevices in the ice; the polecat (*Putorius putorius*) is said to paralyze common grass frogs by a bite in the spinal cord and bring them together in a cavity during the fall.[66] Certain colonial insects, such as honeybees and harvester ants (*Messor*), gather supplies, the former honey and pollen, the latter seeds.

Seasonal migration *

Finally, seasonal changes cause more or less distant migrations of many homoiothermal animals, which enable them to escape the un-

* The preponderant use of the word migration for the seasonal movements of birds, and for analogous cyclic movements, leads us to restrict the term *migration* to this meaning, employing "dispersal," "emigration," "mass movement," etc., for non-returning population movements of geographic extent.

favorable seasons. This is true for regions with dry seasons as well as for those with cold winters. The best known of these phenomena are the annual bird migrations, in which a great number of birds of the temperate and cold zones move to warmer regions in the late summer and autumn. Only a few such migratory birds breed in tropical regions also, and these may be thought of as native to the tropics with stragglers that breed in temperate regions. Northern South America has two separate season populations of migrant birds in addition to the permanent residents. A large number of species arrive at the end of the northern summer and are somewhat replaced in the months following February by a smaller number of forms including a half dozen flycatchers, a martin, and two swallows from their breeding grounds in Argentina and southern Brazil. One species, the warbling vireo (*Vireo virescens*), has races in both groups. None of these transients breed in their winter range.[101] We usually consider the breeding place the natural home of our summer birds. Among the many mooted questions of bird migration, there is one of distinct geographical significance: the question of migratory routes. All observations show that every avian species has its own peculiarities in the development of migration,[99] despite which there are common routes that are followed by many species. These may be relatively narrow and specific tracks or may be broad courses. They generally follow the seacoasts, borders of inland lakes, or river courses, entirely or in great part. The association of so many species of birds, differing in habits, habitat, and power of flight, on the same course at different times makes it apparent that birds react to specially differentiated belts in the atmosphere and probably to places with frequent ascending air currents rather than primarily to visual landmarks. Birds may also migrate without the aid of such rising air, as is shown by those whose migration is on a wide front, such as finches, swallows, the American robin, and others. Birds that migrate over water out of sight of land and notably the few that migrate from the North American Arctic across the Atlantic to Europe and Africa obviously dispense with visual landmarks.[95]

The curlew migrates from the Yenesei delta in northern Siberia to Australia, Madagascar, and Africa. The golden plover from arctic Canada tends to fly south in autumn along an Atlantic coastal route and over the western Atlantic to northern Brazil. It winters in the South American pampas and returns by a midcontinental route. A Pacific subspecies migrates from Alaska to Hawaii, the Marquesas, and the Low Archipelago. The arctic tern of eastern North America holds

the present long-distance record. It breeds in Canada and northern Greenland, crosses the Atlantic to western Europe and migrates down the African coast, or recrosses the Atlantic to Brazil and continues along the South American coast. Arctic terns from both routes overwinter near Antarctica. The total distance flown is about 25,000 miles each year.[95] The Greenland wheatear, a close relative of the European form, also crosses the Atlantic twice yearly in flights between its breeding grounds in northern Quebec and Greenland and its winter range in Spain and North Africa.[6]

Birds that feed on flying insects—swallows, swifts, and flycatchers—are migratory in Europe and North America. Migrants also include grain- and grass-eaters, most of the water birds, and many birds of prey. In the north polar zone all the birds are migratory, though the amplitude of the movement may not be great in ptarmigans, ravens, and snowy owls. Horneman's redpoll (*Acanthias*) breeding in Greenland and Iceland is said to winter in its breeding range. The number of permanent residents among birds increases towards the middle latitudes. Certain species leave in autumn but are replaced by related forms from the north, which remain during the winter, as for example, the junco. On the other hand, birds that are permanent residents in one region may migrate in other localities; the partridge (*Perdix perdix*), a strictly non-migratory bird in Germany, migrates in eastern and southeastern Russia, southwards to the Volga delta; the starling migrates in northern Germany and in the eastern United States; on the Faeroes with oceanic climate they are non-migratory. The migrating habit does not depend wholly on the peculiar nature or on the history of the species, but is obviously associated also with climatic factors.

Such extensive seasonal migrations as are common among birds also occur among some mammals. The migrations of the bats are most nearly comparable to bird migrations. Many northern bats travel to warmer winter habitats. In northern America, the bats inhabiting hollow trees migrate southward as far as the Bermudas. Returns from banding of bats indicate wide summer dispersal of the European noctule (*Nyctalus noctula*) from a hibernation cave near Dresden.[3]

Many ruminants undertake regular migrations at the beginning of the cold season. Especially impressive were the migrations of the American bison, whose enormous herds moved towards the south in the fall, though not to the extent that they migrated from Canada to the coastlands of the Gulf of Mexico; it is true that bison were migrating over the entire distance, but it was a parallel displacement of the entire mass, of such a sort that the most northern herds did not go

beyond the Republican River, the northern source of the Kansas (40° N. latitude), while those from that region moved farther to the south. Such migrations are also known among deer. The wapiti of Yellowstone Park migrate to the high valley of Jackson's Hole in the Rocky Mountains, where as many as 40,000 of them are found together in the winter;[117] and caribou regularly migrate from the tundra into the northern coniferous forests. The fur seal *Callorhinus* of the Pacific migrates northward to its breeding place in summer; in the autumn the seals move southward and lead a pelagic life. The great majority of non-migratory birds and mammals of the high mountain ranges withdraw in autumn into lower, protected valleys; even hibernators such as the marmots make their winter quarters at lower altitudes.

The alternation of rainy and dry seasons also occasions periodic migrations. In Africa great bat migrations have been observed at the beginning of the dry period. Antelopes, zebras, and ostriches often congregate into large herds and abandon the hot arid steppe; during the dry season the elephants move into the mountain forests and climb to high altitudes in the mountains of Abyssinia, on Mount Kenya and Mount Kilimanjaro, or withdraw into the galleried forests along the river courses.

Few invertebrates, considering even highly motile insects, perform periodic migration on a geographic scale. The monarch butterfly (*Danaus plexippus*) of North America is a notable exception, executing massed autumnal migrations to the south and less conspicuous northward migration in the spring. This is the only species of which the same individuals are known to make the return journey.[8,156,157] Many invertebrates make short migrations from exposed summer habitats to protected winter niches.

The substratum

The nature of the substratum is of great importance to many air-breathing animals, especially to those that must live in burrows in the ground itself. Animals that move about upon the ground also show effects of certain characteristics of the substratum and adaptations to its peculiarities. Animal species living in the ground include burrowing forms such as earthworms, Enchytraeidae, nematode worms, spiders, countless insect larvae or mature burrowing insects, such as the mole cricket (*Gryllotalpa*), amphibians, lizards, snakes, and mammals. Associated with these active burrowers are many other species

that are unable to burrow extensively for themselves but occupy the excavations made by others.

It is evident that solid rock offers no habitat for such animals. A Colorado bee, *Perdita opuntiae,* which excavates burrows in sandstone,[26] affords an exception to the common statement that no air-breathing animals can burrow into rocks as do the boring mussels and sea urchins. Other soils, composed of more or less compact particles, are favored by various animals according to their compactness. Clay soils are too hard for many burrowers; the rabbit, for example, does not dig readily in clay. However, many animals build their nests in clay because a certain durability is supplied by the firmness of the earth. Perpendicular clay walls are often perforated by the brood burrows of bees and wasps. Birds likewise establish their nests in such clay walls, particularly if near water, as do bank swallows and kingfishers. Since such places are limited, these birds nest together and often in such great numbers that the cliffs are riddled. The nests of bank swallows are so close together in the Transcaspian oases Pindé and Mero that there is not more than 3 cm. between them,[160] and on the banks of the Essequibo (British Guiana) four species of kingfishers (*Chloroceryle amazona, aenea, inda, americana*) breed close together in entire harmony.

Humus of more or less spongy nature is the especial habitat of the earthworms, enchytraeids, and nematode worms; nevertheless, it must not contain free humic acid. If it is especially spongy, mole crickets and insect larvae may also occur in it; however, the last are also found in sand, for example in dunes. Earthworms and insect larvae compose the greater part of the food of moles, which share their subterranean habitat. In humus and sandy humus soils pocket gophers build their tunnels; mice and voles have their runways in such soils, and the larvae of certain tiger beetles (*Cicindela*) dig round burrows in which they lie in wait for their prey. Many predatory and solitary wasps (*Cerceris, Bembex, Ammophila*) dig their brood holes in sand. In South America and in hot parts of Africa the sand flea (*Sarcopsylla*) lives in sandy areas. The ant lion (larva of *Myrmeleon*) forms its pit traps in the sand; rhagionid fly larvae of the genus *Vermileo* dig similar sand pits. Tenebrionid beetles burrow into the sandy soil of the African dune regions and in the American desert. In certain places, these sand insects determine the character of the fauna.[41] Many reptiles conceal themselves in sand, like the skink (*Scincus*) and the horned viper (*Cerastes*). Sea birds, including many petrels,

dig their brood holes in the sand of the dunes.[129] The consistency of the soil is a determining factor for the soil-inhabiting animals.

Certain non-burrowing animals are also directly dependent on the nature of the subsoil. Birds such as the barn swallow, which nest in the houses of man, are inhabitants of rocky regions in nature. The baboons are usually found in rocky regions. Petrocole hyraces live in rocky areas of southwest Asia and Africa and are fitted for climbing by suction pads on their soles. Many hoofed animals, such as chamois, mountain goats, and sheep, are animals of rocky regions; other hoofed animals (horses, wild cattle, antelopes) require at least hard firm ground that affords a good foothold for running. The speed of the runner increases with the decrease of the hoof surface on the ground; and relatively small, delicate hoofs appear to be an adaptation in this direction. The horny hoofs of such animals are adapted to great wear and are continually growing; where the animals are kept on too soft ground, like the horse on the boggy ground of the Falkland Islands, the hoofs become elongated because of lack of wear. Most two-legged jumpers among the mammals (with the exception of the tree-dwelling *Tarsius* and the arboreal kangaroos of New Guinea) are limited to firm ground. In Europe, Asia, Africa, and America these are rodents; * in Australia they are marsupials. Among birds, most of the large Ratitae (ostrich, rhea, and emu) are inhabitants of such ground. Adaptation to running is attained in these birds by the reduction in number of toes to three or even two. Many invertebrates are also limited to rocky regions; [68] rock snails such as *Patula rupestris* and many Clausilidae are examples. The mountain butterfly, *Parnassius mnemosyne,* is found in waste places that are covered with large boulders; it avoids meadows.

Looser, yielding subsoil, like sand, hinders the rapid movement of heavy animals. For this reason, it is important that their soles be wide. Deep sand is difficult terrain even for the camels with their very broad soles and long legs.[92] The white gazelle (*Gazella loderi*) and the antelope (*Addax nasomaculatus*) in the drifting sand district of the inner Sahara have broad hoofs, differing thus from their relatives. Small mammals and birds are less inconvenienced by loose sand. Even so, sand-inhabiting mammals, birds, and lizards often have fringed toes, which give them traction on the sand.

Deep snow and marshy ground also offer difficulties for larger animals. Mammals inhabiting such regions also possess a broad foot.

* *Dipus, Alactaga, Pedetes, and Jaculus.*

Tapirs, hippopotami, and pigs are hoofed animals of the swamps. The reindeer is much better adapted to such yielding ground than the true deer; spreading its broad hoofs, it runs quickly over yielding crusts and through deep snow in which a deer could not advance 50 m.[140] The European elk and its ally the American moose have large, spreading hoofs.

In the arctic hare, the soles of the feet are unusually tough and covered with spreading hair; *Lepus americanus* is called the "snow-shoe rabbit" by hunters.[67] Like their prey, the predators are also adapted to running over the snow: the Canada lynx has characteristi-



FIG. 118. Digits of lizards characteristic of sandy habitats to show parallel development of fringe-scales that give improved traction. Left, *Scapteira ctenodactyla*, family Lacertidae, of South Africa; right, *Uma notata*, family Iguanidae, southwestern North America.

cally large feet; the puma hunts deer only at times of deep snow. The webs of the feet of aquatic birds, in addition to their function in swimming, may aid in keeping them from sinking into soft mud; the webbed toes of flamingos chiefly serve this purpose.

The various types of soil differ from each other in their relation to heat. Rocky and gravelly soils on south and southwest slopes, and especially alkaline soils, are heat accumulators. The southern flora, for example, extends farther to the north and up mountain slopes on alkaline soil than on moist clay; certain plants found only on calcareous subsoil in north Germany and the British Isles are not thus restricted in milder climates.[32] Rocks and hillsides consequently form a favorable habitat for stenothermal, warmth-limited animals. The rough calcareous cliffs like those of the upper Rhine plateau below Basel and the vineyard-covered spurs of the Vosges with their calcareous soil are foci of southern life.[70]

Soil

Some direct chemical effects resulting from the nature of the soil are evident. Lime is a necessary part of the food of many animals, particularly of snails and mammals. Snails use lime for their shells,

the operculum, and the viscous mucus of the skin; mammals require lime for their bones, and male deer especially need it for the development of the annual antlers, which, in the red deer, weigh up to 8 kg. and more. Snails, as has long been known, are especially abundant both in species and individuals on limestone soils. Thus, of the 91 species of land gastropods recorded from the Basel area by 1909, 81 occurred on Jurassic terrain, 33 on Tertiary and diluvial soils, 60 on the Triassic Muschelkalk, and only 35 on igneous rock.[16] So, too, in the Solomon Islands, the land snails are more numerous in the limestone areas than in those of volcanic subsoil.[51] There has been much discussion as to whether the success of gastropods on limestone soil is directly related to the presence of lime. It has been suggested that the cause of this phenomenon lies rather in the number of fissures and recesses in limestone, in contrast to their paucity in igneous rock, and the greater heat capacity of the limestone soil. Undoubtedly, these are also of significance. It is important to note that slugs are not less common on igneous rock than on limestone. It is certain that calcareous soil is more favorable for the building of the shell. If the weight of the empty shell of *Arianta arbustorum* is compared with the total weight of the animal, it is seen that the shell is but 15–25% of the total weight on soils poor in lime, whereas it is above 35% on soils rich in lime. However, the total weight shows no dependence on the lime content.

Lime is beneficial to many mammals. The roe deer bears stronger horns in regions on lime-containing subsoil, other things being equal; body weight is also greatest on lime-rich soil. In order to avoid sources of error, it is necessary to compare roe deer from similar climates, so that other factors such as those involved in the Bergmann Rule do not enter into consideration.[62] Cattle suffer at times from brittleness of the bones in regions of igneous rock, as in the Black Forest and in Norway, because the food does not provide the necessary calcium for the proper development of the skeleton. On the other hand, the Kentucky blue grass pastures, which overlie limestone, are famous for their fine horses and cattle. Comprehensive investigations have been made for man in Germany, showing that in places where drinking water has higher calcium content than is usual, the number of sound teeth is greater, the alkalinity of the saliva more pronounced, the proportional number of men fit for military duty much greater.[125]

Lack of calcium in the drinking water seems to favor the appearance of rickets.[98] Smaller herbivorous mammals are more readily able to secure the necessary amount of calcium since the quantity of food con-

sumed is relatively greater and the weight of the skeleton relatively less than that of the larger animals. To the carnivores, the calcium supply of the ground is as truly important, even though they secure their calcium from their prey.

Some vertebrates seem to be negative to calcium. The fire salamander (*Salamandra salamandra*) is absent in central Germany on lime formations, but is numerous on sandstone, slate, red marl, and granite; the larvae cannot develop in hard water.[45]

Soil containing common salt is peculiar in its flora and fauna. It is characterized especially by a number of small beetles of the families Carabidae and Staphylinidae and by various other types of insects, which occur in widely separated regions where corresponding conditions exist, and are absent elsewhere.[50] Of the land snails, *Helix pisana* for example, in southwestern Europe as far as southern England, and *Pupa maritima* in Cuba, are limited to the sea coasts. In all these animals, nothing is known of their more intimate relations to the salt content of their habitat.

Herbivorous mammals, especially the ruminants, usually require sodium chloride; they use sodium to compensate for the large amount of potassium that they secure from their plant food.[20] Hunters and fisher folk that live on a diet mainly of flesh may dispense with salt, but not farm laborers who eat many vegetables. Natural salt licks are eagerly sought by wild animals; the so-called "bracks" in the southwestern African steppes are a gathering place for antelopes, which there satisfy their salt requirements toward the end of the dry season.[144] For many species, a large supply of sodium chloride is absolutely indispensable. According to Pallas, the Siberian fat-tailed sheep degenerate when they are kept away from certain salt meadows. The camel is dependent upon salt-containing plants; it also eats greedily the white salty efflorescence on the ground of the desert. The camel loses weight on the most fertile meadows if its needed halophytes are not available. Where salt licks and halophytes are absent in the mountains, wild camels are absent also.[92] Animals living in regions poor in iodine have the enlarged thyroid glands known commonly as goiter. In some districts, such as the region of the Great Lakes in North America, goiter is endemic, affecting other animals as well as man. Animals living near the sea are relatively free from goiter. Goiter can be experimentally controlled in young animals by regulating the supply of iodine.[69]

Another peculiarity, for which there is no satisfactory explanation, is the dependence of many animals groups upon the geological forma-

tions, a fact for which several statistical observations are at hand. According to Gadow,[44] red sandstone is most favorable for amphibians and reptiles on the Iberian peninsula; for amphibians, granite, Tertiary, Palaeozoic, and Mesozoic limestone become less favorable in the order named; for reptiles, the Mesozoic limestone takes second place and the rest follow in the same order. In Matabeleland, the elephant shrew (*Elephantulus rupestris*) occurs mostly on granite, *Nasilio brachyrhynchus* only on shale; [22] not a single species of lizard was found to be common to these two formations; there are parallel series of representative forms. These observations will deserve further discussion only when a more thorough analysis of the environment is available.

Chemical elements of more or less importance in the soil in trace concentrations include cobalt, fluorine, selenium, boron, iodine, manganese, molybdenum, zinc, arsenic, barium, cadmium, chromium, lithium, rubidium, strontium, vanadium, and perhaps lead.[19] Cobalt is usually present in the soil in concentrations of 10–15 p.p.m. or less. When present in less than 2 or 3 p.p.m., as in New Zealand, sheep suffer from a deficiency disease that can be avoided if as little as 5–10 p.p.m. of cobalt is added. Selenium occurs in all soils; it reaches toxic concentrations in those evolved from Cretaceous shales in semi-arid climates. Some plants concentrate selenium enough to give cattle eating them the "alkali disease" that is rather common in some drier parts of western North America.[101]

Plan of treatment of terrestrial habitats

The different major habitats of terrestrial animals may be grouped in the following manner: forest; dry open land (prairie, steppe, desert); moist open lands (swamps, bogs, tundra, river banks, and seacoasts); high mountain chains; polar areas; islands; caves; and cultivated lands.

The biochores are not sharply distinguished from one another, and the animal communities they harbor are not confined to them exclusively. Still, there are characteristics common to the inhabitants of each of these major types of habitat that differentiate them from every other, so that these groups of biotopes may appropriately be treated in separate chapters.

The close adjustment between animal life and the principal plant formations is expressed in the broader ecological concept of the *biome*, for the major biotic distributional complexes of the earth. The map of world vegetation (see end-sheets) is accordingly of primary impor-

tance in the discussion of the distribution of terrestrial animals [1] (see Chapter 9).

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21. *Forest Communities*

FORESTS ARE DIVERSE IN CHARACTER, AND THE CONDITIONS OF LIFE IN THE different types of forest present many gradations. Favorable climatic conditions, including a certain minimum of temperature and moisture, are required for the development of forests. If we define a forest as an aggregation of trees at least 8 m. in height, forest growth is associated with an average temperature for four vegetative months of at least +10°. Such a mean summer temperature corresponds to an annual mean of +3° in the north, where warm summers alternate with cold winters, and to one of +8° in the southern hemisphere, where the winters are warmer and the summers cooler. The southern hemisphere has no abrupt change of seasons, and deciduous forest, which is characteristic in the north temperate region, is reduced and largely replaced by temperate broad-leaved evergreen forest. In the northern hemisphere the northern limit of forest is extended along the west coast of Europe and America by warm ocean currents. The continents of the southern hemisphere, Antarctica aside, do not reach far enough toward the poles to have their forests limited by temperature, as they are to the north before the tundra is reached, or as they are by the low temperatures of high altitudes.[2]

A second condition for forest development lies in the presence of sufficient ground and atmospheric moisture. There must be a minimum rainfall of 50 mm. during each of the four chief vegetative months. On long stretches of the west coast of the Americas from 40° N. latitude to central Chile (except locally), and on the west coast of Africa south of the equator, the rainfall is insufficient to provide the necessary soil water for forest growth. Forests may be absent even where there is a rainfall of 50–100 mm. in the vegetative months, if the average humidity is less than 50%, as it is, for example, in the North American plains and the steppes of south Russia. Only stunted

trees and bushes thrive in regions where these vital factors approach the minimal requirements for forest growth. As will be shown in Chapter 22, the absence of forest in well-watered temperate regions like the high-grass prairie of North America or the Argentine pampas is not yet fully understood.

The forest itself has an influence on the temperature and moisture conditions within it. Warming as well as cooling takes place much more slowly than in open country. In the forests of north Germany the mean yearly temperature range during the course of the day is 2.1° less than in near-by fields and 3.2° less if one considers only the vegetative months. Field temperatures are lower at night than those in the forest, and rise higher during the course of the day. In the winter the heat of decay of the humus, together with the increased insulation furnished by fallen leaves, keeps the temperature of the forest floor above that of the ground in the open country; at an air temperature of $-7°$ to $-10°$, the temperature under the leaves is still $+2°$ and $+3°$ [8] and so provides suitable winter quarters for many forest inhabitants. The temperature differences between forest and open country are even more important in the tropics, where the lower strata of the forest provide a very constant temperature, while near by in the open country there may be abrupt diurnal changes.[1] Since the leafy covering prevents sunlight from falling directly on the soil, its moisture is maintained much longer; and since there is great evaporation from the leaves, a high moisture content is assured in the air. Below the forest canopy this moisture cannot be carried away readily by the winds, since the trees act as effective windbreaks. These conditions permit stenothermal and stenohygric animals of many sorts to become forest dwellers. Snails, myriapods, land isopods, amphipods, and amphibians are everywhere, and in the tropical forests there are land planarians and terrestrial leeches. Forest-dwelling reptiles have less effective adaptations against evaporation than those of open territory.[13]

The denser the forest, the less it is penetrated by air currents; winds are entirely absent in thick tropical forests of tall trees.[1] This is of importance for many forest inhabitants. Forest butterflies may have weak powers of flight without being injured by the wind. So we find that in temperate America the satyrids, many geometrids and tortricids, and that in the tropics *Morpho*, *Hestia*, and many others, are weak fliers; the strong-flying sphingids or, in the African tropics, *Charaxes*, are not excluded. Forest mammals, on the other hand, are less aided by their sense of smell than are mammals in open country.

Similarly, dense forest offers hindrances to vision. Many animals that do not secure their food in the forest come to it for concealment, and at night. The importance of the sense of sight as a means of distance orientation is decreased. For this reason, vultures, which as carrion feeders require the freedom of view of open lands, do not occur in the forest, though they frequent its borders. The sense of sight is said to be less developed in the African forest-inhabiting okapi than in the antelopes of the grasslands,[28] and the same is true for other mammals of the dense primeval forest with the exception of the apes; elephants, for example, and all species of swine permit close approach. In contrast, the sense of hearing is the most important one in the forest. It serves as a means of holding together monkey bands and flocks of birds, which call continually in their course through the woods. Birds and mammals of the forest are more noisy, in general, than those of the grassy plain.

Terrestrial mammals in the forest

The non-arboreal mammals of the forest include, besides the larger forms to be enumerated below, a series of small creatures. These are frequently inhabitants of the humus stratum, where they are protected even from the rigors of winter in the northern forests. In temperate forests the long-tailed and short-tailed shrews, *Sorex* and *Blarina,* are confined to this forest floor and barely subterranean stratum, and with them are found various rodents such as the pine mouse *Pitymys,* the red-backed mouse *Evotomys,* the lemming mice *Synaptomys,* and the partly arboreal ubiquitous white-footed mice of the genera *Peromyscus* in America and *Apodemus* in Europe. Certain moles may inhabit the forest, like the star-nosed mole of northeastern North America. In the tropics numerous small rodents inhabit the forest floor; and shrews of the genus *Crocidura,* in Africa and in the Orient, replace the familiar *Blarina* and *Sorex.*

An important selective factor in the forest habitat lies in the fact that rapid locomotion is prevented. The larger mammals are especially impeded. Of large mammals, only the elephant, buffalo, okapi, wild hog, and leopard occur in the African rain-forest; all the remaining hosts of large African mammals are limited to savanna or to open country. Movement in the dense forest requires certain adaptations; strength and weight of body, short limbs, and a wedge-shaped head are effective in moving through undergrowth. Antlers and horns are little developed among forest mammals in the tropics. The small buffalo and the rare forest antelopes of the Congo have strikingly

small horns. Antelopes characteristic of the African forest region include the bushbucks (*Tragelaphus*) and the bongo (*Boocercus*). In general, ungulates in thick forest are small; species of *Nesotragus* and *Cephalophus* live in tropical forest and are able to wind through the dense underbrush; the forests of Chile shelter the dwarf deer, *Pudu humilis,* which is only 34 cm. tall; the dwarf musk deer *Hyaemoschus* of the African tropics and *Tragulus* of the Asiatic tropics are true forest dwellers.

The arboreal habit

The animals of the tropical rain-forest are characterized by great development of the arboreal habit. This is particularly noticeable among vertebrates. In the densely forested New Guinea and in northern Queensland, kangaroos of the genus *Dendrolagus* have developed this habit despite the fact that their structure is not adapted to living in trees. The arboreal habit imposes certain size limitations that are particularly striking among mammals. Climbing not only involves great muscular effort for large animals, but the branches and vines offer inadequate support, so that swinging from tree to tree, so easy for a monkey, may become impossible with increasing size, and the gorilla, largest of the apes, is mainly a ground dweller. Of the three species of American anteaters, only the smallest is completely arboreal, whereas the largest is entirely limited to the ground.

Climbing mechanisms are varied among arboreal animals, but numerous convergent adaptations can be discovered. Sharp claws are often present among climbing birds, mammals, lizards, or insects. In the neotropical sloths, the claws have developed into powerful hooks. Many tree-dwelling vertebrates have developed opposable toes. The tree frogs of the ranid genus *Chiromantis* of West Africa have two opposing digits of the hand,[49] while both inner finger and inner toe are opposable in the neotropical *Phyllomedusa;* chameleons and a few other lizards have opposable digits on fore and hind feet. Many birds, notably woodpeckers, have two toes permanently turned backwards; others can so turn a second toe at will. This allows a stronger hold upon branches than when but one toe is so turned; parrots furnish a further example of a bird group with two toes directed forward and two backward. Among mammals the thumb and the great toe are opposed to the other digits of the hand and foot, respectively. Didelphidae among marsupials have only the hind feet modified for grasping; Phalangeridae have the hands modified also, which of course is conspicuously true of the monkeys.

The presence of sucking disks on the feet or digits is a widespread adjustment for climbing. Such disks are well-developed and evidently independently evolved in various families of frogs and toads, especially in the Leptodactylidae, Hylidae, Rhacophoridae, and Ranidae. Adhesive organs on the feet of geckonid lizards are elaborate and varied from genus to genus. The bat genera *Thyroptera* from Brazil, *Tylonycteris* from Southeastern Asia, and *Myzopoda* of Madagascar have suction disks variously developed. *Tarsius* has expanded finger tips, and such diverse forms as the tree porcupines *Erethizon* and *Coëndu,* the tree coney *Dendrohyrax,* and the Japanese macaque *Inuus speciosus* have adhesive pads on the soles of their feet. Tree-dwelling snakes tend to become elongate, a tendency which is also shown by the arboreal agamid lizards of the Old World and by the unrelated iguanid ones of tropical America.

Some heavy-bodied snakes, such as the vipers and pit vipers, have developed prehensile tails in the tropics of both hemispheres; chameleons and a few other lizards are similarly supplied. The prehensile tail has been developed independently by many different sorts of arboreal mammals. In its typical form, a prehensile mammalian tail is free from long hair and is hairless at the tip; the bare area is provided with sensitive ridges like those of the palm of the hand, which aid in giving a sure grip. Usually these are on the ventral side, but in an arboreal mouse (*Pogonomys*) of New Guinea [27] and in the American tree porcupines [14] they are dorsal. Prehensile-tailed animals are especially abundant in heavily forested regions of South America. There oppossums, arboreal anteaters, numerous rodents, kinkajous, tree porcupines, and many, though not all, monkeys have prehensile tails.[26] African and Asiatic monkeys lack the prehensile tail, but other Old World groups of mammals have it, for example, the climbing marsupials of Australia, some scaly anteaters, certain mice, and the binturong *Arctictis* of the Sunda Islands.

Climbing mammals, most primates excepted, tend to have relatively short posterior legs; thus the ground-dwelling hares among rodents, and the Indian cheetahs and the serval among cats, have long limbs in comparison with related climbing forms. Comparatively long hind legs are characteristic of animals of the plains; some jumping animals with elongated hind limbs that have taken to arboreal habits, like the tree kangaroos (*Dendrolagus*) of New Guinea, are clearly secondarily arboreal. Other arboreal forms, like many lemurs and the tarsier, may have elongated hind limbs as part of their primary adjustment, to judge from the extraordinary agility of some diurnal Madagascan

lemurs. When locomotion from branch to branch by swinging from the arms (brachiation) becomes highly developed, as in the New World spider monkeys and the Old World gibbons, the arms are much longer than the hind limbs.

Parachutes have evolved among diverse arboreal animals, and, flying animals excepted, are not found elsewhere. The essential principle involved is the development of rigidly supported membranes that enlarge the under surface of the body and permit gliding flight. Lizards of the genus *Draco* have elongate ribs for the support of broad membranes. Parachuting mammals may have extensive membranes connecting the legs. Such membranes have evolved independently in the marsupials, among the squirrels, and most notably in the so-called flying lemur, *Galeopithecus*, of the Malay region, in which they extend to the throat and to the tip of the tail. In ordinary squirrels, the bushy tails are flattened and partially serve the same purpose. The presence of these gliding adaptations in forest animals has led to the speculation that the flying habit originated among such vertebrates in the forest.[10]

A great number of predatory beetles whose relatives elsewhere are terrestrial are arboreal in the Amazonian forests and have developed arboreal adaptations, particularly in foot structure. Thus a tree-dwelling group, the Odontocheilae, has evolved among the usually ground-inhabiting tiger beetles Cicindelidae. The larvae of the Odontocheilae burrow into twigs instead of into the soil. In the Amazonian forests these are four times as abundant as are the tiger beetles proper.[25] Ants frequently establish themselves in trees and even make paper nests there in the tropical rain-forest. Such forests furnish food and shelter for tree frogs, for leaf- and wood-feeding insects and their larvae, for snails that range to the topmost branches, and, in the Philippines, lay their eggs in leaves folded together for their protection[9] (Fig. 119). The great majority of the known species of frogs of the family Hylidae are from the American tropical forests, and the family Rhacophoridae is equally characteristic of the forests of Africa and the Malayan region. Among birds woodpeckers are infrequent outside forest regions and are absent, for example, in Egypt.[23] The curassow (*Crax*) and the hoatzin (*Opisthocomus*) have retained the primitive bird foot with the hind toe no higher than the rest.

In densely forested tropical regions, arboreal mammals predominate over terrestrial forms, a statement supported by the analysis of the mammalian faunae of Trinidad, Borneo, Sumatra, and New Guinea. The insectivores as a group are largely arboreal in the

tropics.[36] Monkeys and squirrels are characteristic forest animals; of the latter Siam has 26 and Borneo 31 species.[18]

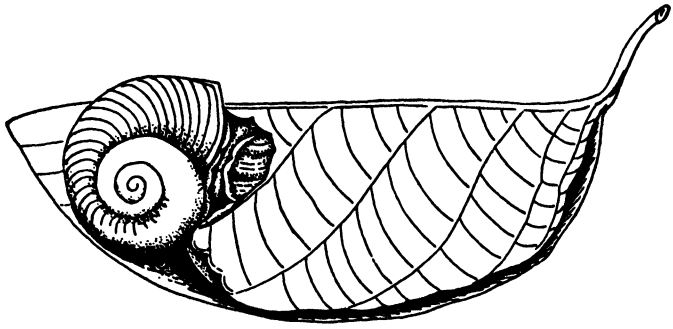


FIG. 119. Deposition of eggs by *Helicostyla leucophthalma*. After P. and F. Sarasin.

The forest margin

The depths of the forests are relatively poor in animal life, much poorer than the open country. Forest margins, which make a transition zone, or ecotone,[2] between the two, are richer than either. Under these conditions the advantages of both communities are available, and their disadvantages are compensated. The forest furnishes a hiding place for terrestrial mammals during the day and a resting place at night, while the neighboring grasslands supply food. In continuous primeval forests of the North Temperate Zone, such animals as deer and wolves are more abundant in a belt 5–8 km. wide near the forest edge.[17] In Java deer, wild boar, and leopards lie concealed in thickets during the day and feed in the open at night.[22] The forests bordering the African grasslands afford food and shelter during the dry season for antelopes, buffaloes, rhinoceroses, and elephants. The flying foxes (*Pteropus*) sleep among the forest trees and fly out in search of food. This is a common habit among birds, which can range far from their sleeping places in search of food. Isolated forest islands in the Asiatic steppe are crowded with the nests of eagles, falcons, rooks, and other birds that feed on the steppe.[31]

The forest is a refuge for man as it is for other animals. The camps of the American Indians were pitched along the forest margins. More primitive peoples still seek shelter within forests from powerful aggressors—witness the pygmies in Africa and Malaysia.[46,47] The forest is not only a center of refuge from more powerful enemies; it is also a refuge from climatic extremes. The relatively constant humidity

and the reduced temperature variations permit a survival in forests of northern Europe and of the United States of species that occupied open country in glacial times; thus the modern German snail fauna in the forests resembles that of non-forested Lapland and north Russia.[8]

Forest types

The botanist recognizes a variety of forms of forest that are of importance to the student of animal geography as the matrices for distinct animal communities. Animals clearly react to the following:

I. Forests characterized by broad thin leaves.
  1. Evergreen; tropical rain-forests.
  2. Deciduous.
    a. With alternating dry and wet seasons.
    b. With alternating warm and cold seasons.

II. Forests characterized by broad thick leaves; sclerophyll forests in regions of winter rain.

III. Forests characterized by narrow thick leaves; coniferous forests.

The tropical rain-forests

A vast forest girdle encircles the earth between the tropics, extending across northern South America, central Africa, parts of India and the Malay peninsula, the East Indies, and northern Australia. This rain-forest reaches its largest continuous extent in South America, where half the continent is covered by a tropical rain-forest, approximately 4000 by 3000 km. in extent. These rain-forests vary greatly in different regions, being affected by the height above sea level, the character of the soil, the regularity and amount of rainfall, and the amount of insolation, all of which effect the species of trees to be encountered in any particular fraction of this world forest. Despite these differences, there is an astonishing similarity throughout this tropical region with regard to the general growth form, the luxuriance of the vegetation, and the great multiplicity of species among the trees present. Conditioned by these factors one finds reduced illumination, high and relatively constant humidity and temperature, a lack of air currents, and, along the margins or around openings, a maximum of impenetrability. As might be expected from these conditions, the animal life of the tropical rain-forest is distinguished from that of other world communities not only by its species composition but also by its internal relations.[24, 30a]

The tropical rain-forest presents a vertical series of strata availa-

ble for animal occupancy, which suggested Humboldt's description of forests above forests and Marston Bates' comparison with the sea.[4] The lower strata may be poorly developed in the subdued light of the forest interior. The stratification found in the rain-forest in Panama illustrates the characteristic structure of such forests, although the width of the different strata and their distance from the ground may vary from place to place.[2,32] For Panama [1] we distinguish the following strata:

8. The air above the forest (not permanently occupied by any species).
7. Trees extending here and there above the main forest roof, 125 ft. or more high.
6. The upper forest canopy, 75–80 ft. high.
5. Lower tree tops, 40–60 ft. high.
4. Small trees, 20–30 ft. high.
3. Higher shrubs, 10 ft. high.
2. Forest floor and low herbs.
1. Subterranean stratum.

Animal life in tropical rain-forests is much affected by the fact that, unlike forests in the temperate zones, there is an astonishing number of different species of trees within a small area. Even in temperate mixed forests barely 10–15 species of trees are present, while uniform stands of oak or beech and maple or pine may stretch for miles. On the other hand, 400–500 species of trees and some 800 species of woody plants have been described from the Cameroon forest; seldom do two specimens of the same tree stand side by side, and fruit-bearing trees are usually widely separated. More rarely the stands are uniform, as when palms dominate a low-lying region to the exclusion of other types. In the usual mixed forest of the tropics some trees may be losing their leaves while others have a fresh foliage; still others may be in blossom while fruit hangs ripe on the neighboring tree. Only in such a forest can stenophagous, nectar-feeding or fruit-eating forms exist the year round.

The leafy canopy casts a heavy shade that prevents grass from growing within the denser types of forests and limits grass-eating animals to non-forested regions or to the forest margin. Brilliantly colored animals, birds in particular, disappear in the leaf and branch tangle of the tree tops and appear gaudy only when one has the animal in hand. The dense vegetation retains the internal forest moisture and makes for such constancy of temperature that it rarely falls below 21–22° or rises above 28–29°.[45] Such hothouse air is in marked contrast with that of the open tropical grasslands and, together with

other factors in the forest environment, makes forest-dwelling mammals tend to be smaller than neighboring varieties from the open country. Thus the tapir of the Guiana forests is smaller than that from the savanna; [38] and the forest buffalo and the leopard of Africa are relatively dwarfed forms.[19] The same tendency is dimly discernible among the human inhabitants.[35]

At first sight, the tropical rain-forest, with its luxuriance of plant life, appears discouragingly impoverished in animals. This results in part from the hiding of the animals behind the tangle of vines, trunks, roots, and branches or from the fact that they live unnoticed in the high forest canopy, or, indeed, on the forest floor. Frequently, if adequate trails are lacking, one must rely on hearing rather than sight for evidence of the presence of animal life. Many of the mammals, including some monkeys, move about the forest mainly after sunset. During the day, silence may reign, a stillness that some travelers describe as oppressive, although the monotony is broken now and then by the cry of a bird, the passing of a noisy flock, the humming of a swarm of bees, the calls of a group of monkeys, or the chattering of squirrels.

In or near the clearings produced naturally by the crashing of a giant tree, by streams, or at the natural forest margins, where uniformity ceases, where air movement is increased, where light penetrates and temperatures fluctuate, life becomes astonishing abundant. No place offers a richer insect life than does a recently cut forest clearing. Here the butterflies may appear in clouds; metallic golden buprestid beetles, magnificent cerambycid beetles, gay hemipterans, and hymenopterous insects are abundant. A collector may take more species in a month in such a locality than in a year in the depths of an undisturbed forest.[18]

It is in such places that the traveler experiences the many-voiced, ear-deafening nocturnal concerts of the tropical rain-forest. With the sudden approach of darkness, as if by command, various Orthoptera burst into a chorus of sharp metallic sounds; various tree frogs join; [42] flocks of parrots and parakeets settle noisily into their nesting places; and in America, the voices of the howling monkeys add to the uproar. In places this evening music increases at sundown to become an inharmonious roar of life such as Humboldt described on the upper Orinoco.[20] Later the larger animals become quiet, and only the concert of the insects and the tree frogs continues during the night. With the approach of dawn comes another period of noise. Orlando Park [2] describes these choruses for Barro Colorado Island in quantitative

terms. The harsh voices of birds of the tropical forests appear to be developed as group or species signals replacing visual stimuli as a method of group integration.

Within the forests, the invertebrates are generally well hidden. Worms, snails, millipedes, centipedes, scorpions, isopods, spiders, and insect larvae retire under loose bark or decaying logs or into the axillae of palms. Land planarians crawl into the ground during the day, and peripatus lives during the drier periods well buried below decaying logs or stumps.

Land leeches not only live on the ground but also climb bushes, whence they attach themselves to warm-blooded animals.[44,48] Of forest insects the bugs (Heteroptera) are abundant; among Orthoptera, blattids, mantids, phasmids, and locustids are well represented, whereas crickets and acridid grasshoppers that dominate the steppes are relatively less important. In the interior of the forest, mosquitoes, mites, and wood ticks attract attention by the annoyance they give the collector. Ticks penetrate the scaly skin or even the horny carapace of a turtle and obtain blood. The earth-dwelling bumblebees are entirely absent and are replaced by forms that make their nests in wood or hang them from the branches.

Termites, which are prominent in savannas, are also abundant in tropical rain-forests. Their nests, found in all strata of the forest, are made by cementing together soil or woody particles, and are connected to the ground by covered passages through which the termites travel. In particularly rainy regions the nests of some species are equipped with ridges that carry off excess water. Termites are especially important in the forest economy because their wood-eating habit greatly hastens the decay of woody materials. They share, with the similarly social ants, the insect dominance of these forests.

Ants are to be found everywhere in the tropical forests. Many species are entirely arboreal; the American *Azteca,* with more than 70 species, is so limited. These are to be contrasted with the leaf-cutting but subterranean nesting *Atta* and with the driver or army ants, which roam through the forest in hordes, putting to flight all animals able to escape. Like termites, ants exhibit a great variety of nests.[12] The ground nesting habit is less common, since, as with other forms, there is a general moving upward into the shrub or arboreal strata. Cavities in trees and branches are much occupied; paper carton nests hang like stalactites from branches. *Oecophylla* in the Indo-Malayan forests and *Camponotus* in Brazil use their spinning larvae to fasten living leaves together into a nest (Fig. 120).[51] The *Eciton* ants of the

American forest make their nest from their own living bodies, which, when the time comes, disentangle and move off with the horde through the forest.[5, 37] Certain arboreal ants have established epiphytic plants on their tree-top nests, especially bromeliads, gesneriads, and aroids, thus making the so-called flower gardens of the ants. Many ants live in special cavities, internodes, hollow thorns, etc., of specially adapted ant plants that provide food for them in addition to concealment. This has been interpreted as a return evolved by the plant for the protection supplied by the ants.[6]

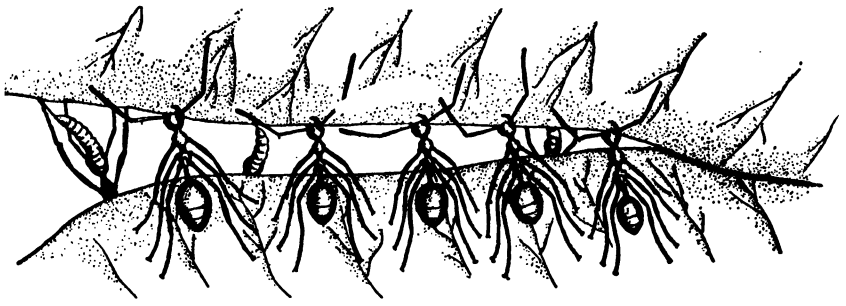


FIG. 120. Row of workers of the tropical forest ant *Oecophylla smaragdina* drawing the edges of leaves together while other workers use the silk-spinning larvae as tools to bind the leaves firmly with silk. (From Wheeler, after Doflein.)

The warm air constantly saturated with moisture makes the tropical rain-forests a paradise for frogs and toads; slender forms from many families are almost entirely arboreal in habit, so much so that they do not descend to deposit their eggs in water as is the usual habit for amphibians. Certain of them, such as *Rhacophorus* in the Old World and *Phyllomedusa* in the New, lay their eggs in leafy sacs on branches that overhang water, into which the larvae fall on hatching. Frogs of the genus *Eleutherodactylus*, with more than a hundred species in tropical America, glue their large eggs to a leaf, place them in the axils of leaves, or conceal them beneath stones. The young go through a curtailed metamorphosis in the egg and hatch in adult form. Still other frogs carry their eggs about until the young emerge as adults (Fig. 121).[49] Many of these species have seldom been seen and the number of individuals is estimated principally by the many-voiced chorus of the males after sundown.

The relatively abundant [11] but mainly voiceless reptilian life of these forests attracts still less attention. Aquatic or semi-aquatic forms may usually be seen along watercourses. Forest lizards belong

principally to four groups, chameleons, geckoes, agamids, and iguanids. The chameleons have grasping feet and prehensile tails and are found in greatest diversity in the forests of Madagascar and Africa. The agamid lizards, confined to the Old World, and the iguanid forms, found mainly in the Americas, although sharply separated in anatomical characters, have parallel series with astonishing similarly compressed bodies. Both families have ground-dwelling, riparian, and arboreal forms. In both families arboreal forms have long tails and are laterally compressed, whereas the ground forms have relatively short tails and dorsoventrally depressed bodies. A few veranids enter the rain-forest in the East Indies. Snakes are not so conspicuous in these forests as would be expected from many popular accounts; but the extremes reached in their adaptation to arboreal life attest their important rôle in the forest canopy.

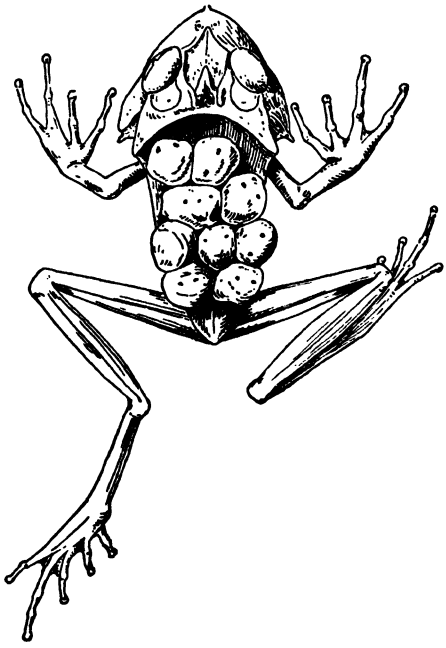


FIG. 121. Female of the tropical American frog *Cerathyla bubalus*, carrying eggs attached to her back. After Boulenger.

Birds are the most striking inhabitants of the tropical rain-forest and are present in all its strata. Since they are largely diurnal, their richness of form and color stimulates interest as does the variety of their habits. The birds of the upper forest seldom if ever come to the ground; they are accustomed to slipping between the tangled branches, but may have relatively poor powers of flight and are limited to forested regions. Parrots, with stronger flight, may be seen outside the forest, though they are characteristic of the forest crown. Ground birds also exist, usually smaller in size and dull in color, but conspicuous because of their raucous voices. Wood hewers in South America search over the tree trunks like our common creeper.

Forest birds frequently combine into groups when not in the breeding season; these groups may be composed of many species and even

of different genera.[3, 43] This sociability may be correlated with the search for food; thus among the birds of the tropical forest there are many fruit eaters, parrots, doves, toucans, hornbills, musophagids, cotingids, and others; and the isolated forest trees with different times for maturing fruit compel birds to roam from one to another. Hordes of birds collect in trees with ripe fruit. Such flocks as wander together are oriented with regard to each other by their loud voices.

The woodpeckers are the most striking of the insectivorous birds. They are particularly abundant in the American and Indian tropical forests, while Africa has relatively few. The ground birds eat mainly insects and are entirely characteristic of the shaded tropical forests, whose moist dimness is essential to them, so much so that they are sometimes called "shadow birds." [41] Birds of prey are sparingly encountered within the forest; nectar-feeding hummingbirds are abundant.

The scarcity of mammals in the forest appears greater than it actually is, because, with the exception of apes and squirrels, the majority are nocturnal and hide during the day. Thus one may wander for months in the Cameroons without seeing a single river hog, although tracks show that these animals are constantly about.[40] The same is true of forest antelopes of Africa and of the tapir in America.

The South African wild pig is an important animal of the wooded regions; it extends out of the tropical rain-forests proper into other forests; moist forests are occupied, whether montane or lower lying, particularly if water and ferns are present. The pigs go about in droves and defend themselves well. They are nocturnal and follow trails made by elephants, getting food from the faeces of the latter and from roots and trees that the elephants have dislodged. Baboons follow the wild pigs and obtain scorpions, earthworms, and insects turned up by the pigs, and eat roots and the like that they have missed. Pigs root up the soil to a depth of several inches, eating buried seeds, roots, rhizomes of ferns, and insects but not much bark or foliage. They take also fruits of forest trees, the seeds of some of which resist digestion and are scattered. Although there are large numbers of wild pigs in favorable forests and they are dependent on the forest for food, the damage done is negligible and is more than offset by their work in improving the seed bed and in keeping insects in check.[34]

As in other groups, the majority of mammals of the tropical rain-forest are arboreal and seldom set foot on the ground, and must

therefore be relatively small. One thinks of monkeys as the prominent arboreal mammal of such regions, yet, at least in Old World forests, squirrels supply a greater number of species. The social habits and noise of the monkey hordes make them noticeable to the ear, though not all with such vehemence as the howling monkeys (*Alouatta*) of America, whose bull-like bellowing fills the forest at sunset or when a passing airplane awakens them. The majority of monkey species belong to the warmer forests of the world, and, like other arboreal animals, they are structurally adapted to arboreal life. Many are frugivorous and move through the forest canopy from fruit tree to fruit tree.[50] The American monkeys differ markedly from those of the Old World in important anatomical characters, but are essentially ecologically equivalent.

Ground-dwelling jungle mammals are able to climb trees without being predominantly arboreal. Gorillas belong to this type, but their great weight and size limit their climbing. Jaguars, leopards, small cats, scaly anteaters, various rodents, and many insectivores ascend trees on occasion.

Ground-dwelling mammals tend to be small stealthy forms that wind their way through the forest; such forms include the smallest of all ungulates, the tiny, primitive musk deer *Tragulus*, and the forest goat antelope *Nemorhoedus* of the Malayan region, and *Hyaemoschus* and the dwarf forest antelope *Cephalophus* of Africa. In South America these are replaced by the ecologically equivalent agoutis and many other rodents and by the pig-like peccaries. Certain large African animals such as okapi, swamp antelope *Tragelaphus*, striped antelope *Booceros*, and the dwarf hippopotamus, have similar habits. The elephant stands out in contrast as a forest wrecker, moving through the forest by sheer strength. Hippopotami, rhinoceroses, buffaloes, lions, leopards, and even hyenas, as well as forest pigs and baboons, use the elephant-made trails, leaving them yet more passable for other animals. The tapir represents this type of trail-maker in the American jungle. Many of these animals are active principally at night.

Tropical rain-forest changes gradually into gallery forest limited to river courses and projecting far into grassland and steppe regions, producing the savanna type of country. Typical forest forms disappear and are replaced by the teeming life of the forest margins. The tropical forest overhanging rivers also deviates from type in many particulars, especially in the scarcity of tall trees, whose giant size cannot be supported in the yielding alluvial soil, and in the increased

density of the forest canopy. Unlike gallery forests, such river bank forests exhibit a decrease in terrestrial and an increase in arboreal types, although in tropical America tapirs and peccaries are characteristic inhabitants. Ground birds tend to be absent, though finches, icterids, and flycatchers, characteristic of grasslands, invade the river bottoms. Water and shore birds, ibises, kingfishers, herons, and storks enter this habitat *via* the river highway [41] (see Chapter 23).

The characteristics of animal populations of forest lands are shown to best advantage in the tropical rain-forest. The further the forest deviates from these conditions—i.e., the less dense the tree trunks, the lighter the forest crown, the more sparing the underbrush, and the richer the growth of grass, the more light penetrating to the ground, the greater the air movement, and the more limited number of species of trees—the fewer are the forest-limited animals present. Arboreal habits give way to semi-arboreal ones, and the number of invaders more characteristic of the open grasslands becomes greater. These changes may be evident even in the tropics, particularly in regions of monsoons, where well-defined dry and rainy seasons alternate, and in mountains with their more extreme conditions. The differences become still greater in temperate and cold regions. The height of the trees diminishes until, at the timber line, whether at the tundra or on mountains, a man may look over the tree tops to the horizon.

Bears are absent in the dense tropical forests of Africa and South America, and though some species occur in the Malayan forests they are more common in the less densely forested temperate regions. Deer, which are not characteristically forest animals in the tropics, invade the temperate forests. In Asia a few monkeys and the tiger are found in forests north of the Himalayas. The species or genera of animals in the northern forests become more similar on the two sides of the Atlantic, or better, on the two sides of Bering Strait; these faunae are taxonomically more clearly related than those of the different world divisions of the tropical forests.

An expanded account of the animal life of the rain forest, intended especially as an amplification of Hesse's section devoted to this biochore, is presented by Mertens,[30a] and the reader is referred to it for a vivid and well-illustrated exposition based largely on personal knowledge. The distribution of animals in their biotopes within the forest; the inanimate environment; body form and locomotion dependent on rain-forest conditions; food supply; cryptic and mimetic

coloration and form; and societal relations are some of his chapter headings.

Cloud forest

The characteristics of lowland rain-forests are modified in various respects, especially in the great increase of epiphytes, in the cloud-forests of tropical mountains and mountain ranges that extend into or through the cloud zone. Cloud formation is produced by condensation of water vapor in the upwardly deflected winds, and a cloud zone is thus especially characteristic where on-shore winds (like the trades) reach a mountain range not far from the sea coast. Thus an even more humid atmosphere at considerably lower temperatures is characteristic of this zone, and everywhere in the tropics this finds its reflection in characteristic amphibian faunas and in other moisture-limited animals. Larger mammals may often range upward into cloud-forests from the adjacent rain-forests below. Bird life is usually sharply distinct in the two zones.[4a, 36a]

Animal communities of temperate deciduous forests

The more typical temperate forest mammals are certain deer, the pig, squirrels, flying squirrels, dormice, martens, wildcats, and lynxes. The more striking animals of these forests are ground dwelling and cursorial, like wild boar, red deer, and roe deer. Badgers and foxes are at home along the forest margin. Wolves range out into the neighboring grasslands, obtaining concealment in the forest.

Woodpeckers, nuthatches, thrushes, certain hawks, and owls find their food even in deep forest. Many warblers and vireos are forest birds in North America. As in the tropics, many other birds are to be found in the forest margins, including ravens, the black stork and herons in Eurasia, and crows, cardinals, flickers, and brown thrashers in America.

The reduced number of species of trees is far less critical for higher vertebrates than for other animals, especially for those forms that approach stenophagy. There are mammals and birds that are confined to the temperate deciduous forests and are absent in the coniferous ones.

Temperate deciduous forests are forests of broad thin leaves that have a cold winter season. These differ from tropical forests in that they are located in higher latitudes with a mean annual temperature of 10°–20°. The rainfall is from 75 to 150 cm., approximately equally distributed throughout the year. The ratio of rainfall to evaporation

varies from about 80 to 130%. Such forests are less luxuriant than the tropical forests and lack the low underbrush except in openings or near the borders. They are also deficient in lianas except in the lush river valleys where, in North America, trumpet vine, wild grape, and five-leafed ivy grow luxuriantly.

The distribution of these forests depends on moisture, temperature, and soil. In the main they occur in the moderately moist southern part of the temperate zone but are not well developed in sandy or peaty soil. Specifically, such forests occur in the United States mainly east of the Mississippi River except for evergreens in the Appalachian Mountains and a southeastern belt of conifers; in Eurasia they occupy a belt from northern Spain to southern Sweden, west through Siberia into Japan. These forests are mainly replaced in the temperate zone of the southern hemisphere by an evergreen broad-leaved forest, the sclerophyll forest.

Stratification of the deciduous forest is less complex than that of the tropical rain-forest. In eastern North America the forest is varied with walnut, oak, hickory, and tulip, and many other more southern types, and the more northern birches, beeches, and sugar maples, sometimes locally intermixed with hemlock and other conifers.

Many of the terrestrial mammals of the North American deciduous forests have subterranean dens; among these may be mentioned red fox, gray fox, skunk (an invader from the tropics), chipmunks, and shrews. Wapiti (the American counterpart of the red deer), bison, Virginia deer, and beaver formerly ranged throughout; only the deer and a few beaver remain. Muskrat, beaver, otter, and mink belong to the forest near streams; the cottontail rabbit, the jumping mouse, the raccoon, and the burrowing woodchuck, *Marmota monax*, live in the forest margin. Squirrels, flying squirrels, and bats compose the arboreal animals. In all, Seton [39] lists 13 species of mammals that are mainly arboreal, 18 that belong to the ground stratum, and 3 that are mainly burrowing forms. The arboreal opossums and porcupines in North America are unrepresented in Eurasia.

Among birds, the great horned owl, several hawks, the great crested flycatcher, various thrushes, and woodpeckers are characteristic of the north temperate forest in America. Turtles are present around the forest ponds and streams, and the black chicken snake, a constricting species, may drape itself over bushes along the forest margins. The timber rattlesnake and the copperhead are the common poisonous snakes. Salamanders of the genus *Plethodon* lay their few large-yolked eggs in moist places under decaying logs. Tree frogs and

Rana sylvatica are also characteristic inhabitants. The invertebrates of such forests include burrowing earthworms, millipeds, snails, and land isopods of the forest floor, a restricted termite fauna, and wood-boring larvae of various insects, especially beetles, and leaf-feeding insects of various sorts of the shrub and tree strata. The larva of one of these, *Papilio ajax,* a butterfly, is monophagous, feeding on the leaves of the pawpaw, a shrub or low tree with tropical affinities.

In the temperate forests of southern South America the antarctic beech is the principal tree. The forest is damp and mossy. Darwin's fox, the dwarf deer known as the pudu, *Rhyncholestes,* a representative of the primitive marsupial group Caenolestidae, and several genera of frogs are confined to this region. The tiny Darwin's frog *Rhinoderma darwini* has a remarkable life history, in which the eggs with already well-developed and active embroyos are taken into the greatly enlarged vocal sac of the male, where they grow and transform, emerging from the parent's mouth as fully developed froglets.[33]

The European deciduous forests have been much under the influence of man, and even where they have been left intact in extensive stands they are by no means primeval on account of having been long maintained as hunting preserves and by the practice of scientific forestry. In England in olden times bears and wolves were present; wild cattle hid their young in coverts and grazed in the open.[52] Animal life apparently approached that in similar regions in America. The wild boar, absent in America, ranges the forests of Europe and Asia.

The tiger is found in the birch forests of southern Siberia. Its absence in Ceylon and Borneo is evidence that it has only recently crossed the Himalayas into the tropical regions in which it is now so much at home. A monkey, *Simia speciosa,* lives in temperate deciduous forests of Japan.

As the forests are cleared by man, only the forest margin animals remain in the scattered groves and fence rows; of these the burrowing forms are most likely to persist. The climate that produces the deciduous forest is a stimulating one for the white man; the soil is suitable for varied crops, and the climate is favorable for both northern and southern types of domestic animals. In fact, this region in America now supports more cattle and sheep per square mile than are found in the semi-arid regions where they are more conspicuous.[15]

Animal communities of coniferous forests

The evergreen coniferous forests extend as a broad belt between the tundra to the north and the temperate deciduous forests to the south, throughout the northern land masses. There are southern extensions along the mountains and regions determined by soil or moisture in other sections, as in the southeastern United States. The present account will deal with the geographically extensive world belt, known as the northern coniferous forest or taiga. The northern limit is set by the summer warmth; the southern depends on rainfall, absence of drying winds in winter when the ground is frozen, and character of the soil, which favors the growth of conifers if peaty or sandy. The leaves remain on the trees the year around; the trees often bear nuts, berries, or seeds that are present above the snow for animal food. The coniferous trees provide more shelter than the deciduous hardwoods.

The coniferous forest is particularly liable to forest fires and has been so in all ages. Now as in preceding periods they may be started by lightning. The effects produced are of importance to forest animals, since berry bushes of many sorts grow in the burnt-over areas and provide much food. Willows and birches are common along streams, and poplars occur locally (also after fires), so that the forest is not completely monotypic. Lianas and creepers are absent.

Many animals of the deciduous forests extend into the northern coniferous zone. The most important mammals are deer, rodents, and carnivores, with a few bats and insectivores. Contrary to usual opinion, deer are increasing in numbers in this region in America since man has been holding the wild carnivores in check, and probably there are more moose, caribou, and mule deer in these forests now than when the white man first came. The distribution of many of these animals is determined almost as much by the distribution of their feeding grounds in forest openings as by the conifers themselves.

Ungulates living in tropical rain-forests are mostly small with laterally compressed bodies enabling them to slip through the tangled plant growth. But those of the coniferous forest are large, often with spreading antlers in the males, suggesting that they may have only recently moved into the forest. In both Canada and Eurasia one finds the representative caribou, reindeer, moose, and elk. These are mainly forest-browsing forms that eat twigs, leaves, berries, nuts, lichens, and mosses, grass being a less important food. All may range southward, but they find their best development in this belt. The woodland

caribou are larger than the barren-ground form of the tundra to the north, being better fed and better protected.

The important rodents are the squirrels, beaver, varying hares, and Canadian porcupine. This last is largely arboreal, although it nests on the ground. These northern forests show a paucity in true cats, which are abundant in tropical forests. An abundance of members of the weasel tribe replaces the tropical cats and civets. Bears are characteristic, although they occur elsewhere. In both America and Siberia one finds lynxes, wolves, foxes, martens, gluttons, weasels, minks, and badgers. The Asiatic tiger contrasts with the American puma, and neither the European wild cat nor the wild dog, *Cyon,* of Siberia have close relatives in America. The skunk is absent in Europe. Siberia has a brown bear in place of the American black bear; in addition there is the American grizzly bear in western North America.

The absence or scarcity of snakes makes for safety for birds, as does the absence of monkeys and other arboreal tropical mammals. Weasels and other mustelids take a heavy toll. Among birds especially abundant in the northern coniferous forests are grouse, grosbeaks, crossbills, woodpeckers, nutcrackers, and Jays, with a host of migrants of other groups in the nesting season. The black woodpecker *Picus* and the common green woodpecker *Gecinus viridis* are characteristic in the forests of Eurasia. The three-toed woodpeckers of the genus *Picoides* are circumpolar in the coniferous forest, as are the less exclusively northern spotted woodpeckers, of which the American downy and hairy woodpeckers are representative.

The Amphibia are represented by a few Hylidae, which are more numerous in America; in Eurasia they barely reach the coniferous belt. True frogs (*Rana*) range into the taiga in both hemispheres.

Insect life is rich. In Asia wild bees reach the Arctic Circle; in America they penetrate only into the southern part of this forest. Conifers are much more vulnerable to insect attacks than are beeches and maples. Repeated complete defoliation is fatal. Beetles are important pests from the viewpoint of the forester. Burrowing bark beetles are killed in healthy trunks by the rise of sap, but after repeated attacks, aided perhaps by injuries from wind, snow, and ice, the beetles may establish themselves and kill many trees.[21] Wood wasps, *Sirex gigas,* pine sawflies, *Lophyrus pini,* pine geometrids, pine processionary caterpillars, *Cnethocampa,* and others often attack in masses with severe results. Termites, the pests of the tropics, are absent.

Animals of the northern coniferous forests exhibit two types of

migration. In the spring comes the great northward migration of birds that nest in the north woods, and in the winter, with their departure, there is the great migration from the north of caribou, of arctic hares, and, to some extent, of arctic birds, which overwinter in the forest.

This northern coniferous forest is the great fur-producing region of the world.[29] The finest furs come from the north, where dense hair coats are produced as a protection from cold; from near fresh water, where furs take on an attractive sheen; and finally from wooded areas, which protect the luster from being faded by sunlight. Otter, weasel or ermine, mink, marten, fisher, sable, and wolverine, belonging to the family Mustelidae, supply the finest of all furs; and the staple supply, of only slightly less fine quality, is afforded by the beaver and muskrat, though these extend far to the south. In the main the fur supply is decreasing, although closed seasons and protection of females and young are preventing extermination.

Like the tropical forest, coniferous forests spread into temperate grassland along river courses, and such gallery forests, like tropical savannas, are relatively rich in animal life. The outer edges of such forests advance or retreat as climatic or biotic conditions favor or retard the growth of trees. Animals influence such changes more than is generally appreciated. Thus in England forest margins advance where rabbits are carefully excluded, whereas neighboring unprotected regions are stationary, and in Manitoba in the poplar parkland region, after a year of unusual rabbit abundance, such as commonly occurs in 9- or 10-year cycles,[30] the majority of small trees along the woodland margin are killed by rabbits.[7]

At the climatic limits of forests, whether in the far north or in mountains, the trees become dwarfed to mere bushy thickets, which may, however, extend for miles. In polar regions such forests consist of scrub spruce, dwarfed birches, willows, and alders, often no higher than three feet and frequently so light in stand that one can readily make his way through them. Arboreal creatures are absent. Such dwarf forests, however, serve as nesting sites for a large bird population; the birch siskin is as characteristic of the dwarf birch forests of Iceland as is the crossbill of the conifers.[16]

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49. Werner, Franz, 1912–1913, "Lurche und Kriechtiere." *Brehms Tierleben*, 4th ed., 2 vols., illus. (vol. 1, p. 333).
50. Weyers, J. L., 1895, "Oiseaux et singes des forêts de Sumatra." *Rev. biol. nord. France*, 7:132–138.
51. Wheeler, W. M., 1926, *Ants, their structure development and behavior.* N. Y., Columbia Univ. Press: xxv, 663, 286 figs.
52. White, Gilbert, 1875, *Natural history and antiquities of Selborne.* London, Macmillan: xxx, 591, illus., 1 map [orig. ed., 1789].

all the phenomena appear that depend upon their fluctuations. The reduced moisture of both soil and atmosphere in the grasslands, which must be regarded as one of the main causes of the disappearance of the forest, and the irregular distribution of rainfall during the course of the year, are of importance to the associated animal life. Relatively small amounts of precipitation are characteristic of extensive plains, which may become very hot in summer, and such regions absorb moist air masses without the cooling necessary for precipitation.

Although water relations generally condition the type of vegetation, this generalization cannot be applied unchanged as an adequate explanation of the existence of all glasslands. Despite much study, it is impossible as yet to account for the extension of the tall-grass prairie as a great peninsula through Illinois and northwestern Indiana. This region has many climatic characteristics similar to those in the woodlands into which it penetrates. Possible causal factors given to explain the presence of such grasslands include (*a*) a drier period in former times; (*b*) the continuing high ratio of evaporation to rainfall at least during parts of the year;[68] (*c*) the effect of fire; (*d*) poor drainage on flatlands, leading to excessively wet soils at times and the exclusion of swamp trees by drought effects in dry years or seasons; (*e*) soil modifications; (*f*) the probability that mycorrhiza are necessary for some forest trees and that these fungi are not present in grassland;[76] (*g*) the excluding effects of an established species to a potential invader.[14]

The concentration of the small amount of rain within limited and often short periods affords temporarily favorable conditions for plant and animal life. There is great danger even for well-adapted animals in the irregular recurrence of rains and in occasional unusually prolonged droughts. During the dry winter of 1863, whole herds of wild animals were destroyed in the South African steppes.[33] During the great droughts in the pampas along the La Plata, both domestic animals and the native species die, thousands of pampas deer (*Odocoileus bezoarticus*) among others; in certain parts of India, ten years or more are required after a drought to restore the full numbers of native species.[20] Parts of northeastern Brazil and of the plains of North America are conspicuously subject to disastrous drought of this kind.[45,65]

In general, only animals that tolerate dry air are best adapted to the conditions of open country. Animals that require moist air, such as snails, isopods, and amphibians, are not entirely absent; but they do not attain great numbers of species and individuals, and their

occurrence may depend on special adaptations or on local conditions. On the other hand, a large number of reptiles and insects thrive in the open country, especially insects with incomplete metamorphosis such as many hemipterans and grasshoppers, which are easily able to survive on account of their independence of rain and their toleration of high temperatures. Birds survive in dry areas because their powers of flight bridge the stretches between water supplies and because in the main they are sparing in their use of water.

Mammals are principally represented by forms relatively independent of water, either because of the slight development of the cutaneous glands (rodents), concentrated urine (antelopes), dry faeces, or all of these. Many rodents, a large number of antelopes, the aardvark, and many armadillos (e.g., *Dasypus minutus*), may survive for months without drinking; for these the limited water taken with their plant and animal food, together with the water produced in the processes of metabolism, is sufficient to satisfy their fluid requirements. Camels are able to get along for five days, even ten to twelve days if necessary, without water. Elephants, except for herds with young calves, need to came to water only every two or three days. Many ungulates, like the zebra and white-bearded gnu (*Connochaetus albojubatus*), do not hesitate even to drink alkaline water, such as is found in many steppes; indeed they thrive on it.[61] On the other hand, rhinoceroses, water buck (*Cobus*) and reedbuck (*Cervicapra*), monkeys, and even rabbits usually need water to quench their thirst daily. Many mammals of the steppes have a keen sense of smell for moisture. Distant rains in the South African veld cause a migration of wild animals, and elephants are attracted from a distance of 100 km. by the first downpour of the wet season.[67]

Temperature and winds

A universal characteristic of open country is the fluctuation of temperature, particularly from day to night but often also between summer and winter. There is no protecting leafy roof to ward off the rays of the sun by day, nor to prevent radiation by night, which is further favored by a cloudless sky. In the Cameroon savanna, a midday heat of nearly 40° C. in the shade is followed by a night temperature of 3°; indeed, in the Sahara a night frost of −5° following even higher day temperatures may occur, and in southwestern Africa, fluctuations of 40° within 24 hours are not unknown. In the Arizona deserts, sudden wind changes may bring temperature rises of 36° within 8 hours. In high Tibet, midday heat reaches almost 40° in summer,

and the winter temperature may descend to −37° and lower. There is, therefore, no place for surface-dwelling stenothermic animals in such regions, and even eurythermic forms like the homoiothermic birds and mammals need protection against the extremes of heat and cold. This is especially true in open plains and deserts where there is little or no vegetation shelter from the direct rays of the sun. Studies of the temperatures of desert and other reptiles have shown that these creatures keep within a rather narrow range mainly by moving about in their environment.[18]

Air currents have a free sweep in open lands. Winds and storms, which are seasonally frequent, drive unhindered over the level or rolling land, at times with terrific force; they carry along dust, sand, or snow, and may carry off even full-grown sheep. The furious winds of the African and Arabian deserts, the sand storms and sand hurricanes of the Transcaspian, and the blizzards and tornadoes of the North American plains are notorious for their destructive effects. There is no protection against them in open lands.

Finally, there is little cover, which is important to herbivores as protection from predatory animals and to carnivores in stalking their prey.

The burrowing habit

The extremes of temperature, wind, and visibility explain the relative prevalence of burrowing animals in open terrain. In underground burrows, or merely within the soil or sand, such animals are assured of protection against heat and cold, against storms, and from many predators. The fluctuation of temperature at the surface decreases progressively, until at a depth of 0.5 m. the soil temperature approaches the average annual temperature of the region. The soil, even at moderate depths, is considerably cooler in summer and warmer in winter than the surface. Thus burrowing animals find protection against the heat of the day and the coldness of the night, against summer heat and winter frost. Many animals of the steppes close their burrows during the day against the penetration of heat,[33] just as the hibernating marmot (*Marmota bobac*) does regularly to ward off the winter cold.

Ants and termites of open lands belong primarily among the burrowing animals. The ants, whose nests rise in high, loose mounds on the ground in the forest or hang free from the boughs of the trees, build their nests in open country under stones or burrow deep into the soil. The surface mounds disappear, the more the region is exposed to winds; in meadows and grassland, earth mounds are built up above

the subterranean part of the nest; in deserts, the entire nest is in the soil, and the wind very quickly blows away the sand mound formed about the entrance during the building of the nest. In tropical and subtropical forests, termites burrow out the trunks of trees or build carton or earth nests on the branches in addition to their subterranean nests. In open tropical savannas they burrow into the ground and overlay their burrows with lasting, resistant structures built from the

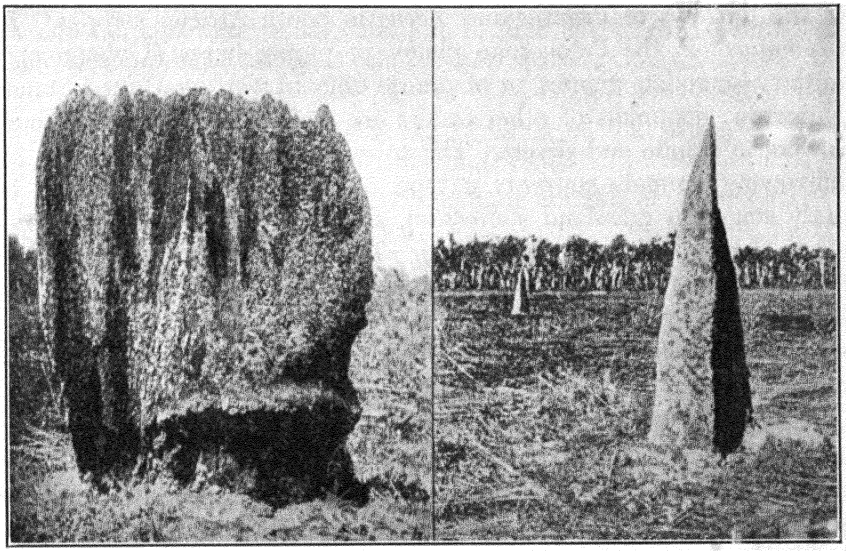


FIG. 122. "Compass nest" of an Australian termite, from Port Darwin, North Australia. After Saville Kent.

excavated material with the help of their excretions; these hillocks are able to resist wind and weather because of the hardness of their walls and are well insulated in the innermost parts by the numerous air chambers. The shape of the nest may be adjusted to insolation, as in the so-called compass nests in northern Australia, which are long, narrow, and high, and without exception have their long axis directed north and south, so that a reduced surface is turned toward the strongest rays of the noonday sun, whereas the wide flat surfaces are exposed to the rising and setting sun (Fig. 122). The whole arrangement makes for temperature stability.

Burrowing is common among reptiles of open country. Tortoises like *Testudo horsfieldi* and various monitor lizards (*Varanus*) are able to burrow even into the driest loam. Many snakes burrow in the soil

and have modified snouts, shortened tails, and other characteristics in adaptation to this habit.

Rodents are the most numerous burrowing mammals; rodent burrowers are found in all parts of the world and are often structurally similar because of similar modes of life despite remoteness of relationship. They dwell side by side in suitable places in the open country in such numbers that the ground is undermined over wide stretches. Saddle horses are constantly endangered by the caving in of the burrows of *Pedetes* and *Xerus* in South African steppes,[33] of *Ctenomys*[4] in the Patagonian plains, of piping hares (*Ochotona*)[57] in the Mongolian steppes, or of prairie dogs in western United States. Numerous mammals of other orders are included in the list of burrowers in steppe and desert. The subsoil brought to the surface by burrowing animals supports a type of vegetation characteristic of early stages in grassland succession, and hence extensive burrowing alters the appearance of grassland. The ground excavated by such burrowing activities is spread by winds and may form, as in the Kalahari, a sand layer of 0.5–1.0 cm. in depth.[56] The soil as a whole is modified by the opening of the substrata to ready penetration by air and water.

A large number of birds nest on the ground, such as larks, bustards, and gallinaceous birds; if there are no groves or rocks, even large birds of prey like the eagle nest on level ground.[52] The hardships of winter and the drought of summer influence bird migration. Burrowing habits are also found among birds, a number of which breed in holes in the ground in open country, though they seldom prepare burrows by their own efforts, but tend to use the abandoned burrows of rodents or occupy the same hole with them. The burrowing owl, *Speotyto cunicularia,* may prepare a nesting hole in the ground; it does this, for example, both in Uruguay and in the savannas of Guiana,[63] but where opportunity presents itself, it enters into a tenant relationship with rodents and is found as an inhabitant of the abandoned holes of the prairie dog (*Cynomys*) on the plains of North America and in those of the viscacha in the pampas. Two small birds live as tenants in the burrows of the South American viscacha, the mud dauber *Geositta cunicularia,* which builds its own brood nest in the steep entrance of the burrow, and the swallow *Attycora cyanoleuca.* The burrows of the piping hare in high Tibet are used by three small species of finches (*Montifringilla*), and many other examples could be given.[36]

The cursorial habit

Tree trunks, underbrush, tangled roots, dead trees, lianas, aerial roots, and all the barriers opposing free movement of animals in the forest are absent in open country. Many animals of open terrain develop great speed and endurance in their movements, which are the more to their advantage as there are fewer hiding places. The stimulus to such evolution is greater, the more open the countryside, the greater the temperature variation from summer to winter, and the scarcer the watering places. Because of their speed, such animals are able to escape their enemies, to traverse daily great distances to water, and to migrate from summer drought and winter frost. This swift-moving element in the animal communities of the plains contrasts strikingly with the burrowers discussed above.

The frequent occurrence of quick-moving animals in open country is striking among reptiles. The lizards of the steppe regions are for the most part slender, very active, and agile, like the species of *Eremias* in Africa, and *Callisaurus* in the southwestern United States. Slender and swift types of snakes are characteristic of such regions.

Among the birds of open country, such as larks and many gallinaceous birds, cursorial habits are much more important than among forest dwellers; at the same time there are unusually skillful fliers, like swallows and sand grouse. Speed in running has undergone extreme development in birds of the plains, often even at the cost of flight, as among larger forms. Emu, rhea, and ostrich are all birds of the open plains and are convergently transformed by increase in size, atrophy of the wings, strengthening and lengthening of the hind limbs, reduction of the number of toes, lengthening of the neck, and degeneration of the feathers.[12] Many carinate birds of the plains have also adopted the running habit. These include the road runner of southwestern North America, the secretary bird of Africa, the desert jay of the Asiatic plateau, and, conspicuously, the bustards of the Old World and the tinamous of the New. Among these, the secretary bird has only recently taken up running, as is shown by the fact that the young are slow in developing the habit. Many plains birds with excellent powers of flight do not take to the wing until pressed.

Mammals have contributed the principal cursorial types. The most outstanding runners are horses, asses, and zebras; camels and also giraffes may be numbered with them. The greater number of antelopes, and among these the swiftest types, inhabit open country. The North American prongbuck is a typical cursorial animal. Many preda-

tory animals of open country are long-limbed and thereby adapted to fast running, particularly the wolves, the Cape hunting dog *Lycaon,* the South American maned wolf *Chrysocyon,* and the long-limbed cats such as the serval *Felis serval,* caracal *Lynx caracal,* and cheetah *Acinonyx.* Measurements of the speeds of such mammals have been summarized by Howell.[39]

Jumping animals, with long hind legs, are also characteristic of open country. Twelve genera of kangaroos with more than forty species are found in the plains of Australia, together with a large number of species of rat-kangaroos and mouse-like jumping marsupials.[71] Jumping rodents have convergently assumed the bipedal form of locomotion, although they belong to quite different groups, in the savanna regions of other continents. Such jumping mammals are characterized by an enormous development of the hind limbs and tail and an atrophy of the forelimbs. The African jumping hare (*Pedetes*) among the hystricomorphs, and among the myomorphs the Australian jerboa rats (*Conilurus*), the Old World Dipodinae (*Jaculus, Alactaga*), and the North American Heteromyidae (*Dipodomys, Perodipus*) have evolved this form of locomotion. It is difficult to understand what advantage this affords the smaller forms; Spencer [66] believes that their zigzag, ricocheting movements aid them in escaping predators. In South America, where the rodent fauna is varied and abundant, this rodent type has not been evolved; the hare-like viscacha, though with long hind-legs, retains well-developed forelegs and is essentially a runner rather than a leaper.

Sight is of great importance in open country, and we find both mammals and birds that are especially keen of vision. Many species habitually survey their surroundings; rodents sit up on their haunches to look about, like the prairie dog, *Cynomys;* kangaroos and hares have this habit. The flashing white of the buttocks of the prongbuck serves as a signal from great distances and from herd to herd. Despite the importance of vision, the sense of smell is even more vital to mammals of the grasslands. Sound, though of secondary importance, is audible at greater distances than in the forest and may serve to orient steppe animals, which make use of warning signals like calls and whistles. In general, however, birds and mammals of the plains tend to be quiet, as they are able to keep together by sight; and noisy groups, like troops of monkeys and flocks of parrots of the forests, are infrequent.

The flocking habit

It is particularly striking that animals congregate more often in herds in grasslands, much more so than in the forest. The digging rodents and the ungulates are usually found in large companies. Rodents of the same species have their burrows close together, often over wide stretches. Bison, yak, antelopes, and guanacos live in herds. Several species of antelopes may mix freely in the same herd, and zebras associate with these, just as the kulan (*Equus hemionus*) of central Asia feeds in company with various wild sheep, Tibetan antelope, and the yak. Ostriches often join such herds in Africa, and guanacos and rheas are found together in Patagonia. Kangaroos, too, are gregarious. Many carnivores, which are ordinarily solitary, occur in packs in the open country, as do jackals and hyenas; indeed, even lions hunt together in what are thought to be family groups. Among the birds of the open country, the formation of flocks is common, as among the emus, rheas, and ostriches, the bustards, and partridges. Sand grouse of the genus *Pterocles* live a solitary life in the Kalahari desert, but during the flight to watering places come together into flocks that contain up to sixty thousand individuals.[56] Although certain survival values are evident, there is still no completely satisfactory explanation for such gregariousness.

Animal communities of savanna and steppe

The amounts of atmospheric moisture and of rainfall, the duration of the dry season, the nature of the soil, and the number of grazing animals are together decisive for the development of vegetation in open country. Reserving the terms arid and xeric for the extremes of dryness reached in true deserts, the contrasting savannas and short-grass plains may be referred to respectively as subhumid and semi-arid.

Tropical savanna includes the savannas of tropical Africa, the grass wildernesses of the East Indies, the llanos of the Orinoco region, and the Amazonian campos. There are numerous modifications of tropical savanna with transitions, sometimes by very uniform gradients, into the drier steppe, characterized by shorter grasses that still tend to form continuous sod. In the African Sudan (extending from Senegal to the upper Nile) there is a complete gradation from the rain-forest border to the Sahara. The temperate analogues of tropical savanna are the high-grass prairies of mid-continental North America and the Argentine pampas.

Steppe, in the sense of geography and climatology, includes those extensive dry areas with sparse vegetation, in which, however, grasses are still characteristic and tend to form areas of sod, the vegetation being adjusted to a longer or shorter annual rainy season. An extensive, more or less continuous belt of steppe in the subtropical and temperate zones extends around the earth in the northern hemisphere, with an analogous series of widely separate steppe areas in the southern hemisphere. The northern steppe belt includes the high and low steppe of central and southwest Asia, with an extension into south Russia that continues into Hungary, and a broad connection through Asia Minor and Syria with the North African and Sudanese grasslands. In North America "steppe" is commonly referred to as short-grass plains, and includes the Great Plains, part of the transition to the high-grass prairie, and parts of the Great Basin. The southern hemisphere has great steppe areas in Australia and South Africa, with the somewhat less extensive Patagonian plains in South America.

Interspersed in the steppe belts and areas lie deserts of varying extent, characterized by a minimum of precipitation and plant growth. The north African steppe passes gradually into semi-desert to the south and into the Saharan extreme desert. In North America, every transition from grassland to desert is to be found in the Great Basin and in the Sonoran region of the southwest. Such transitions are equally evident in South Africa with the Kalahari and southwest African coast, in Patagonia east of the Andes with interior deserts at the north, and in the Australian grasslands with the central desert area.

Steppes are even more varied in type than are savannas. They are found in subtropical as well as temperate climates, at low levels as well as at high altitude. The vegetation does not attain the luxuriance of the savanna grass areas; all gradations are present, from knee-high to short grass, which may even be broken by more or less wide stretches of bare ground. With the grass are found many kinds of flowering plants, plants with root bulbs, poppy, thistle, and low woody plants such as *Artemisia,* which may predominate. Where such flowering plants are wanting, one naturally misses the pollen feeders and nectar-sucking animals such as bees, butterflies, hawk moths, and noctuids. In many steppe areas, e.g., in the South African or Asiatic steppes or in the western United States, there are stretches where the soil is rich in salts and supports only a sparse growth of halophytes.

On the plains the abundance of animal life depends directly on the density of the vegetation, all parts of which serve as food for animals,

whether as just sprouted seedlings, ripe, hardened stems, dried, stiff, and often thorny stalks, leaves, seed, and fruit, or roots and tubers. To work up such food, strong masticating apparatus is necessary. Grasshoppers and termites possess powerful, efficient mandibles. Rodents and ungulates are equipped with front teeth fitted for clipping vegetation and have strong molars with broad roughened crowns for grinding; in rodents, rabbits (Fig. 123), and horses, these rear teeth are adapted for long, heavy use by the capacity of continued growth. Grain-eating birds, such as sand grouse and weaver-birds, grind such

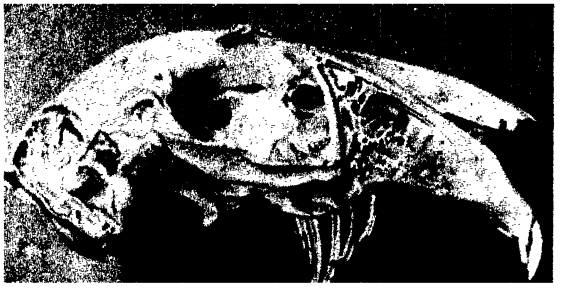


FIG. 123. Skull of a hare, with abnormally elongate molars, resulting from lack of use and wear.

food by means of their muscular gizzard. These grass and grain feeders constitute the key industry animals of the fauna of the steppes. The food interrelationships of such a community are suggested in Fig. 124 for the aspen parkland region in Manitoba.[10]

For the most part, steppes proper are entirely treeless. Where trees occur, they give a varied character to the formation. Thus at Kilimanjaro, one may recognize fruit-tree steppes and acacia steppes, to which the bush steppes join; the high campos of the Amazon are comparable with fruit plantations. With even isolated trees, arboreal animals come into the steppe, introducing an element foreign to grasslands proper. Tree-nesting birds, which find abundant food in the steppe, nest in large numbers in such trees. There are weaver-birds and other seed-eaters in the African steppe, and ovenbirds with their mud nests in the Patagonian plains.[40] Eagles, hawks, rooks, and others are closely packed into the forest islands of the Siberian steppe.[48]

Of arboreal types of mammals it is mainly monkeys that range into the steppe, either as residents in the islands of trees, like the howling monkeys in southern Brazil, or as permanent ground-dwelling steppe

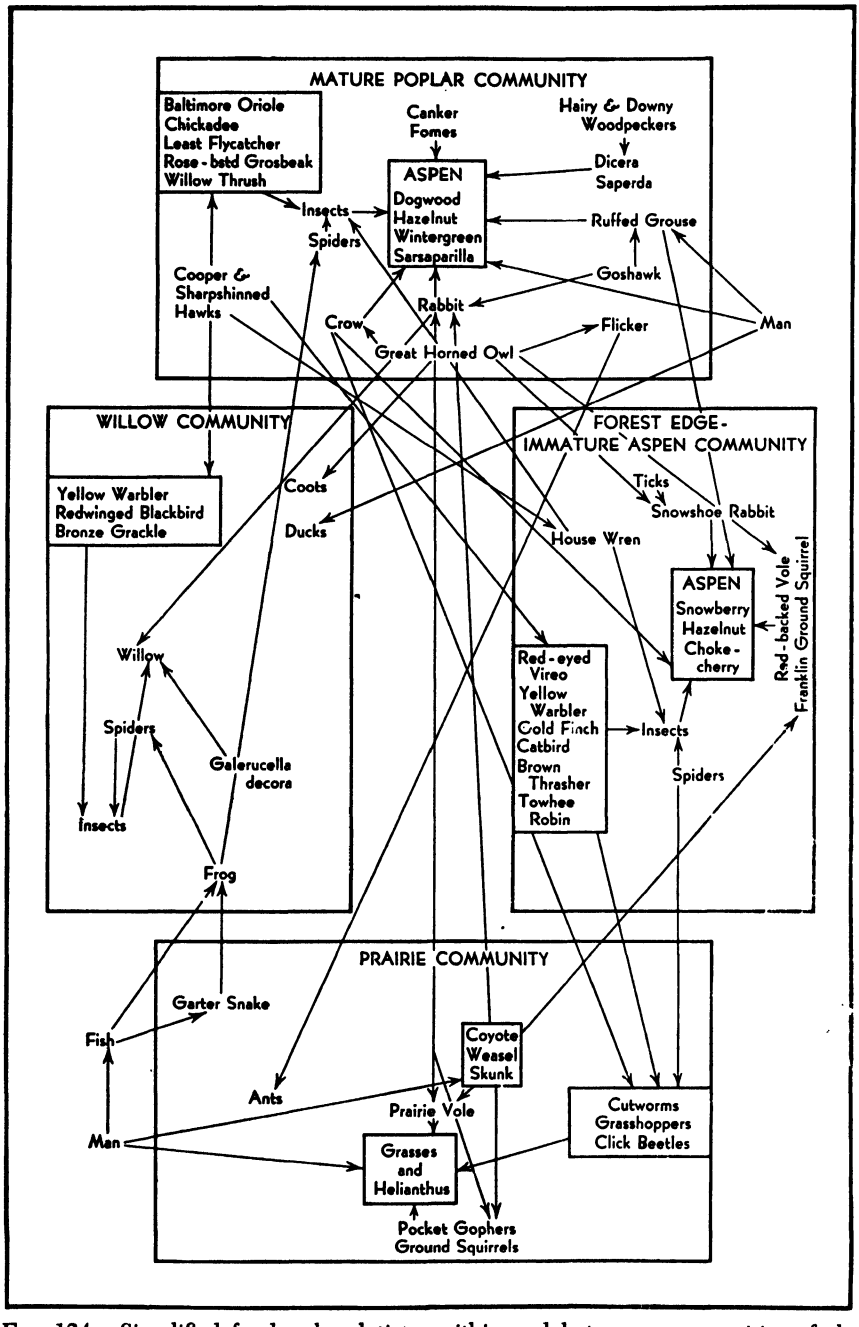


FIG. 124. Simplified food-web relations within and between communities of the aspen parkland region of Manitoba. The arrows point toward the food of indicated animals. From Allee after Bird.

inhabitants, like baboons in Africa. Many mammals seek the isolated trees of steppes for shade at mid-day.

The conditions of life during the favorable season are of less significance for the organization and relationships of the animal population of the grassland than those during the least favorable season. Whether there is a dry open winter or a snowy closed winter makes a significant difference. Tropical and subtropical grasslands and steppes have the former, the grasslands of the North Temperate Zone have the latter.

The dry season produces an apparent reduction of life everywhere in grassland and steppe; the blazing heat of the sun is as detrimental as frost. Many insects and reptiles and all snails and amphibians aestivate; many mammals like the African aardvark pass the unfavorable season in this manner. The Columbian ground squirrel of northwestern United States combines aestivation with hibernation, retiring to its burrow in August and emerging in late February or early March.[64] Some animal life remains active. Termites and ants survive heat and drought, finding enough moisture in the deeper parts of their subterranean nests.[32] Other insects and spiders may be found under stones; small and dull-colored grasshoppers occur under dried brush. A number of species of reptiles remain active. The number of birds is somewhat reduced by migration, but birds are by no means absent in the dry season. Like the mammals that remain active, they find food in the stems and seeds of the great amounts of dry grass.

The chief problem for birds and mammals is the water supply. Succulent plants and juicy fruits may satisfy the liquid requirements. In the llanos, *Cactus melocactus* serves to quench the thirst of mules after they have knocked off the thorns with their hoofs.[41] Large herds of antelopes and zebras of the South African steppes live on melons (*Citrullus coffer*), which are juicy and green just at the beginning of the drought; later, they scrape juicy tubers out of the ground.[56] Elephants and kudus chew out the juice of the bowstring hemp (*Sansevieria*) in order to secure water.[61] Mammals gather at watering places, at permanent springs, at pools that have not yet dried up, at the remnants of ponds and lakes, even about brackish water. The more limited the watering places, the greater the assemblage of animals. Some stay in the immediate vicinity; others range to greater distances. Monkeys never wander farther than 4–6 km. from water; rhinoceroses, waterbucks (*Cobus*), and reedbucks (*Cervicapra*) keep close to water; and in the Australian steppe the small finches *Taenio-*

pygia castanotis are indicative of the nearness of water. The elephant, however, travels 30 km. or more from water, and the Namaqua sand grouse may live 175 km. from any body of water. At the water holes, there is an astounding amount of animal traffic. At dusk and during the day, birds are the principal visitors, many in flocks that darken the sun; the mammals come particularly by night, herbivores and carnivores, singly, in troops, or in herds.[67] Even well-filled springs with an abundant flow may be entirely emptied during the night.[6]

When the springs are exhausted and the last pools have dried in the steppe, difficult times ensue for mammals; they must then migrate and seek new habitats that offer more favorable conditions. Domesticated animals are equally dependent on water, and their owners are compelled to wander with their herds in search of it. The migrations of steppe mammals are usually regular; such migrations are carried out by zebras, antelopes, and ostriches; and the carnivores—lions, leopards, and hyenas—follow them. At times, however, in especially rainless seasons, such migrations may end in tremendous catastrophes. In the winter of 1863 in South Africa, duiker antelopes (*Cephalophus mergens*) perished by thousands, often, driven by hunger and thirst, coming to the vicinity of human habitations, even into villages.[33] Regular migrations of tropical birds may be associated with the dry season; thus a number of species of African birds are known to come to the eastern Sudan at the rainy season for breeding; [38] the sun bird, *Nectarinia famosa*, lives in the Karoo from December to April and in the Knysna and East London areas from May to November.[62] The subject is reviewed by Chapin [15] for African birds.

With the first rains, the vicissitudes of the dry season are over. In a surprisingly short time the grass shoots forth, the trees and bushes become green and blossom, and the animal life changes accordingly. The wild life, which was assembled at water holes, scatters widely over the steppe; with fine scent, it detects distant rains and is drawn to them. In places where a few weeks before immense numbers of antelopes, elephants, and zebras were present on the South African steppe, they disappear, and at this season the large herds divide into flocks and families.

The aestivating animals reappear. One hears the croaking of frogs everywhere, and their oviposition quickly begins in recently formed pools. Tadpoles hatch after an astonishingly short interval and grow at a surprising rate under favorable conditions, for the water is warm and affords abundant food; it teems with crustaceans, especially phyllopods, and contains numerous insect larvae. Enemies are also pres-

ent in abundance, such as predaceous water beetles that prey upon the tadpoles, and various water birds, which appear like magic as soon as the rain falls. The surviving frog larvae shortly are ready for metamorphosis, and, if the brief rainy period comes to an end, may bury themselves in the mud for aestivation as young frogs.[66]

The winged sexual forms of the termites and ants rise in clouds from their nests. Butterflies emerge from their pupae. Gnats and flies whose larvae develop in the water are soon present. The grasshoppers (acridids) hatch in large numbers from eggs, which had been laid in the soil and may have lain there for several years until the degree of moisture necessary for development is reached.[32] A gay swarm of flying insects (Hymenoptera, beetles, Diptera) gathers on the flowering trees. The shorter the rainy season, the more the development of insect life is compressed into a short period. A single species of beetle may suddenly appear in enormous numbers, only to disappear after a few days to be replaced by another.[23] Snails, too, are awakened by the moisture and come forth to feed on the revived vegetation.

Conditions are different in the high steppes with cold winters such as those of the North Temperate Zone—in southeastern Europe, central Asia, and North America. In these steppes the dried grass is covered with snow, and decays. All snails, insects, and spiders, all amphibians, reptiles, and small mammals hibernate. Many burrowing rodents remain active but feed on their stored food supplies; hamsters (*Cricetus*) in Eurasia and ground squirrels (*Citellus*) in both Eurasia and North America store grains and other food material. *Ochotona dauricus,* of the Asiatic steppes, gathers haystacks up to a weight of 10 kg. in the vicinity of its burrows. Birds, which were for the most part summer visitors, have disappeared; but in the Gobi region, where little or no snow falls, larks and buntings overwinter in spite of temperatures as low as −37° if sufficient grass seed and other food is at hand.[57]

Large mammals are less affected by cold; they have a relatively small surface and may have an enormously thick winter coat of fur. They eat twigs and dry leaves, and scrape dry grass, lichens, and moss out of the snow. The bison of the North American plains, and the yaks and feral camels of the highlands of Tibet, defy the winter. Many mammals are nevertheless compelled to migrate. Antelopes and wild asses (*Equus hemionus*) leave the wintry Gobi, not on account of the amount of snow, but because the water is frozen; thirst, not cold, forces them to depart. The prong-horned antelope of North

America migrates to places where grazing is good, often many hundreds of kilometers distant, and overwinters there in large herds; the open plains are made well-nigh uninhabitable for them by the snowstorms. The bison herds in the nineteenth century moved southward in winter, though without getting out of the range of winter snows, and northward again in summer. Through use during innumerable years, the "buffalo" paths in places became almost as deep as the animals were tall. Vast numbers of bison existed on the Great Plains, up to the time of the building of the transcontinental railroads. The great number of skulls and other remains of bison found in northern Colorado and Wyoming are thought to be the remains of herds that perished in blizzards.[34] Now all have been exterminated by man save an insignificant remnant that is holding its own under human protection.[1]

After a snowy winter in the steppe, there is a slow revival in the animal world as well as in the plant world, quite different from the overnight awakening following the breaking of the dry season described above. The temperature rises slowly, grass and herbs spring forth, the hibernators awaken, insects develop, the migrating mammals and flocks of birds return.

A comparative survey of semi-arid grasslands shows that in small steppe areas, like those of Spain, characteristic steppe animals are lacking, though a number of characteristic plant forms have developed. The inhabitants of such areas are species from the surrounding regions that are able to live in the steppe, which is there characterized only by the severe selection of the animals and by the mass appearance of individual species that are also distributed near by.[49] Only in regions with large steppe areas in the vicinity is there invasion of typical steppe animals from the larger into the smaller.

In general, the fauna of semi-arid regions shows about the following composition:

Aquatic animals are the scarcer, the more temporary the bodies of water. Forms with a short developmental period and a resistant, quiescent stage are the most common; hence the large number of phyllopod species in the steppe. Many more species of these crustaceans are known from Australia with its extensive arid regions than from well-investigated Europe, which is one-fourth larger; almost one-half of all the known phyllopod species come from Australia and Africa together.[77] Not uncommonly, a number of genera occur side by side in the same pool, e.g., *Limnadopsis, Limnetis,* and *Estheria;*[66] the smaller the species, the more numerous they are, for their developmental

period is so much shorter. With them are found aquatic insects and insect larvae such as water beetles, water bugs, and especially gnat and mosquito larvae.

Of hygric animals, only a few are able to subsist in arid, open country; they appear in decreasing number of species as the environment varies from grassland to desert. The snail fauna of the steppe is impoverished, for only species occur that can endure a long quiescence during drought, sometimes more than a year. Within the same species, this ability may vary according to the locality; *Helix lactea* in the Sahara may awaken from an aestivation of several years; individuals of the same species from Madeira are dead after a like number of months.[30] The llanos of Venezuela have a relatively rich snail fauna; [11] in the North American prairies, however, they are limited mainly to the tree-grown banks of the rivers.[2] The pampas are almost lacking in mollusks,[14] and in central Australia snails are very uncommon. All these snails have bright-colored, whitish, rather thick shells; the stronger the shell, the greater is their resistance to the drought. Desert individuals of widely distributed species of snails, such as *Helix pomatia*, are much thicker shelled than typical specimens and tend to lose their color bands.[17]

Amphibians are few in species in the steppe, and all are burrowers. During the short moist period they must accumulate a food surplus (fat), and many Australian frogs (*Cheiroleptes, Heleioporus*) also store a water supply; individuals distended to the shape of a lemon have been found, and investigation showed that the urinary bladder was filled with clear water.[66] The natives know how to find these frogs in their hiding places and use this water in time of need.

Insects of the steppes

Insects are found in enormous numbers. Even during the dry season, they are not absent in grassland and steppe, though their number is much reduced. Three groups are predominant, grasshoppers, ants, and, in the tropics and subtropical areas, termites. At times they have a major influence not only on the organization of steppe life, since they afford a basic food supply, but also on the landscape.

Grasslands are richer than other biochores in grasshoppers, most of which belong to the family Acrididae. Many related groups rich in species and individuals are represented. It has become customary to refer to gregarious acridids as locusts, whether members of nymphal hopping bands or of mature winged swarms. In contrast, the popula-

tions consisting primarily of more solitary individuals are called grasshoppers.[72]

Migratory locusts with myriads of individuals inhabit the steppes of all continents, being more common in semi-arid regions. Examples include the migratory locust *Locusta migratoria,* which is widely distributed in the warmer parts of the Old World and is notably present in the Caspian basin and eastward; the Moroccan locust *Dociostaurus maroccanus* from the Mediterranean region and Transcaucasia; the desert locust *Schistocerca gregaria* from north and east Africa and Asia Minor; the brown locust *Locustana pardalina* in South Africa; the South American locust *Schistocerca paranensis,* and the Rocky Mountain locust *Melanoplus spretus* formerly abundant in western United States.[72]

These locusts require a certain alternation of dryness and moisture in order to thrive; their eggs become moldy with too much moisture and dry up with too little. The newly hatched nymphs with their thin exoskeleton likewise need moist air and tender grass. Later, moisture kills them. They are not able to exist long in regions with extended rainy seasons, such as tropical savannas, but continually emigrate into whatever invasion areas are available, coming as adults from more arid areas to last at most a few generations. They are absent from forests. Locust-grasshopper maintenance in non-humid outbreak centers in tropical grasslands and temperate steppes is aided by the drought resistance of the eggs, which may lie in the ground for several years if there is too little moisture for hatching. Under favorable conditions they appear in exceedingly large numbers and thereby become a plague. They have been known to bring trains to a standstill in east Africa and in western United States. The mature animals undertake long flights in such large numbers that they rise into the air like dark clouds. Where the females lay their eggs in the soil, the ground is so full of burrows that it looks as though it had been recently worked by man. Before the advent of the white man, their voracity laid waste the regions they entered in the Great Plains of North America to such an extent that the bison are thought to have been compelled to migrate.[3] Today in Russia, South Africa, and elsewhere, they are kept in partial control by grasshopper patrols that scatter poisons from airplanes over adults or over their breeding places.

Locusts notably occur in immense destructive swarms that appear at irregular intervals. They often invade fertile regions distant from the hatching grounds and then suddenly almost or completely disappear. Uvarov proposed the phase theory to help explain this striking

variation in population density. The theory regards locust species as being polymorphic, postulating, for example, that the form called *Locusta danica* Linneus (widespread in Europe, Asia, and Africa) is in reality the phase *solitaria* of *Locusta migratoria* L., which was originally described from what is now known as phase *gregaria.* Phase *transiens* is also known.

The polymorphic character of the species is revealed by differences in coloration and by the much greater activity shown by individuals of phase *gregaria.* There are also significant differences in such adult characters as body size, shape of the pronotum, and relative length of hind wings and hind femurs. The theory explains the apparent disappearance of swarming locusts by stating that the species is still present but transformed in body proportions and colors toward those typical of non-swarming grasshoppers.[27,72] The grasshopper-locust phase theory is the working basis for locust-control officers [46,47] and is gaining general acceptance both from the accumulation of field observations and particularly from transformations effected in rearing populations of controlled densities.[27]

The Rocky Mountain locust (*M. spretus*), swarms of which were formerly abundant and destructive,[58] has now disappeared both as a pest and as a species unless it represented what is now known as phase *gregaria* of *Melanoplus mexicanus* (*=atlanis*). This suggestion is consonant with the results of hurried breeding experiments.[28] Further rearing of nymphs of *M. mexicanus* under crowded conditions is sorely needed. Grasshoppers and their relatives are particularly important because they transform the hard grass of the summer steppe into easily digested materials and so provide nourishment for a large number of animals. Scorpions and solpugids, lizards, many snakes and turtles, hawks and owls, marabous and storks, guinea fowl and ravens, and many others feed upon grasshoppers. Hosts of buzzards follow the swarms in South Africa, and the rosy starling (*Pastor roseus*) is drawn far from its normal distribution area during the grasshopper years in pursuit of the swarms; grain-eating birds feed them to their young. Their scarcity during the dry season is an important cause of bird migration in Africa.[22] Many mammals also take grasshoppers as food, from weasels to jackals, baboons, and man.

The cellulose-eating termites may feed on dry grass, and thus find abundant food, year in and year out, in subtropical, semi-arid regions. They construct their "anthills," which may be enormously large, or small and exceedingly numerous, in forms characteristic of the individual species. These nest forms are extremely varied: rounded

knobs, conical spires, high towers, and the wall-like compass nests already mentioned. Such structures may reach a height of 4 m., and even 6 m., in many species; Livingston indeed estimated some to be up to 9 m. in height. They are almost impenetrable to rain and may even withstand violent tropical storms. A rich fauna is associated with termite nests. Hostile ants conquer a part of the stronghold and establish their nests in them, as do other insects, especially carabids, like *Anthia guttata* in South Africa. Numerous amphibians, lizards, and snakes feed exclusively on the termites. Various mammals burrow into termite structures, like the jackal (*Canis mesomelas*), mongoose, and the aardvark (*Orycteropus*).[32] Monitor lizards lay their eggs in the nests. They serve as alighting places for birds of prey as they search the plain for food; antelopes use them as shade for their noonday rest in the treeless steppe.

Ants are found in the ground as abundantly as termites, but are even more widely distributed. Being eurythermal and euryhygric in contrast to the stenothermal, stenohygric termites, they range also into the areas of cold winters. They are active as long as the temperature permits, and continue to feed throughout the year in the subtropical and tropical regions. Whereas forest ants seldom go below the surface of the soil, all the grassland species build their nests in the ground; they reach depths of 3–5 m., sometimes down to ground-water level. The earth is piled up in conspicuous rings about the entrance. Their work supplements that of the burrowing rodents, accomplishing the same end in dry soil that earthworms do in moist ground; they produce a constant renewal of the surface layer, which is especially important for germinating plants; they promote the circulation of air in the ground and the penetration of rain water; and they fertilize the soil with their excrement and metabolic wastes.

Ants are different from termites in that they are not exclusively plant feeders but take food of every kind, and especially animal food. In times of greatest drought, their menu is limited; it is on account of this that certain ants that store food live in the dry steppes. *Tetramorium caespitum* [26] carries seeds into its nest in Germany only in the warmest summers; in Algiers this species regularly stores large quantities of grain. In the Mediterranean region, the grain-gatherers of the genus *Messor* always do this, as do the North American species of *Pogonomyrmex*. The so-called honey ants have a peculiar method of storing up supplies; they feed individual workers so full of honeydew that the abdomen is made to swell up like a ball, and in times of need this stored "honey" is regurgitated. This striking habit has

been convergently developed in semi-desert areas in North America, South Africa, and Australia by species only distantly related.

Ants and termites are among the "key industry" animals in the open lands and form the base of important food pyramids. Mammals and birds track them even into their nests and dig them out, together with their larvae and pupae. The pampas woodpecker *Colaptes campestris,* the North American flickers of the same genus, and the South African ground woodpeckers *Geocolaptes* live almost entirely on ants. The number of ant- and termite-eating animals becomes even greater when the winged sexual forms swarm forth at the beginning of the rainy season, some by day, some by night. Predaceous beetles, frogs, toads,[22] and lizards lie in wait for them on the ground, and wasps, innumerable birds, from hawks to goatsuckers, and a host of bats, pursue them in the air.

The richest bee fauna appears to be developed in sunny steppes with loose soil; in damp ground the food supplies for the brood might be endangered by mold.[31] Burrowing wasps likewise play a large part in steppe regions; thus, more than 80 species of *Cerceris* occur in South Africa. Brood parasites are found with these Hymenoptera, such as mutillid wasps, bombylid flies, and blister beetles (Meloidae), which predominate in steppe regions.[53] Finally, several families of beetles occur in large numbers in open country. Correlated with the abundance of ungulates, the dung beetles appear, finding abundant food for themselves and their brood. The carcasses of dead animals attract carrion beetles. Numerous and varied tenebrionids range wherever there is bare ground and loose sand, and are abundant in dry, hot regions; South Africa alone has more species of them than all tropical America; the Near East and central Asia have more than the Indo-Malayan area; of the 48 species of beetles, for example, that Escherich [25] collected on the island of Djerboa (Tunis), almost half belonged to this family. Insects of the remaining orders are of less importance in comparison with those already discussed, although Hemiptera, Diptera, and Lepidoptera are of sufficient importance to deserve mention.[16] Other insects are for the most part scarce on the grass floor, the more so, the closer the area approaches desert conditions.

The number of insects present in season is impressive. In Manitoba they may number 9,500,000 per acre in the spring when many insect-eating vertebrates are still hibernating and before flocks of migrant birds arrive. Insect numbers are reduced to only a million per acre

in late June.[10] Insects vie with herbivorous mammals in the amount of grass consumed.

A peculiar group of animals limited to arid steppes and desert regions is composed of the agile spider-like solpugids, which are found in suitable localities in Eurasia, the whole of Africa, and subtropical North America up to Colorado. They prey upon insects, mostly termites, and the larger species even attack small vertebrates. True spiders and scorpions are also present, but are less distinctive of the steppe.

Vertebrates of the steppes

Open country is the domain of the reptiles. Favorable living conditions are offered for these warmth-tolerant animals, which, when the heat is not too great, expose themselves to the direct rays of the sun and thus raise their internal temperature to their optimum, almost corresponding to the temperature of homoiothermic animals. They inhibit a further rise by increased respiration, by moving into shade, or by burrowing. Lizards and snakes are present in large numbers of species and individuals in grassland; although they are not common everywhere, they may occur in large numbers; land turtles like the ornate box turtle (*Terrapene*) of western North America may be abundant. Many reptiles are fossorial, and dig into the ground or at least make use of burrows already present. Sandy soil readily permits them to burrow, and they are especially numerous on such terrain. The food of lizards is primarily insects; only the largest species, such as the monitors, also capture vertebrates. In cold steppes, reptiles hibernate; but in the subtropical regions, many remain active all the year around. They form one of the chief sources of food for carnivorous mammals and birds; jackals, civets, mongooses, and other predators feed on lizards and snakes; and marabous, storks, hawks, the secretary bird *Sagittarius*, and other birds may live primarily on them.

The abundance of insects, reptiles, and small rodents, and immense numbers of various seeds make favorable feeding grounds for birds. Unobstructed view is important for birds as eye-dependent animals. Many steppe birds have given up flight and become cursorial. Flying forms are better able than other animals to avoid temporarily unfavorable conditions. On the other hand, the conditions for the establishment of their nests is less favorable in open lands; most birds must breed on the ground, even eagles or storks, which elsewhere seek unapproachable nest sites. They are mostly praecocial, especially the larger forms and more especially the ground birds proper; but there

are also altricial birds among those nesting on the ground, such as larks, buntings, rosy starlings, or birds of prey. Linsdale [44a] found a sharp coincidence of the range of the black-billed magpie in North America with the climatically defined "cold-type dry steppe."

Grassland fires present scenes that are constantly repeated in the African steppes,[61] in the prairies of North America, in the llanos of the Guianas,[63] in the Asiatic steppes,[59] and in the grassy wildernesses of New Caledonia.[60] When the dry grass begins to burn, the rising clouds of smoke are the signal for many birds to hurry to the scene of the fire, for the flames drive ahead of them all creatures that cannot escape below ground. Hunters of creeping and burrowing animals such as marabous and storks run about snapping up their prey before the fire; hawks fly over the fire, while insect-eating swallows, flycatchers, and shrikes follow their prey almost into the flames.

Among mammals, herbivores naturally predominate in grassland. Rodents surpass all others in number of species and individuals. In Tripoli [43] two-thirds, in the Russian steppes [52] three-fourths, in California three-fifths, of the species of mammals are rodents.[35, 65, 66] Because of their small size, fecundity, and resistance to drought, they have the advantage over other mammals. They are mostly fossorial in habits, and the young are protected in nests. They form a principal food for many predatory animals: eagles, hawks, owls, wolves, foxes, certain cats, and others; but their fecundity balances all losses. Ungulates join them as grass-eaters according to the location: wild horses, asses, zebras, antelopes especially, giraffes, bison, pampas deer, camels, and guanacos, and, in addition in the African steppes, elephants and rhinoceroses. With these larger animals, the young must follow the mother soon after birth. Though the non-rodents bulk larger as individual units, the amount of food consumed by rodents may run as high as 75% of that available. Next to the rodents, ruminants such as antelopes, cattle, deer, and camelids are the most abundant. The large predatory animals—lions, leopards, hunting dogs, and wolves—are attracted in turn by these large herbivores; they follow the herds and flocks, congregate like them at the water places during the dry season, migrate with them, and disperse again with them over the grassy plains during the moist season.

The abundance of life in open tracts of land is variable. Many of them represent areas where the maximum amount of life is crowded together. This is naturally dependent upon the amount and condition of the grazing afforded. The stiff, hard grass of the Cameroon savanna, which is as high as a man and higher, is less favorable than

the low, fine grass of the "Süssveld" of South Africa. Opportunity to escape the effects of drought by migration is also important. In tropical South Africa, where the total rainfall is small in amount, the rain is distributed over the entire year in such a way that there is a zone of winter rain in the west, a zone of summer rain in the east, and a transitional zone in the middle.[55]

The amount of mammalian life that filled many stretches of the South African plains in earlier times is almost beyond belief; and even yet there are regions that abound in animal life. Livingstone and other travelers of the beginning and middle of the nineteenth century tell of wonderful sights, and in the present century Berger [9] estimated the number of zebras seen daily by him in British East Africa as 1000, the number of hartebeeste as 3000 to 5000, with other large mammals similarly abundant. Many parts of north Tibet are likewise rich in animal life, but do not by any means equal the African steppes. Przewalski [57] describes a rich fauna in the pasture land along the Schugo River; "Only by moving about from one place to another could they find the necessary food on the wretched meadows." More recently Andrews [7] writes of seeing thousands upon thousands of Mongolian antelopes that poured in a yellow flood over a mountain rim and spread out into the fertile plain. Sometimes a thousand or so would dash away from the main herd, only to stop abruptly and feed. At one time on the Great Plains of North America the bison were so numerous that the herds extended as far as the eye could see. In a similar manner, but in smaller herds, the guanacos characterized the Patagonian plains over which they were scattered by the thousands.[4] Many of these mammals, feeding primarily on the grassland plants, have played an important rôle in preventing the invasion of trees into parts of these plains whose soil and rainfall would otherwise have supported forest growth.

Desert communities

The desert forms the extreme of aridity in the open lands. Permanent flowing water is entirely absent. Rain occurs seldom and irregularly, and in extreme cases may fail for several years in succession. The yearly rainfall is subject to wide fluctuations, and rains when they do come may be torrential. In many regions there is not even dew. The clearness of the unclouded sky results in a decided heating during the day and quick cooling by night, so that the daily temperature range may amount to 50° or more. In many desert regions much adjacent territory should be referred to as semi-desert or desert-

steppe, but a sharp distinction is not possible; all transitional conditions can be found from grassland through scrub to desert.

The principal desert areas of the world are for the most part adjacent to or enclosed by steppe. Desert conditions may merge into grassland by insensible gradation, by interdigitating areas, or by sharply marked transitions of vegetational types. Ancient, long-persistent deserts are characterized by plants and animals highly adapted to lack of water in air and soil, and, accordingly, by water-conserving devices and physiological and ecological adaptations. Rock desert may be even more extremely barren than sand desert. In sand desert vegetation tends to hold the moving sand wherever the rate of movement is reduced to a critical level, which presumably varies from region to region. A striking desert type results when sand and soil are removed from pebbles by wind, which may then form a residual "pavement desert," with polished pebbles covering a soil substratum and with vegetation and animal life only where the surface is broken by an arroyo.

The great deserts of the world form a pattern related to mountain ranges, breadth of continental areas, and climate,[69] with local deserts conditioned by more strictly edaphic factors. Interrupted somewhat by steppes, a chain of great deserts extends from southwest Africa via the Kalahari and east Africa to Arabia, and across north Africa from the Atlantic coast to the Red Sea, and from the great Arabian desert through central Asia to Mongolia. The principal American deserts are in southwestern North America, from Lower California into the Great Basin and to the Mexican plateau. This Sonoran Desert has its origin in part in the cool climate produced by the upwelling oceanic waters off California and Lower California. Though such cool waters may condense fog in the winds that blow over them, the cool air has its moisture capacity increased as it reaches the warmer land, and no rain falls. The relation of the coastal Chilean and Peruvian desert to the climatic effects of the Humboldt Current is even more evident. Desert conditions extend to about 3500 m. on the western slopes of the Andes, and reappear in many interior valleys.[51] East of the Andes there is an isolated desert area in the northern Argentine (Catamarca). The great interior Australian desert is quite isolated from all others. Desert conditions on islands, often with characteristic desert plants, may be found even in humid regions where calcareous bed rock permits the rain water to leach through. Elsewhere, as in Hispaniola, arid conditions and small desert areas are clearly associated with "rain shadows."

A limited number of forms are able to survive the unfavorable environment of deserts and to become adjusted to it. Since vegetation is very sparse, only a small amount of animal life can develop. In general, only small animals occur; the desert fox is one of the largest in the Sahara; the gazelle (*G. loderi*) stays in the semi-desert and disappears where the vegetation is too sparse. The lion is not a desert animal; it does not find enough food there. Where vegetation is entirely absent, as in the stony desert south of Biskra or in parts of the Libyan sandy desert, at most only a few dung-eating insects are able to survive, by feeding on the dung of camels traveling through the desert, with a few birds and lizards that feed on such insects.

There are biotic limiting influences, in addition to food supply. The elf owl (*Micropallas whitneyi*) lives in arid parts of California and Arizona. It nests exclusively in holes made by two woodpeckers, *Centurus uropygialis* and *Colaptes chrysoides mearnsi*, in stems of giant cactus, *Cereus giganteus*.[24] The range of the elf owl is limited by the distribution of these two biotic elements of its environment. The woodpeckers, unlike the pigmy owl, are not limited to this one cactus for nesting; they excavate nest holes in other trees and plants. The owl is limited by absence of cactus even though woodpeckers are present and limited by absence of woodpeckers even though cactus is present.

Many animals live in the crevices between rocks or burrow among them. Rock-dwelling animals are called petrocoles and include snails, spiders, other arthropods including ants, and various small lizards and mammals. Petrocole lizards are characteristically flat, as is an east African land turtle (*Testudo tornieri*) that also lives among rocks. Animal life is more abundant under stones lying somewhat loosely on the ground.

In spite of the extreme dryness, a number of animals whose taxonomic relations are all with inhabitants of regions of moist air are able to survive in the desert. Amphibians occur only in oases and extend into semi-arid lands from more humid regions. As has been stated, a number of species of snails and isopods have been able to enter and adjust themselves to the desert. In North Africa, where vegetation appears to be quite absent and where the temperature at noon rises to 43°, one may find the ground at times thick with the shells of *Otala lactea*, and *Theba pisana* occurs in clumps as large as two fists.[17] The success of snails in these dry areas is shown also by the fact that the individuals of *Leucochroa candidissima* attain twice the size of European individuals.[70] *Helix* (*Eremina*) *desertorum* seems

to extend as far in the Sahara as night dew falls: 20 km. inward from the seacoast, and 4 km. around the oases.[74]

The shells of desert snails in widely separated regions may possess a striking similarity, without close relationship of the species. There is an analogy, for example, between the snail fauna of Arabia and that of Lower California: *Helix* (*Micrarionta*) *areolata* in California differs from its relatives from the moist regions of that locality and resembles the Arabian subgenus *Eremina;* furthermore, the Lower Californian *Bulimulus* of the subgenus *Sonorina* parallels the Arabian *Buliminus* of the subgenus *Euryptyxis,* and the *Bulimulus* (*Orthostomium*) *pallidior* of Lower California in general form and sculpturing of the beginning whorls is very similar to the *Bulimunus* (*Cerastus*) *fragosus* of Yemen.[5] The species of the Lower Californian *Bulimulus,* and others from similarly dry and desert areas in Peru and Chile, carry the stamp of their environment so plainly that in many instances similar forms from California and Peru were formerly placed in the same species, and only after careful investigation could it be established that their resemblances are the result of independent convergence.[19]

White isopods occur in the north African and Asiatic deserts. Their high curved backs provide a relative reduction of surface, particularly in the genus *Hemilepistus,* but also in species of *Porcellio* and *Metoponorthus;* as in our northern species of *Porcellio* and *Armadillidium,* evaporation is reduced by a reduction of the epidermal glands.

As elsewhere in open lands, running, jumping, and burrowing vertebrates play an important rôle in the desert. Lizards are runners, as are the larks and coursers (*Cursorius*) among the birds. Jumping mice and jerboas are the best representatives of the jumping animals. Burrowing forms are at home in sand desert. Reptiles are especially abundant and are able to dig themselves into the sand very quickly. The species of *Phrynocephalus* in Asia and *Phrynosoma* in the American Southwest produce horizontal movements with their flat bodies and disappear rapidly into the sand. The rostrum is particularly well developed and extends beyond the mouth in many snakes and lizards of the desert; they burrow through the sand by means of lateral movements of the head. Beetles, too, burrow into the loose soil. In the Sahara the crested larks, *Galerida cristata,* are said to have longer beaks in sandy than in rocky desert, which enables them to extract such prey out of the sand.

Wherever the desert floor is sandy, many animals have adaptations that prevent them from sinking into the sand and so facilitate running over the loose ground. Among lizards, the toes are provided with

lateral rows of scales or fringes, a convergent development shown by the iguanid *Uma* of the Colorado desert, the geckonids *Ptenopus* in South Africa and *Teratoscincus* of southwest Asia, the agamid *Phrynocephalus,* and the African lacertid *Scapteira* (Fig. 118). The feathering of the tarsi and toes and the web in the sand grouse *Syrrhaptes,* and the well-developed lateral hairs of the soles of the feet in the kangaroo rat *Dipus* exhibit similarly increased surfaces for running over sand. Even in tenebrionid beetles of the north African, Asiatic, and Sonoran deserts, the flat tarsus is widened by long chitinous hairs.[29] Snakes may be driven to the novel "sidewinding" type of locomotion.[50] Some snakes and lizards (*Uma, Scincus*) "swim" in loose sand.

Desert animals in all parts of the world tend toward a resemblance in color and pattern to the pale colors of their environment, though with exceptions, equally world-wide, in which a striking black coloration is developed. Because of the lack of cover, color adaptation to the substratum has been shown to have biotic importance for desert animals.[8,21,42] The pale yellowish or reddish color of the desert floor recurs in many. Numerous Orthoptera,[73,75] most of the snakes and lizards, very many birds, and mammals of numerous genera have this yellowish or reddish coloration. The crested larks *Galerida,* which have dark brown colors on the dark cultivated fields of northern Algeria, are sand-colored in sandy wastes to the south and grayish in the rocky deserts.[37] A resting grasshopper, a lark, or a desert courser, sitting quietly, is unusually difficult to distinguish. A large number of animals with nocturnal habits have the desert type of coloration, especially among mammals and reptiles, as well as those tenebrionid beetles that are not black. It seems evident that faded colors may arise as the direct result of climatic influences and thus occur in both diurnal and nocturnal animals, though only in the former case do they have full selective value from coincident biotic adaptation. Besides these, numerous black animals occur in deserts that contrast strikingly with the substratum. These seem to be protected in some peculiar manner [13,54] from possible injury resulting from the penetration of the shorter wavelength radiation rather than by direct biotic advantage.

The concentration of life at certain localities under the extreme conditions in the desert is striking. Wherever a depression carries down to a greater proximity to the ground-water level, a more abundant plant life springs forth, and there animal life also congregates. Every bush, every briar, is an oasis in itself, full of specialized forms

of animal life. In many places, as in the Algerian desert, every large stone affords protection for a number of insects, myriapods, arachnids, isopods, often also for lizards and snakes and even for small mammals and birds. With conditions close to the limits of existence, a few advantages are decisive.

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23. *Animal Life of Swamps and of Shores*

SWAMPS AND MARSHES, THE GREAT NORTHERN TUNDRA IN SUMMER, RIVER banks, bottom land, and the borders of lakes and seas contrast radically in their environmental conditions for animal life with those of the dry steppe. Of all other types of environment, only the tundra, known sometimes as the "moss steppe," extends over areas comparable with those where grassland or savanna conditions prevail. The borders of streams and bodies of standing water, though also of great extent, are essentially linear. Trees may be present, as in the cedar-bordered lakes of the northern United States or the mangrove formations of the tropics; forest may be replaced by bushy vegetation but is more frequently absent. Even where there is forest growth, free space both within the water and above it is available to the inhabitants of the shores. The trees themselves provide an upward extension of a firm substratum much used, especially by birds.

The presence of water largely governs the composition of the swamp and shore fauna, for its constant abundance of life affords a sure food supply, which attracts a great number of air-breathing animals to these situations. The air-breathers are to some extent aquatic, and most of these are able to swim. They exhibit a transitional stage between the complete return to the water of the secondarily aquatic forms, like whales, ichthyosaurs, or sea snakes, and land animals proper. This amphibious fauna is dominated with respect to both quantity and composition by the seasonal periodicity of its habitat. In the polar and temperate zones the water freezes for a varying period in winter, and in the tropics and subtropics swamps and even rivers may dry out completely. This condition forces a periodicity on the shore fauna as well, and it is composed of wandering or migratory animals or of those capable of hibernation or aestivation.

Amphibious habits among animals

All the phyla of land animals include amphibious forms. They are fewest among the snails, though not entirely wanting. The species of the genus *Succinea* live in both fresh water and on land, and *Assiminea* is found in salt marshes along the seacoast both above and below the water surface.

Amphibious forms are numerous among insects. Many orders have completely aquatic larval stages, with air-breathing adults, as in some neuropterans, and all mayflies, stoneflies, caddisflies and dragonflies. A great number of Diptera have aquatic larval stages and even an active aquatic pupal stage, as in mosquitoes. These aquatic Diptera are present in such great numbers, in both tropical and temperate zones, that they afford an important food supply to many other creatures. Lake Myvatn in Iceland derives its name from them. Its waters harbor a host of mosquito larvae, whose adults hover over the water in dense clouds in summer. The circumpolar tundra zone is infested with these blood-sucking hordes, and the humid tropical regions are equally renowned for their insect plagues. Numerous Hemiptera and Coleoptera have carried these amphibious habits further, and have returned to the water in the adult stage as secondarily aquatic animals.

All the classes of vertebrates include animals with amphibious habits. The water frequently serves only as a place of refuge from drought, heat, or enemies, as for the common frog or the hippopotamus. Conversely, the water may be the hunting ground, from which the animals retire to land for their other activities, as do the penguin and otter. The amphibious members of the several classes of vertebrates have acquired certain characters in common, such as the relation of eyes, ears, and nostrils in the hippopotamus, crocodile, frog, and *Periophthalmus* already mentioned (Figs. 35 and 83), or the development of webbing between the toes.

Only a few fishes are in any sense amphibious. The gobies have given rise to a number of forms that leave the water in active search for food in tropical tide flats, notably *Periophthalmus* and *Boleophthalmus.* Certain blennies (*Alticus saliens* of the tropical Pacific, for example) have similar habits on rocky shores. Fishes like the lungfishes and mud minnows, which are able to aestivate in the mud of dry swamps and ponds until the return of water necessary for their activity, are more numerous.

Amphibia are by implication amphibious. Some of them have be-

come secondarily completely aquatic, and others completely terrestrial. Most frogs and salamanders begin life in the water and spend their adult life either on land or as air-breathers in or near water. Some frogs, like the European *Rana esculenta* or the American bullfrog *Rana catesbiana*, never wander far from water. Others, like the common North American leopard frog, inhabit upland fields and meadows during the summer. Similar variation in the degree of permanency of relation with water is found among the salamanders. Hibernation in temperate climates and aestivation in the tropics are the usual means of surviving unfavorable seasonal conditions.

Among reptiles numerous forms are semi-aquatic, notably all the crocodilians and a majority of turtles; both these groups reverse the life history of frogs in that they spend their active life in the water but repair to the land for egg-laying. They hibernate or aestivate in muddy ponds or swamps. Among the few lizards that have adopted a riparian life, the monitors of the East Indies and Africa, and the aquatic East Indian agamids such as *Hydrosaurus*, with their close parallel *Basiliscus* among the American iguanids, must be mentioned. Many species of Old World monitor lizards are riparian, as is the teid lizard *Crocodilurus* in South America. Numerous snakes are closely confined to the neighborhood of water, notably the anaconda of tropical America, the common water snakes (*Natrix*) of the North Temperate Zone, and a great variety of harmless and back-fanged snakes in the tropics. There are a few aquatic water snakes among the poisonous Elapidae (*Boulengerina* in Africa), and among the Crotalidae only the American moccasins (*Agkistrodon piscivorous* and perhaps *bilineatus*). The sea snakes (*Hydrophiidae*) have become completely aquatic, and only the more primitive members of the family come ashore at all.

The semi-aquatic environment is favorable for birds. Their powers of motion make them independent of seasonal variations in the water. Whole orders of birds have arisen by adaptation to this habitat, and these, together with isolated groups of more terrestrial orders, compose the two ecological groups distinguished as swimming and wading birds.

Birds find food and protection in the water and along shores. All the animal life of both marine and fresh water, except the largest forms, is subjected to their toll. This food supply is for the most part abundant, and the birds furthermore adapt themselves to its seasonal variation. Their numbers stand in direct proportion to the available food supply. Thousands upon thousands of birds are seen

at such lakes as Lindu [30] in Celebes, Lake Chad [34] in Africa, or in the marsh areas of great rivers such as the Paraguay or Nile, all of which are rich in invertebrates and fishes. The water itself, the thick vegetation of marshes, and islands and floating vegetation afford protection to birds, primarily from mammalian enemies but also from birds of prey. Predators have, to be sure, adapted themselves to the same habitat in pursuit of the food supply offered in their turn, by the birds. Birds are abundant on the islands and in the marshes of Great Salt Lake, whereas the shores of the Dead Sea are birdless wastes. As stated in Chapter 2, the dearth of life in and around the Dead Sea cannot be the result of its high salinity alone.

Swimming birds are characterized by some form of webbing of the feet. These birds include penguins, loons, grebes, gulls and terns, albatrosses and petrels, pelicans and their relatives, ducks and geese, and a few members of the crane and plover tribes. The waders, characterized by elongate legs, are found in the storks and herons, cranes, plovers, sandpipers, and others. Both swimmers and waders tend to be gregarious, sometimes nesting in vast colonies. This gregariousness may transcend the usual specific limits—a flock of various kinds of sandpipers may be led by a large yellowlegs or a godwit.[22]

The swimmers have a dense oily underplumage, which does not become wet. In the best-adapted forms, such as the ducks, these feathers extend over the wings, protecting them also from wetting. Numerous swimmers, derived from various groups, are skilled divers. The divers have in common close and dense feathering and marrow-filled bones; their greater specific gravity causes them to sink more deeply into the water. The non-diving swimmers float almost on top of the water (Fig. 125). Some of these divers swim under water with their wings, notably the auks, loons, and penguins; penguins, indeed, have the wings completely transformed into flippers. Swimmers are more closely associated with open water than waders, and many swimmers and divers wander far at sea. The fact that none of them have become wholly aquatic, like whales or sea snakes, is plainly a result of the fixity of the egg-laying habit in birds as a class. Among birds the extinct toothed and wingless *Hesperornis* of the Cretaceous, and the penguins have advanced as far as is possible in aquatic adaptation.

The elongation of the legs of wading birds is mainly in the tarsal bones, though the tibiae may also be involved, and long legs are associated with long necks and long bills. These features enable them to wade and feed in shallow water without wetting the plumage.

Though essentially semi-aquatic, they are less dependent on these habitats than are swimmers, and may leave the water entirely to take advantage of a food supply on land. Storks feed on grasshoppers in the African savanna, and the demoiselle crane in central Asia may take to the desert in pursuit of lizards.

A number of other birds, of varied origin, have been attracted to the neighborhood of water in various degrees and for a variety of reasons. Kingfishers, incapable of either swimming or wading, have adopted an almost exclusive fish diet and capture their prey by vertical diving. The same is true of the osprey, which is so successful a fisherman that the American bald eagle robs it systematically.[6] Swallows feed on the adults of aquatic insects, finding free space for their evolutions over the water. The bank swallow (*Riparia riparia*) nests in colonies in holes in vertical banks and cliffs, especially along lakes or rivers. Brehm reports colonies of this bird with thousands of nests on the Obi. Bee eaters frequent watercourses solely on account of a similar nesting habit. Predaceous wasps in the Congo are attracted to shores where midges breed on the mud flats (Bequaert, personal comm.).

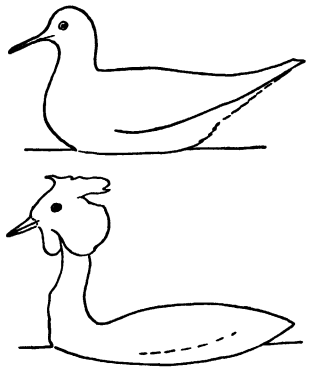


FIG. 125. Upper, a swimming bird incapable of diving floating high on the water (phalarope); lower a diving bird, much deeper in the water (grebe). After *Brehms Tierleben.*

The semi-aquatic habitat has attracted a great variety of mammals. The duckbill of Australia is notably aquatic, with completely webbed feet and close underfur; it nests in burrows with an underwater entrance. Marsupials have an aquatic representative in the similarly web-footed water opossum *Chironectes* of South America. Numerous rodents frequent streams, lakes, and marshes, notably the muskrat and beaver in the north and the coypu and capybara in South America. Aquatic mammals not infrequently have the tails flattened from side to side as a swimming organ, in such diverse stocks as the muskrat and the African insectivore *Potamogale.* Such flattening is ridiculously conspicuous also in the tail of the hippopotamus. A whole series of mustelids illustrates various degrees of adaptation to swimming habits —from the riparian and frog-eating mink to the almost pelagic marine sea otter. The beaver is unique among aquatic animals in the successful control of water level to suit its mode of life. The seals, among

Carnivora, present still more complete adaptation to marine habits, coming ashore only for rest and reproduction.

Swamps and stream borders attract a number of ungulates. These usually have wide spreading hoofs, for support on soft ground. A partial list of such animals includes the hippopotamus, tapir, various pigs, African antelopes of the genera *Cobus, Limnotragus,* and *Tragelaphus,* the northern reindeer and moose, and the water buffalo of the tropical orient.

Swamps and marshes

Swamps and marshes, in topographic succession, represent a transitional stage between open water and dry land. The evanescent character of lakes in general has already been emphasized (Chapter 6). Abundance of lakes characterizes the North Temperate Zone, primarily by reason of the recent glaciation. These lakes are frequently surrounded by a narrow ring of open sphagnum bog; tamarack or spruce and various other trees rapidly encroach on the bog zone as it gains in firmness. Great stretches of older swamp are covered with dense stands of timber—tamarack, spruce, and white cedar, with a substratum of sphagnum. These forested swamps are no longer wet lands with open water, though they may afford rookery sites to aquatic birds that feed elsewhere.

Shallow depressions in the glaciated surface in the north produce more extensive and longer-lived bog conditions, ending in the familiar peat moors of more northern regions. On the prairies, ponds and swamps are familiarly known as sloughs, and disappear because of the encroachment of sedge and cattail rather than of bog moss. These cattail marshes are rich in bird life, notably of the perching birds such as the yellow-headed and red-winged blackbirds and marsh wrens mentioned above, besides a great variety of waders and swimmers. When present, cattails supply food and nest material to one of the most characteristic of the semi-aquatic mammals, the muskrat, which also invades other situations and may depend on other food plants.

Bottom-land marshes of rivers

The history of river bottom swamps and marshes is different from that of lakes, since wide flood plains subject to inundation and retention of water are the end stages of the erosion of all river valleys. Rivers are in general much older than lakes; the river bottom and river delta swamps and marshes have some continuity of geological history,

and an older, more permanent fauna. Furthermore, in the United States at least, lakes characterize the north, and rivers with wide lowlands the south. Such southern river-bottom marshes, with favorable climatic factors, have a luxuriant vegetation, like the canebrakes of the lower Mississippi; this tendency culminates in the tropics in the papyrus swamps of Africa, the giant *Arum* of the Amazon, and the 20-foot high wild sugar cane of the river swamps of New Guinea. The lowlands of the lower Mississippi have a characteristic growth of timber such as cypress, which grows habitually in the water, or the gums and other species that withstand long immersion.

Great river marshes are usually associated with the lower courses of the streams; but this is not a necessary relation, for on the Paraguay and the Nile vast open marshes characterize the upper or middle parts of the river. Rivers flowing through a flat flood plain frequently build up natural levees on their banks, which permit the growth of timber. On the upper Paraguay this fringing strip of timber is often so narrow that one sees through it to the open marsh and plain beyond. As the stream meanders it cuts through these strips of timber so that the former banks and parallel forest strips may be at right angles to the existing course, the old stream bed being filled with herbaceous marsh or floating plants.[33]

Bird life * is the most conspicuous element in the fauna in each of these regions, but the hippopotamus in Africa, the tapir, capybara, and otter in South America, and the smaller but vastly abundant muskrat in the Mississippi are reminders that mammalian life is also important. Reptiles, conspicuously crocodilians, are well represented in this river-marsh habitat. The enormous concentration of the smaller caimans in the lower Amazon is familiar through the fine picture in Brehm.[35] On the Marajo Island, in the mouths of the Amazon, regular drives are made against the local crocodilians (two species of caiman), in which thousands of individuals are killed. Amphibians are abundant, but except in the southern United States with its remarkable salamanders, they tend to be reduced in variety.

Floating vegetation extends outward from the shores in tropical rivers, much as bog mosses do in the north, but here the mats become much more extensive and may choke the entire river course, as on the upper Paraguay, where the floating plants include especially a large species of grass, with finger-thick stems, and great amounts of

* Chapman [5] and Bengt Berg [4] describe the bird life of the White Nile, and Miller [24] and Roosevelt [29] give a view of that of the Upper Paraguay. The bird life of the Mississippi bayous is described by Arthur.[3]

blue-flowered water hyacinth. These mats of vegetation form floating islands when detached, and may remain intact until they reach the sea. One of the most notable of the adaptations of air-breathing animals to floating vegetation is that of the jaçanas, whose elongate

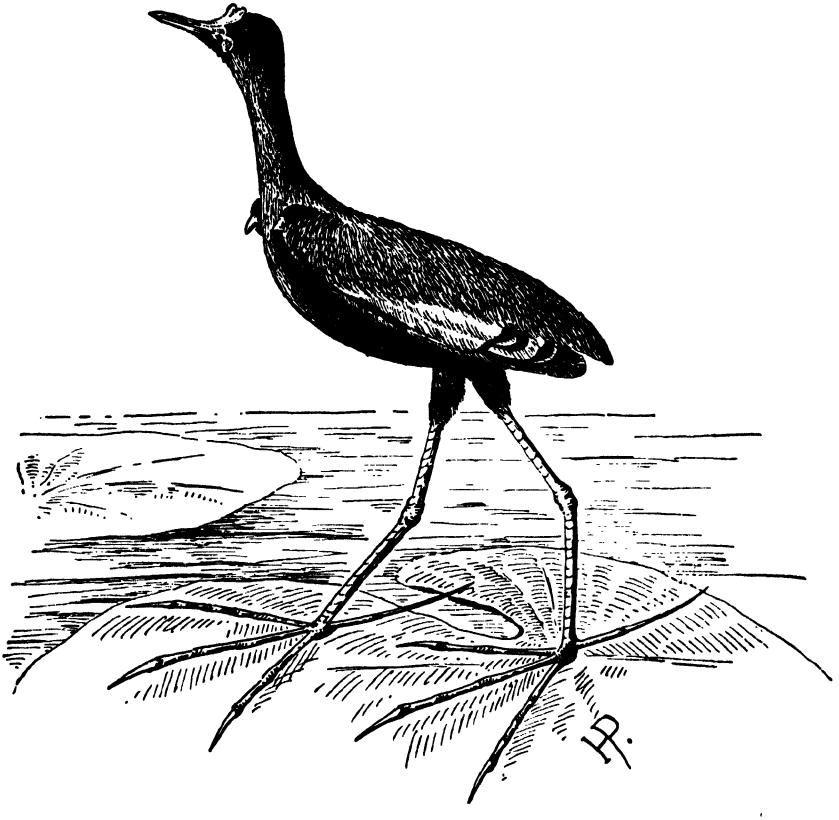


FIG. 126. Jaçana, *Parra jacana,* of South America. After Plate.

toes distribute their weight. They are represented by the genus *Parra* (Fig. 126) in South America, *Actophilornis* in Africa, and *Hydrophasianus* from south Asia to New Guinea.

Bottom lands, subject to seasonal overflow, offer peculiar environmental conditions. Many animals are excluded from such areas either completely or seasonally. These overflow areas may be vast, as in the Amazon basin, which floods more than 500,000 square miles. Fishes and other aquatic animals are left behind in ox-bows and other depressions with the fall of the water, and may then become so concentrated

as to afford a readily accessible source of food for predators. Birds, mammals, snakes, and turtles also become seasonally abundant. In the Amazon region, the majority of water birds breed in this favorable period.[14]

Tundra

The lakes and marshes and bogs of the tundra, with their extremely characteristic faunal picture, cover a vast extent in both North America and Eurasia. The frozen subsoil prevents the escape of water by seepage, so that the melting ice and snow of winter produce innumerable lakes and ponds, while sphagnum bog covers every level stretch not occupied by open water. The vast bulk of the life of the tundra consists of invertebrate forms that flourish only in summer, and of migratory birds, among which water birds are by far the most important element. Birds may be attracted also by the relative absence of enemies and the protection afforded by the bog habitat from such as are present. The permanent inhabitants of the tundra zone are discussed in Chapter 25.

Vertebrate life of the seacoast

The transition from sea to dry land in tide flats, salt marshes, and, in the tropics, mangrove swamps and forests, offers a third semi-aquatic habitat, much frequented by the types of birds and mammals already discussed, but with a reduced reptile fauna and with amphibians almost totally absent.

The mangrove swamps of Florida have many plant communities depending on the stage of succession and other factors.[9] To the north one finds the brackish-water fiddler crabs, *Uca,* abundant; to the south, these are replaced by the West Indian land crabs, which burrow into the muddy flats in the dry season and become active during the rainy seasons. when they swarm forth in ground-covering numbers. Several species of fishes likewise occupy these mud flats and burrow during the dry season. A number of snails are found, one of which, *Littorina angulifera,* although not a pulmonate, has become arboreal and climbs over the mangrove roots, coming down to water only occasionally. The mud-skipper (*Periophthalmus*) is found in similar mangrove swamps in the tropical Pacific and Indian Oceans and in west Africa; it is a teleostean fish highly modified for life out of water, with accessory breathing apparatus and with modified anterior fins by means of which it skips over mud flats or climbs the mangrove roots.

In the salt marshes of the Louisiana coastal margin the muskrat (*Ondatra rivalicus*) is abundant in regions where the tidal influence is not great. The Louisiana seaside sparrow, a marsh wren, the red-winged blackbird, the boat-tailed grackle, the clapper rail, and two species of gallinules and the least bittern nest and feed among the canes and bullrushes. The first four birds mentioned feed in part on insects; other members of the community eat small crustaceans and fishes, as do the herons and snowy egrets, which nest elsewhere. When the marsh becomes more shallow, it is entered by the raccoon, otter, and the mink. Alligators abound in neighboring fresh-water marshes but are absent in brackish ones. The diamond-backed terrapin is limited to these coastal marshes of the Atlantic and Gulf coasts of southeastern North America.

The seacoast itself, as distinguished from coastal marshes and sounds, is inhabited by a great variety of the larger animals that feed on coastal invertebrates and fishes. The preponderance of wading and swimming birds is a feature of this environment, and seacoast bird life is further remarkable for its great concentrations to the north and south. Mammals are well represented, and there are a few reptiles; amphibians, which are intolerant of salt, are almost entirely absent, and there are only a few midges and the water strider *Halobates* to represent the insects.

Few reptiles live in this habitat. The large marine iguana, *Amblyrhynchus,* of the Galapagos Islands is completely adapted to the environmental conditions by its powerful tail for swimming and the strong claws that enable it to land on rocks in the surf, after feeding on the seaweeds exposed at low tide. Two species of crocodile, the East Indian *Crocodylus porosus* and the American *C. acutus,* venture from the salt marshes and river mouths out to sea, and accordingly have a wide distribution. The African crocodile may also enter the sea, and has reached Madagascar. A few small lizards * frequent the beach and feed on invertebrate refuse and small crustaceans.

Two groups of marine turtles are breeding members of the communities of the ocean shores. One of these is the primitive "leatherback" turtle (*Dermochelys coriacea*), which may weigh up to a ton, the largest of all chelonians. This is cosmopolitan in distribution in tropical seas, but is rare everywhere, least so in the west Atlantic from Florida to Brazil and in the Indian Ocean. It breeds on the coasts of Brazil, the Tortugas, and the Bahama Islands. Only juvenile

* The iguanid, *Tropidurus,* and the skinks, *Ablepharus* and *Emoia.*

and mature forms are known, for they visit land only for breeding purposes and otherwise lead a pelagic life. The other family represented is the Chelonidae, which includes the green or edible turtle *Chelonia mydas* and the loggerhead *Caretta,* with a few other forms. The first is a plant-feeder and is therefore restricted to littoral waters; the others eat fishes and mollusks. The breeding season of the green turtle varies in different parts of the world. In the East and the West Indies it breeds from April to June; on the west coast of Africa the breeding season is from September to January. Other wide-ranging tropical and subtropical animals show similar nonconformities in breeding time in different parts of their ranges. The loggerhead turtle ranges farther north and is an occasional visitor on European coasts as far as Great Britain. All these sea turtles deposit their eggs in excavations made on sandy shores.

Mammals of the seacoast include polar bears, sea otters, sea lions, seals, walruses, manatees, and dugongs, besides more casual visitors. The concentration of these amphibious mammals, manatees and dugongs excepted, is notably arctic and antarctic, with almost continuous connecting colonies on the west coast of the Americas, where the upwelling cold waters produce suitable temperature and food conditions. The existing sirenians are confined to shallow coastal waters and rivers in the tropics and subtropics. Seals and eared seals seem notably less abundant in the tropics than in temperate and polar regions.

The polar bear is a land or ice-floe animal, but it is a powerful swimmer; since its principal food is seals, it is almost confined to the ice border and pack ice, where the seals occur. It is circumpolar, and entirely without a south polar representative. The sea otter, which has been almost completely exterminated for its incomparable fur, is confined to the northern Pacific coasts of America and Asia. Its fully webbed hind feet adapt it to aquatic habits much more completely than any other of the Mustelidae, so many of which frequent fresh waters.

The circumpolar walrus (*Rosmarus*) is distinctively a coastal form. As it feeds on mollusks such as *Saxicava, Mya,* and *Cardium* by digging them up with its tusks, it requires shallow water, and is absent from the steep coasts of Greenland. The walrus lives continuously in the water during winter, but comes ashore on land and on ice during summer, especially at the breeding season, and is then covered with hair; during the winter it is hairless. It is gregarious, and was formerly very abundant. Nine hundred specimens were killed in the Bear

Islands in the year 1667 within a few hours. It is now present in numbers only on the northernmost of the arctic islands.

The eared seals (Otariidae) and the true seals (Phocidae) are well adapted to aquatic life, but they repair to land or ice for rest and sun and for longer periods at the breeding season and to produce their young. The eared seals are still able to travel overland and to land and climb on rocky shores, in spite of the transformation of their limbs into flippers. Phocidae, on the other hand, are much less mobile on land, and are accordingly confined to shelving coasts and low ice floes and to the immediate vicinity of the water. The crested seal, *Cystophora,* is sometimes found on ice whose border is 2 m. vertically above the water, and, like penguins, undoubtedly reaches this height by a single powerful leap.

Both seals and eared seals may make long migrations to reach their breeding grounds. The polygamous fur seals assemble in enormous numbers at their rookeries, dominating the landscape as do penguins and cormorants elsewhere. The rookeries of the fur seal (*Callorhinus ursinus*) in the Alaskan Pribilof Islands are well known [20,27] (Fig. 132). Even since the legal cessation of pelagic sealing, there has been a continuing pelagic loss of about 25% of the births for a given year. The killer whales are suspected of being the carnivore mainly responsible for this loss; 18 to 24 seals have been found in the stomach of a single one of these wolves of the sea.[15] The true seals, which are monogamous, do not gather in such large numbers. The Greenland seal (*Phoca groenlandica*) makes great journeys, from Greenland to Spitzbergen and to the Jan Mayen ice, where the young are born; *Phoca barbata* and *Cystophora cristata* do not have a breeding migration.

Coastal birds

The life of the seacoast is dominated by birds. Wherever there is a tide flat, low tide exposes a great number of marine creatures and provides a constant daily food supply for birds, which come in hosts to avail themselves of the opportunity. The supply is especially abundant when the wind is on shore and numbers of swimming creatures are stranded. The birds then follow the water's edge, and do not even avoid small waves. Yellowlegs, oyster-catchers, curlews, godwits, sanderlings, knots, and sandpipers all feed on the tide flats and at the water's edge, each in its own way. Various gulls join them, and ducks work over the residual pools. Driven out by the return of the sea, they fly inland to meadows and pastures, and so alternate

from seashore to dry land in accordance with the tides.[10,16] In seas and gulfs, as in the Baltic or Adriatic, where the tides are slight, such wading shore birds are only scantily represented, and they are likewise absent from precipitous coasts. Sand and mud shores with broad tidal flats afford them a rich food supply; gravel offers them little. Shore birds are largely world-wide in distribution so that the aspect of sandy coasts in this respect is similar in widely separated localities.

Precipitous coasts in all latitudes, lacking waders, may have a rich nesting bird life, mainly of more pelagic birds, and of diving birds like gannets.

The gregariousness of sea birds is literally forced upon them by the limitation of space in their linear environment. It becomes most pronounced in their breeding places, in which the concentration of life reaches a degree scarcely equaled elsewhere in such limited areas. These breeding sites differ according to the species of birds grouped together and according to the varying environment, presenting distinctive aspects in the major climatic zones of the world.

The wealth of marine life in the arctic seas supports an extreme number and variety of wading birds, and still more swimming forms. Relatively few of these live exclusively on fishes; the majority are plankton feeders, notably murres (*Uria*), which feed chiefly on *Mysis* at certain seasons, and terns (*Sterna*), which feed on small amphipods. Such feeding habits necessitate diving, since the spring melting of ice and snow covers the surface with the less dense fresh water, so that stenohaline plankton animals are absent at the surface. A superfluity of food is afforded in these seas only in spring and summer, and the scarcity of food in winter has driven many arctic marine birds to omnivorous habits. Gulls even devour the dung of the polar bear, and scavenge after foxes. The fulmar feeds on everything digestible offered by either land or sea—fish, plankton, carrion, and even plants.[28,31] Some, such as the glaucus gull, *Larus hyperboreus*, become robbers and nest plunderers. Social parasitism, the robbing of other birds of their food, is notable in the skuas and jaegers.

The longest known and most intensively studied of sea-bird rookeries are those of the Arctic. At the breeding season the birds are not uniformly distributed along the coast, since they select breeding sites presenting favorable environmental conditions, ice-free sea, with rich food supply, protection from storm, good insolation, and, above all, protection from predaceous mammals, especially the ubiquitous arctic fox. Some parts of western Greenland are accordingly very

densely populated with breeding birds, while northeast Greenland, with unfavorable ice conditions, has relatively few.[21] The west coasts of Spitzbergen, washed by the Gulf Stream, are more favorable than the east, and here as well as in the Bear Islands, the south and west exposures are protected from the raw north and east winds, and are most heavily colonized by birds.[28, 31] The density of the bird population may vary from year to year at the same locality. In King Charles Land, only 9 species of marine birds were found in 1889,



FIG. 127. A bird island: Eiderholm in southwest Iceland. After Hantsch.

when ice conditions were unfavorable, whereas 21 species were reported in 1898.

Arctic sea birds nest either on steep rock cliffs which rise from the sea or on small islands. The cliffs are inaccessible to predators, and the islands are, or become so, when the ice has broken up in spring. These two types of breeding places are adopted by different birds; the arctic sea birds may be divided into cliff breeders and island breeders.[21]

The northern eider duck (*Somateria molissima*) and the king eider (*S. spectabilis*, Fig. 127) form the principal element in the population of arctic bird islands. They take up their breeding residence only after the break-up of the ice. Where they are undisturbed they may nest so close together that it is impossible to walk without stepping on them.[23] Barnacle geese, knots, phalaropes, and terns are associated with the eiders. All live peacefully together and feed in the adjoining shallow sounds and bays.

Bird cliffs are usually vertical rock walls rising from the sea, populated at the breeding season with vast numbers of birds of rel-

atively few species (Fig. 128). Every ledge and inequality in the rock is occupied. The community may include only a few related species, as in Spitzbergen, or may be a varied assemblage, as in the Bear Islands. At Godthaabs Fiord, in West Greenland, a great cliff is

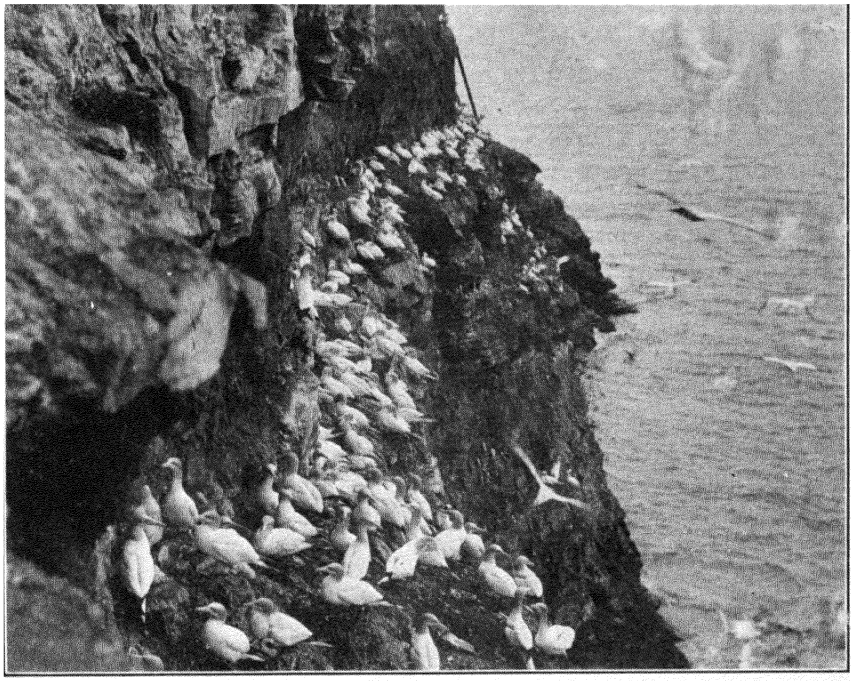


FIG. 128. A bird cliff: breeding colony of gannets on Bird Rock, Gulf of St. Lawrence. Courtesy The American Museum of Natural History.

occupied by the glaucus, Iceland, and kittiwake gulls, while in other localities the breeding birds may be mostly murres.[16] Each species usually has special habits. The vast numbers of birds in such rookeries as the cliffs of the Bear Islands can scarcely be exaggerated.[28]

Most of the inhabitants of the sea-bird cliffs, and especially the auks,* lay their eggs without a nest, directly on the rock. They usually have only one or two eggs, and press these into their body so that they are completely covered. The nest might be said to be in the parent's body. If these birds are driven suddenly up, they usually carry the egg up with them for a short distance.[16] When a boat touches at such a nesting cliff, the hosts of brooding birds rise up

* *Alca, Uria, Fratercula, Cepphus,* and *Plautus.*

suddenly and a shower of eggs may descend.[19] The "broodspot" lies posteriorly on the belly, near the legs; these birds hold themselves erect when brooding, and not in the horizontal position of birds with numerous eggs. The eggs of birds laid on bare rock tend conspicuously to a conical shape, which appears to be an adaptive character of importance, since such eggs roll in a small circle. Gulls built a nest, in which three eggs are usually laid; the altricial young, being few in number, are very amply provided for by the parents.

Birds of the islets have quite contrary characteristics. Ducks, especially divers, and geese have more numerous eggs, and provide them with a nest on a base of plant material, lined with down. The young are praecocial and very soon learn to forage for themselves under the guidance of one or both parents. Diving ducks and swans have relatively large eggs, so that the young hatch at a correspondingly advanced stage.

Many northern sea birds breed inland, on fresh-water ponds and lakes, at varying distances from salt water. This is true of the divers (Colymbiformes) and of most ducks, though the eiders are exceptions. Among divers and especially the sea divers (*Urinator*) the eggs are placed at the water's edge or on floating islands of vegetation. Such a location would be impossible on the seacoast on account of tides, waves, and drift ice.

With the advent of winter the arctic bird cliffs and bird islands are deserted. Some of the birds, like the fulmar, scatter far and wide over the arctic sea. One finds isolated specimens everywhere. Expert divers such as the murres (*Uria*) follow fish migrations. A large number of the European arctic birds wander southward along the Norwegian coast.[18] Shore birds are more completely migratory and spend the winter in the tropics or in the southern hemisphere.

Breeding colonies of birds in the Antarctic resemble those of the Arctic in many ways. The numbers of birds are similar, but the variety of species and the number of higher groups are smaller. The environmental conditions are much less favorable. The winter is less cold, but the summer is less warm, and the constant winds and long-continued cloudiness of the sky make the temperature factor still more unfavorable. The complete absence of predatory land mammals makes it much less necessary for the birds to breed on islets or cliffs. Where glacier ice does not form, the snow is largely carried away by the winds, and the remainder melts in the spring. Such places are densely colonized by breeding birds, which range onto high terrain. (Fig.

129).[1] At such sites there is abundant summer bird life. Penguins compose the principal element in antarctic bird populations. The penguin group is primarily antarctic, ranging from the coasts of Antarctica to the southern coasts of the land masses of the southern hemisphere, and ranging northward to the equator only in the cold waters of the Humboldt Current (see Chapter 20).

Penguins are like auks in many respects, owing to convergent

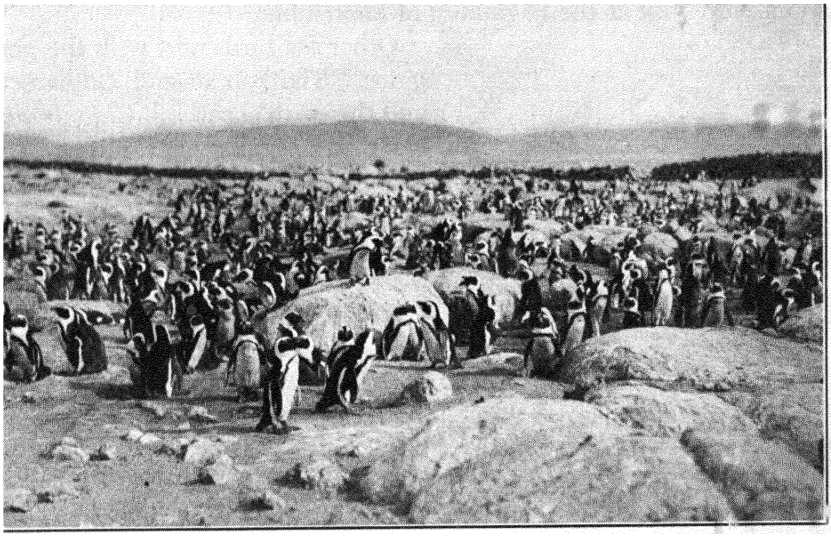


FIG. 129. Breeding place of the penguin *Spheniscus demersus* on Jutlen Island, South Africa. Photo by Rudyerd Boulton.

adaptive evolution, for they are not closely related. They are skillful divers, and their short strong wings are used as oars. The birds are reduced to complete flightlessness, as was the extinct great auk (*Pinguinis impennis*). The close-lying and oily plumage and the short legs placed at the extreme rear end of the body give penguins and auks a similar appearance when sitting. Penguins feed on fishes, cuttlefishes, crustaceans, etc., secured by diving. The Adélie penguins, for example, feed primarily on euphausids at certain seasons. The breeding places are recognizable from afar by the odor of fish and ammonia. Where the Adélie penguin breeds, the whole area is reddened by the pigment of the euphausid crustaceans in the dung of the birds. At the beginning of winter the breeding places are abandoned, and these penguins, in contrast with the emperor penguin, *Aptenodytes forsteri*, range northward in the sea, following the borders of the

pack ice. *Pygoscelis adeliae* migrates still farther to the north and does not return to its breeding places before the regular breeding season, even if ice conditions permit.[1] Like the auks, penguins have only a single egg (rarely two) and brood this by pressing it into a featherless brood pocket situated posteriorly on the belly, protecting it from below with the feet (Fig. 130). This effective protection of the egg makes it possible for the emperor penguin to breed in the antarctic mid-winter. The eggs are laid toward the end of June, and the young hatch out at the beginning of September.[2,7,12]

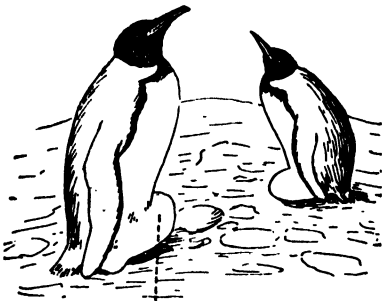


FIG. 130. Brooding penguins, *Aptenodytes patagonica*. After Murphy.

Other sea birds nest with the penguins. The robber-gull *Catharacta* and the small sheathbill *Chionis alba* carry on a regular egg robbery. The giant petrel *Macronectes gigantea* and a cormorant *Phalacrocorax atriceps* join the breeding colony. The three antarctic petrels, *Pagodroma nivea, Thalassoica antarctica,* and the Cape pigeon, *Daption capensis,* breed on inaccessible cliffs.[1]

Breeding places of sea birds in the tropics offer somewhat different phenomena. The birds gather from wide areas to small, uninhabited islands. Their numbers may be vast if suitable islands are far apart. The breeding seasons of different species may differ, or be successive, since there is no requirement of seasonal concentration of the breeding activity. Thus on Laysan (26° N. latitude in the Pacific) there are sixteen species of breeding birds, which distribute their breeding activities through the year. In July and early August tropic birds (*Phaëthon*) and terns (*Sterna*) are breeding; *Oestrelata hypoleuca* arrives promptly between the fifteenth and eighteenth of August; these in turn give way to the albatrosses in October, which arrive in such numbers that every available space is taken and many are compelled to go farther for lack of room.[32] This phenomenon may help to explain the varying breeding season of the same species on different islands. The shearwater *Puffinus assimilis baroli* breeds in Tenerife from February to April, in Porto Santo (Madeira) from March to May, and in Montana Clare (Canary Islands) from May to June. The same is true of the petrel *Oceanodroma castro*.[17] Such tropical breeding places may exhibit a concentration of bird life equal to that of the bird islands of the north. It is

curious that the birds often sit with bills pointing in the same direction and against the wind, which would otherwise ruffle their feathers (Fig. 131). The constant feeding operations of the parents in the north are replaced by a single daily feeding, which frequently is made at a particular time of day with pedantic regularity; on Laysan the albatrosses return with full crops between 3 and 4 P.M., while the tropic

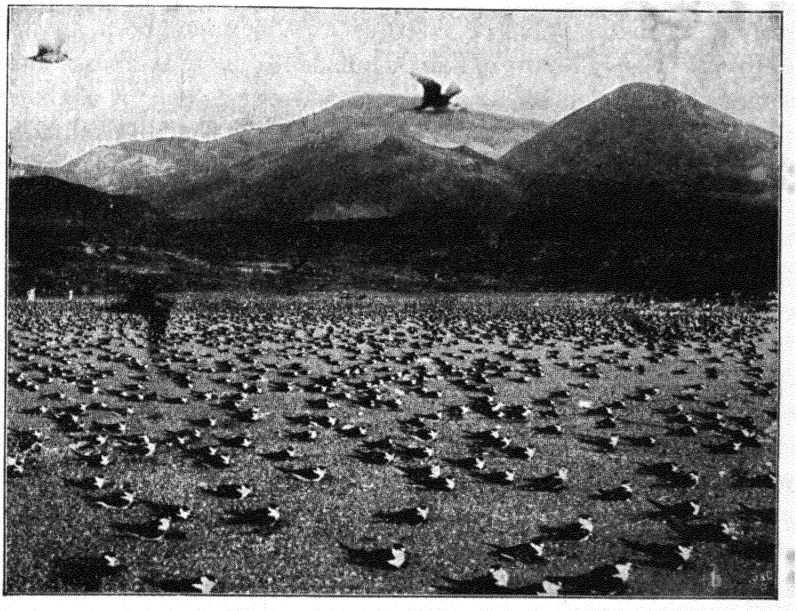


FIG. 131. Breeding place of *Sterna fuliginosa* on Ascension. All the birds sit with the bill against the wind, to avoid ruffling of their feathers. After v. Drygalski.

bird feeds its young between 9 and 10 in the forenoon. This procedure is possible because of the reduced food requirement of the tropical climate and is associated with the fact that the time for the development of the young is not so sharply limited.

Guano production on tropical islands has been mentioned above (Chapter 11). Wherever rainfall is slight or absent, as on the islands off the coast of Peru, the dried bird excrement may accumulate to great depths, originally more than 30 m. on the Chincha Islands. Dried by the tropical sun, the guano retains its nitrogen, which is not given off as NH_3. More than ten million tons of high-grade guano were shipped from these islands between 1851 and 1872. The principal guano producers are the cormorant *Phalacrocorax bougainvillii*, a pelican (*Pelecanus thagus*), and next to these the boobies (*Sula* spp.).

On the south island of the Chincha group a cormorant colony covers 60,000 sq. m., with three nests to the square meter, so that the assemblage includes 360,000 adult birds. Shearwaters (*Puffinus*) and dwarf penguins (*Spheniscus demersus humboldti*) breed in holes excavated in the guano. *Larus dominicanus* and two vultures * are the principal nest robbers.[8, 25]

The use of the guano on the Peruvian islands has a most instructive history. When the value as a fertilizer (which had been known to the Incas) was rediscovered in about 1843, an era of exploitation began that continued for some decades without a thought of the possible exhaustion of the accumulated deposits. The birds that produced the guano were disturbed, driven away, and even wantonly slaughtered. By the end of the century the outlook for further guano production was gloomy. The Peruvian government then took the wise step of a scientific survey, and a succession of foreign scientists was engaged to report on the problems of conservation and restoration involved. These were, successively, Robert E. Coker (1907–1908); H. O. Forbes (1913); Robert Cushman Murphy (1919–1920); and William Vogt (1939–1942). The organization of the guano industry under the control of the privately managed but government-controlled Campañia Administradora del Guano is now exemplary in its conservation of the producing birds and legitimate use of their guano as a "renewable resource." The story is well told by Murphy in *Bird Islands of Peru*,[25] and by William Vogt.[34a]

In coral islands used as breeding sites by oceanic birds situated in more humid regions, the guano is leached into the underlying limestone to form a valuable lime-phosphate fertilizer.[13]

The extent to which certain marine birds are "tied to the land" in South American waters forms a gradient as follows:

pelicans
cormorants
man-o'-war birds
boobies
tropic birds

Pelicans apparently never lose sight of the coast, and have occupied no remote islands except the Galapagos. Only the tropic birds regularly venture into the more distant stretches of blue water.[26] In the North Atlantic [36] the arrangement is:

* *Carthartes aura* and *Coragyps foetens.*

Inshore (the outer limit a few miles from the coast)—most gulls, cormorants, ducks.

Offshore (out to the edge of the continental shelf)—gannets, auks, murres, guillemots.

Pelagic (the open ocean)—petrels of all kinds, kittiwake gulls, and skuas; and jaegers and phalaropes at some seasons.

The distribution of sea birds in the Arctic during the nesting season is quite different.[11] Their feeding zonation is as follows.

Feeding Place	Sea Bird	Food
Littoral	Arctic tern	Mainly small crustacea
	Eider ducks	Larger crustacea and mollusca
	Mandt's guillemot	Fish
Deeper waters	Kittiwake	Surface plankton
	Brunnich's murre	Mostly plankton below surface
	Dovekie	
	Puffins	Largely fish
Anywhere	Fulmar	Anything

Man

Maritime communities of our own species are an integral part of the vertebrate life of seacoasts. Like those of other land mammals, man's activities are limited to inshore waters of iceless regions unless supplemented by ships. Aided by small boats, many such communities gain

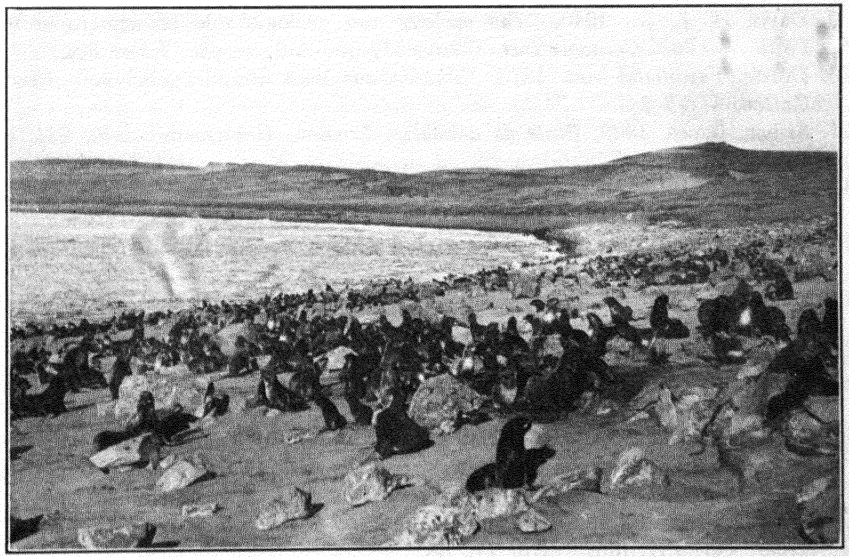


FIG. 132. Rookery of the fur seal *Callorhinus ursinus* on the Pribilof Islands. Photo by W. H. Osgood.

their livelihood by preying upon sea life, returning nightly to the shore. When larger vessels are available independence of the shore becomes greater, but even under these conditions, seafaring men normally rest and rear their families ashore and hence resemble, in their ecological characteristic, the sea turtles, seals, and sea birds that obtain their food from the sea and rear their young along its coasts.

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24. *Alpine Animals*

PLANT AND ANIMAL LIFE OF MOUNTAINS IS DISTINCTIVE AT HIGHER altitudes. Intermediate heights, in so far as they are wooded, have a fauna much like that of the near-by forested lowlands. As the conditions for forest growth change with increasing altitude and coniferous forests replace the mixed hardwoods, the fauna also becomes less varied. At still higher altitude, with lower temperatures and shorter duration of summer, tree growth ceases and new and peculiar environmental conditions present themselves for a characteristic high-mountain biota.

The region above timber line is referred to as the alpine zone in all parts of the world. Few even of the higher peaks and ridges in low mountains, such as the Hartz in Germany or the Appalachians in North America, extend into this treeless zone. Alpine conditions are much better defined when the peaks extend upward into the zone of eternal snow, which flows down into the valleys as glaciers. The zone between the snow line and timber line may be subdivided into a shrub zone, with stunted bushes and recumbent trees, a meadow zone with grasses and herbs, and a sub-snow zone of isolated rocks and patches of ground, which merges into the snow zone proper above. The altitude of the timber line depends on the latitude of the mountain range and on the direction of the slope, especially if north or south, and on the nature of the climate. The highest forests reach 4600 m. in Tibet; the alpine zone begins at 3600 m. on the south slope of the Himalayas, and at 2800 m. in the Colombian Andes; in the western United States timber line varies even at the same latitude (48° N.) from an altitude of 3500 m. in the Rocky Mountains to 2000 m. on Mount Rainier. In arctic Norway, at 74° N. latitude, it is only 260 m. above sea level. In insular New Zealand the snow line lies at about 2000 m. in summer at latitude 39° (mid-Colorado). The alpine fauna ranges downward into the forest zone along the glaciers, which may descend far below the normal timber line.

The peculiarities of the high mountain environment consist of the high altitude above sea level and the correlated phenomena of reduced atmospheric temperature and pressure and increased humidity, and in the steepness of the slopes, which combine to make such areas inaccessible and unfavorable to life. The isolation of high mountain areas from each other or from polar areas with similar conditions by wide stretches of lowland with a very different environment contributes greatly to the production of characteristic mountain faunae.

Low atmospheric pressure

Reduced temperature and lack of food, rather than rarefication of the air, limit upward distribution of invertebrates. Beetles reach the last outposts of meadows in the Himalayas, and butterflies and bees range up to 6400 m. on Mount Everest. Earthworms are found nearly up to the snow line in the Andes. A common Andean lizard, *Liolaemus multiformis*, reaches the snow line in Peru.

Vertebrates show varying resistance to reduction of atmospheric pressure. Distinct effects of lack of oxygen are shown by pigeons and men at 350 mm. (of mercury); by monkeys at 300 mm.; by cats at 270 mm.; by dogs at 250 mm.; by rabbits at 200 mm.; and by frogs not until 100 mm. is reached.[1] Symptoms of distress (mountain sickness) appear long before these pressures are reached in man and in some other mammals. The greatest altitude reached by mountain climbers without artificial oxygen supply is 28,000 ft. (8540 m.), by the Norton brothers in the Himalayas. With the aid of oxygen apparatus 29,400 ft. (8967 m.) has been attained on Mount Everest. The highest altitude where human settlements persist is at 4860 m. in west Tibet, while herds and herdsmen range up to 5500 m. A number of mammals live at higher altitudes in Asia, such as wild sheep and ibex, which reach 5800 m.; yaks, which go even higher; wolves, to 5600 m., and hares, to 5500 m. The more delicate races of dogs die in the Andes at 3900 m. within a few days.

Experiments by F. E. Lutz have shown that insects are extraordinarily resistant, not only to extremely low pressures, but to rapid alternation from low to normal pressures. Insects of various orders were found to survive exposure in a vacuum tube exhausted to the point at which ionic conduction of electricity fails, at $\frac{1}{10,000}$ mm. of mercury.[28]

Thinness of the air in high altitudes presents a mechanical handicap for flight in addition to the reduced amount of available oxygen. Vultures and eagles reach an altitude of some 7000 m.; this is during

flight when the oxygen supply is increased by air resistance.[43] The crow-like chough has been observed at heights above 8000 m. on Mount Everest making its take-off by running downhill. It did not fly far.[22] The condor, capable of living and of soaring flight at high Andean altitudes, can descend and feed at the ocean strand line along the coasts of Patagonia and Chile.

Numerous observations have been made of the effect on man and other mammals of the reduced pressure at high altitudes.[8,10,27,53,58] The first effect seems to be a concentration of the blood corpuscles resulting from the passage of blood serum through the walls of the blood vessels. There seems to be no doubt, however, that this is followed by an actual increase in the total number of red corpuscles with increase in the haemoglobin available for combination with larger amounts of oxygen. This appears to be a direct adaptation to the reduced oxygen supply at high altitudes. Peoples of high altitudes are noteworthy for large chest cavities, with increased lung capacity. This was observed by Humboldt in the Andes, and has been shown by exact measurements of the inhabitants of Cerro de Pasco,

Relation between Altitude (in feet and meters), Atmospheric Pressure (in millimeters of mercury), and the Pressure of Oxygen (in percentage of that at sea level) [4]

Altitude		Atmospheric Pressure,	O_2 Pressure, % of
Ft.	M.	mm. Hg	Sea Level
0	0.0	760.0	100.0
1,000	304.8	733.0	96.45
2,000	609.6	706.6	92.97
3,000	914.4	681.0	89.61
4,000	1,219.2	656.4	86.37
5,000	1,524.0	632.4	83.21
6,000	1,828.8	609.0	80.13
7,000	2,133.6	586.4	77.16
8,000	2,438.4	564.4	74.26
9,000	2,743.2	543.2	71.47
10,000	3,048.0	522.6	68.76
11,000	3,352.8	502.6	66.13
12,000	3,657.6	483.2	63.58
15,000	4,572.0	428.8	56.42
20,000	6,096.0	349.2	45.95
25,000	7,620.0	282.0	37.10
30,000	9,144.0	225.6	29.68
35,000	10,668.0	178.7	23.51
40,000	12,192.0	140.7	18.51

Peru (4302 m. altitude), who have a chest measurement of 92 cm. compared with 79 cm. in lowlanders of equal height.

Ascent to high altitudes by man and various other homoiothermal animals adversely affects their reproductive ability.[34] Eggs from sea level do not hatch at high altitudes; in controlled laboratory tests, pigeon and ring-dove embryos do not develop if kept throughout incubation at oxygen pressures less than ⅔ that at sea level. This reduced partial pressure of oxygen is found at an altitude somewhat below 3350 m.[42] (see table). In contrast the condor nests in the Andes up to 4800 m. at a decreased oxygen pressure of about 54% of that at sea level. Breeding performance of laboratory rats imported from altitudes of less than 300 m. was unaffected during a 2-month period on top of Mount Evans (about 4300 m.).[35] Similar rats subjected to 4-hour daily exposures to a simulated altitude of 5586 m. for 8 months or a year showed significant reduction in rate of reproduction in both sexes.[3]

Reproductive acclimatization in the high Andes takes place with sheep after a few generations, and the following brief table shows that the physiology of human reproduction is normal in regard to the birth rate of inhabitants of Peru.[34]

Altitude	0–2 km.	2–3 km.	3–4.4 km.
Population	2,251,700	1,596,000	1,742,200
Birth rate, %	28	26	26

More studies are needed both with expeditions to higher mountains and in the analysis of steady exposure to simulated high altitudes in comparison with the effects produced by extreme changes in atmospheric pressure repeated day after day.

Low temperature

The air temperature decreases with altitude at the rate of 1° for 140 m. in the Alps, 1° for 165 m. in the Caucasus, and 1° in 195 m. in the equatorial Andes. The long persistence of the snow and the shortened warmer season leave only two seasons in the alpine zone, a long winter and a short summer. The length of the season with mean temperature above 0° varies from six months at 2000 m. to only two months at 3100 m. in the Alps.[20]

These temperature relations exclude many animals from the alpine habitat. The fact that relatively large numbers of poikilothermal animals range up to the snow zone depends on the difference between ground and air temperatures, for, in consequence of reduced atmos-

pheric absorption, the temperature of rocks and soil on which the sun shines is considerably higher than that of the air. The difference between ground and air temperature increases with altitude, amounting to 1.5° at 1000 m., to 2.4° at 1600 m., and to 3.6° at 2200 m. The supply of radiant heat is of special importance to the invertebrates that live on or in the soil. North slopes, consequently, are much more impoverished in their animal life than are south slopes.[20] Snow affords protection against the extreme cold of winter to the hibernating invertebrates under it, for when the air temperature is −17°, the temperature of the snow varies from −15° at the surface to −1.6° at 52 cm. depth.[51]

The number of species present is steadily reduced with increasing altitude in every mountain range. Of the 240 species of snails known from Tirol in 1881, 80 ranged into the alpine zone and only 8 were known from the snow zone.[21] Similarly, of 96 species of butterflies in the coniferous forests of the Swiss Alps, only 27 ranged into the shrub and meadow zones, and only 8 into the sub-snow zone. Insects with complete metamorphosis, which appear to resist temperature changes better than those with incomplete metamorphosis, predominate in high altitudes. Reptiles are sparingly represented.

Low temperatures reduce the rate of development of many animals. All the insects of the alpine zone are accordingly small species that develop in a short period, such as the podurids. Many butterflies with two generations at low altitudes have only one in the mountains, *Pieris brassicae* and *Papilio machaon* being examples in the Alps. Others, which require a year for development in the lowland, require two in the alpine zone; *Pieris callidice,* for example, is abundant in the Swiss Alps on alternate years.[20] The lengthening of the larval period to one or two seasons has the result that the emerging butterflies may exceed the lowland specimens in size, the opposite of the usual size relations. *Echinopteryx silesiaca* is such an enlarged (two-year) form of the lowland *E. pulla,* and *Bombyx quercus* var. *callunae* of the Riesengebirge is similarly a biseasonal form of *B. quercus.*[41] Frogs may similarly be delayed in development and pass a winter as tadpoles.[15] Small passerine birds that normally raise two broods at lower altitudes raise only a single brood at higher levels.[5]

Humidity

The alpine zone in general has a more humid atmosphere than lower altitudes. Fog and clouds hang about the peaks; moisture is condensed and precipitated by the rise of the air to the cooler zone.

Increased humidity is thus associated with high mountains, though not necessarily so for all high altitudes, since the Tibetan plateau and the Great Basin in western North America are extremely arid, robbed of moisture by the surrounding mountain ranges. The storage of precipitation as snow, and the relatively short period during which melting takes place provide abundant and uniform soil moisture during the short growing season. Fogs, clouds, and melting snow aside, the reduced air pressure at high altitudes tends to increase the evaporating power of the air.

The melanism of many mountain animals appears to be correlated with increased humidity. Alpine insects, especially, tend to melanism. This is notably true of beetles of the families Chrysomelidae and Carabidae.[21] The appearance of black forms at high altitudes in Lepidoptera has been observed in the Alps, the Andes, and in New Zealand.[6, 20, 23, 41] Melanism, or dark coloration, is notable also among mountain vertebrates. *Salamandra atra* among salamanders, *Lacerta vivipara* among lizards, and *Vipera berus* var. *prester* among snakes illustrate this phenomenon in the Alps. Various rodents and other mammals are darker at high altitudes or have melanistic varieties that predominate in the alpine zone.[14, 16] This does not seem to be true of birds, certainly not with the pheasants of central Asia, where many birds exhibit a tendency toward blue and violet coloration, but not to melanism.[24] Dark coloration, by its absorption of radiant heat, may be even more important to alpine animals perhaps in association with protection from the increased proportion of ultra-violet radiation.[46]

Wind

Strong winds are frequent in high mountains. Animals of weak flight are adversely affected by such winds, for they are likely to be blown away into snow or ice fields. Alpine insects habitually conceal themselves when the winds blow, and fly only when the air is quiet.

Zonation

The regular reduction in temperature and pressure with altitude, and the inverse variation in humidity produce a zonation of the total environment, primarily for vegetation and secondarily, in partial dependence on the vegetation, for the animal life. These zones compare with the climatic zones that surround the poles, but their much closer approximation in the mountains makes them more immediately evident. In a single day one may climb from the lowland hardwoods through conifers to the alpine and the snow zone. A regular arrange-

ment of animal life corresponds to these climatic and vegetational zones. Thus the successive zones in adjacent mountain ranges may have similar faunae, as is beautifully shown by the chipmunks of the

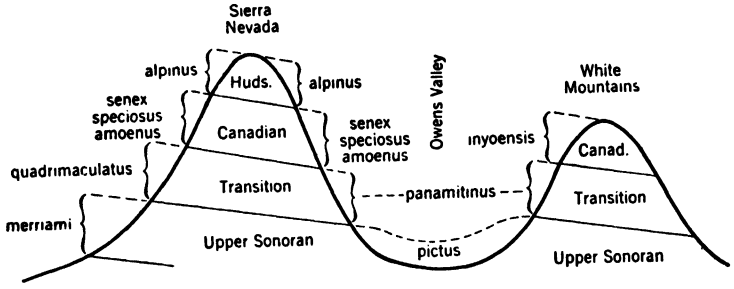


FIG. 133. Zonal distribution of the chipmunk *Eutamias*, shown in a cross section through the Sierra Nevada and White Mountains in California. After Merriam.

Sierra Nevada and White Mountains of California (Fig. 133).[31] The changes in the land snail fauna observable between central Europe and Spitzbergen correspond closely to those found in the Alps from

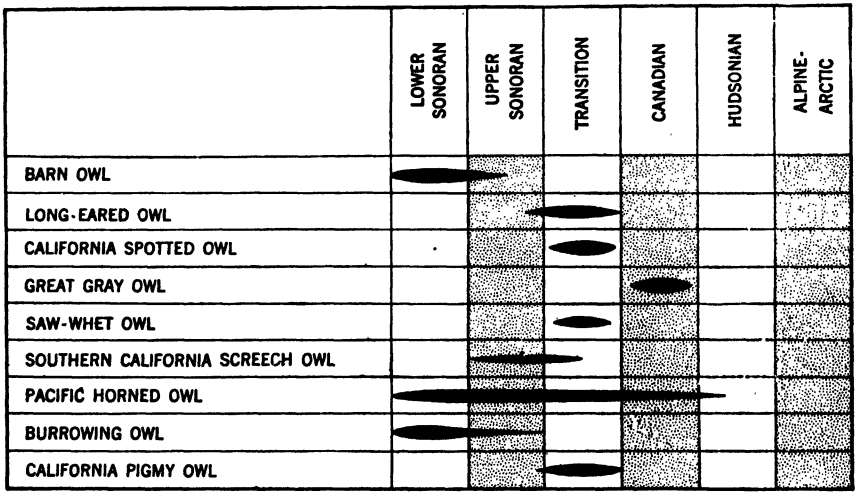


FIG. 134. Zonal distribution of the owls in the Yosemite region; an example of contrasting euryzonal and stenozonal distribution among related animals. From Grinnell and Storer.

their base to the zone of permanent snow.[29] In the ascent to the Abyssinian highland, the insects are essentially Saharan up to 800 m.; between 800 and 2000 m. they are Senegambian; from 2000 to 2800 m. they are Mediterranean, and above this European or even sub-

alpine. In the Chilean Andes two small species of butterflies (*Argynnis modesta* and *A. euterpe*) range to lower and lower altitudes to the southward, until they are found at sea level at the Strait of Magellan.[7] Similarly, the guanaco, a primitive camel, lives on the Patagonian plains and extends towards the tropics, limited to steadily increasing altitudes in the Andes. The most complete interrelations between the circumpolar and mountain zones are to be seen in North America, with its north-south mountain ranges; and animal distribu-

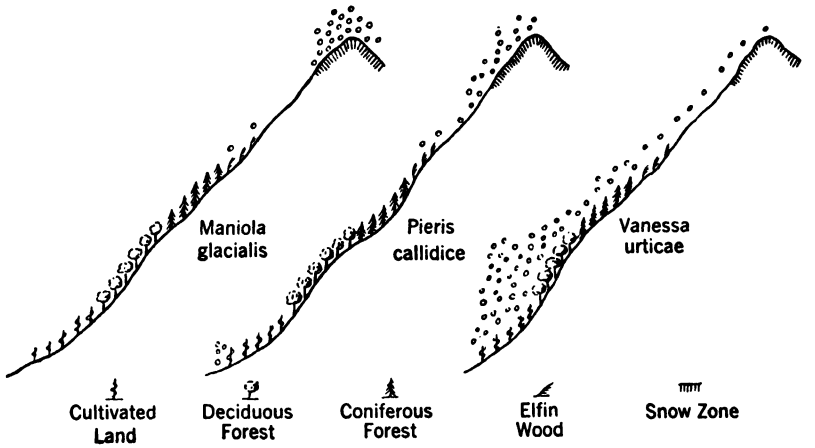


FIG. 135. Distribution of a snow butterfly, *Maniola glacialis;* an alpine form, *Pieris callidice;* and a lowland form accidentally reaching the snow zone *Vanessa urticae.* After Handschin.

tion in this continent has largely been studied with reference to these life zones.

This zonation does not mean that every species of animal is confined to a distinct zone. The closeness of this correlation varies among different animals, and we may distinguish stenozonal forms,[33] confined to a single zone, and euryzonal forms, which range through more than one zone. Grinnell and Storer,[19] in their account of the zonal distribution of the vertebrates of the Sierra Nevada, have diagrammed the zonal range species by species (Fig. 134). Schmidt has studied the mainly stenozonal salamanders of the genus *Oedipus* on the Guatemalan volcanos.[44] Invertebrates may likewise be either stenozonal or euryzonal. In the Alps the moth *Maniola glacialis* is stenozonal, *Pieris callidice* is less distinctly so, while *Vanessa urticae* is euryzonal (Fig. 135).[20] The butterflies of the genus *Parnassius,* favorites with collectors in both hemispheres, are strictly limited to the boreal zone of mountains in lower latitudes.

Difficult terrain

The steepness of slope encountered in high mountains is one of the characteristics of the mountain environment. Erosion is more active, owing to strong winds, steep gradients, and heavy rains. Temperature differences are extreme, and streams, swelled by melting snow, gouge deep ravines in even the hardest rock. Steep and vertical slopes thus are frequent. Rock surfaces may be laid bare even on less steep slopes, and coarse rock débris covers great areas. Rock slides, veritable rivers of rock, extend downward thousands of feet in the arid Chilean Andes, fed by the splintering rock at the highest levels.

Rock-inhabiting animals are thereby favored, in so far as they are otherwise adaptable to alpine conditions. Birds that nest in rocky situations, such as birds of prey and swifts, are abundant. Climbing birds, with the exception of the wall creeper, *Tichodroma muraria*, which has adapted itself to the rock and cliff habitat, are infrequent. Alpine mammals, on the other hand, are likely to depend on climbing adaptations. Chamois, ibex, yak, and mountain sheep have strong spreading hoofs. The American and Asiatic pikas and the chinchillas of the Andes are abundant among rocks. The pikas (*Ochotona*) depend greatly on the rock slides for concealment and for situations in which they store their hay. It must, of course, be remembered that rock-inhabiting animals of many groups may be equally represented in the lowlands or may not range at all into the mountain habitat.

Zonal endemism

The high mountain fauna may be classified according to its vertical distribution into true alpine, tolerant alpine, and accidental alpine forms. The true alpine faunal element consists of the minority of animals confined to the alpine zone, such as, in the Alps, the snow finch (*Montifringilla*), the wall creeper (*Tichodroma*), the marmot (*Marmota*), and the chamois; or ptarmigan and pika in the Rocky Mountains. Alpine-tolerant animals range naturally into the alpine zone from lower levels. The viviparous lizard, the European redstart (*Phoenicurus*), and most of the meadow mice (Microtinae) of the Alps are examples. Accidental alpine animals are those that temporarily or incidentally enter the alpine zone but do not develop there. Migratory birds and insects carried by wind compose the majority of this element of the alpine zone.

Isolation

The wide separation of individual mountain ranges may make their alpine zones insular in character—separated by lowlands impassable to their stenozonal inhabitants. Endemic forms are accordingly frequent in mountains. The high mountains of Eurasia are especially discontinuous, contrasting in this respect with the Rocky Mountains and Andes of the western hemisphere. Speciation results from such isolation. The Old World ibexes, for example, fall into a series of species —the common ibex of the Alps, the Caucasian, Sinaitic, and Abyssinian species, and finally, the various ibexes of central Asia, which are divisible into numerous subspecies. Chamois and wild sheep develop distinct subspecies on individual ranges. The same is true of many birds, such as the partridges (*Caccabis*) of Eurasia, the hedge sparrows (*Prunella*), and the mountain-inhabiting snow finches (*Montifringilla*). Species formation by isolation is notable in the hummingbirds of the Andean peaks. Extremely isolated mountains, like Mount Kina Balu in Borneo, develop a completely distinctive fauna. This subject was discussed at greater length in Chapter 6.

Environmental selection

The peculiarities of the alpine environment all represent divergence from optimum conditions and accordingly operate as selective influences that exclude many animals. This selection increases in intensity with approach to the snow line. Thus the highest peaks exhibit great similarity of faunae. The same systematic groups supply the animals of mountain peaks in Eurasia and Africa. The sub-snow zone fauna of Mount Kilimanjaro of Africa has almost all the beetle genera of the same zone in the Alps.[2] The close relationship or even identity of the species and genera of butterflies in the alpine zone of widely separated mountain ranges is astonishing.[38] The high mountains of Africa, although widely separated in latitude, all have closely similar bird faunae.[9] The high mountains of Java and the Philippines present striking relationships with the alpine animals of Asia.[24,25] It is certain that ecological selection has played a part in these relationships of montane faunae, partly by providing refuges for relict forms freed from some of the biotic competition encountered in the lowlands. The vertebrate fauna of the Alps provides an example of the general tendency for mountains to furnish one of the geographic refuges for relict animals (cf. Chapter 7).

Review of alpine faunae

Insects are important in alpine faunae. Orders with a complete metamorphosis predominate, with Hemiptera and Orthoptera sparsely represented, though Collembola are present in considerable numbers. At high altitudes insects are dependent on the heat of the sun-warmed earth, for they require a certain minimum temperature to function, 12° to 15° in butterflies, which is higher than the air temperature at high altitudes in the alpine zone. Since both ground and air temperatures fall below this limit at night, nocturnal insects are ruled out, and such noctuid and geometrid moths as occur are forced to adapt themselves to diurnal life.[20] Once in flight, the muscular motion generates enough heat to make some insects less dependent on that of the environment. As a means of conserving this internal heat, many alpine insects have a dense hairy covering, especially notable in the bumblebees but also found in many flies and in the butterflies of the genus *Parnassius*.

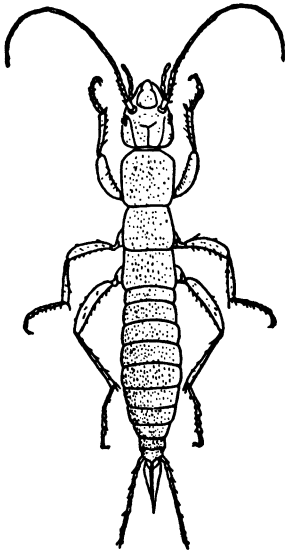


FIG. 136. *Grylloblattodea campodeiformis* (×2), representing an order of insects thus far known only from the alpine zone of mountains in North America and Japan. After Essig.

Many wingless or flightless insects are found in the alpine zone, especially among grasshoppers and ground beetles (Carabidae). The most abundant alpine beetles are wingless, and even genera only with winged species in the lowlands may be represented at high altitudes by wingless forms.[50] Darwin thought that flying beetles tend to be blown away from exposed habitats, leaving a selected wingless stock to occupy islands or island-like mountains.[12] Results from a re-examination of the distribution of ground beetles indicate that populations with reduced wings are found in sheltered as well as in exposed mountain habitats. Underlying causal factors are complex. Carabid mutants with reduced wings show inherent general superiority over fully winged forms and tend to be selected in regions such as mountains in which the survival value of flight is reduced.[11]

Grasshoppers are the only Orthoptera of the alpine zone, and they are found principally in the lower portion where a more abundant

vegetation and longer season enable them to develop. Hingston found grasshoppers as high as 5490 m. on Mount Everest.[36] Only a few species are confined to the alpine zone. *Podisma frigida* in the Alps represents these truly alpine forms, which usually have stocky bodies, are densely haired, and have thick and somewhat bent legs.[40] A large proportion of the alpine Orthoptera are flightless, in both Old World and North American mountains.[45,54] Fifty-four per cent of the mountain species of grasshoppers in Carinthia have reduced wings.[40]

The order Grylloblattodea, a primitive group related to the Orthoptera, is known only from four alpine species in western North America and Japan. These small wingless insects are often confined to the zone of melting snow, where they apparently subsist on the remains of insects and plants that have been killed during the advance of the snow field.[13]

The Lepidoptera of the alpine zone are conspicuous by reason of their vivid coloration and active flight. Their period of activity is short, and, as all the individuals of a species emerge at once and as the suitable areas of occurrence are small, their numbers are apparently great. Alpine butterflies in general fly low, on account of the stronger winds at higher levels. Certain moths and butterflies, the parnassians among them, flatten themselves to the ground in sheltered nooks facing the wind and fly only when the wind is relatively quiet; others make rapid darts from one shelter to another.[22,30] Caterpillars and pupae are found nearly up to the snow line. The adults, which are more exposed to wind action than other insects on account of their relatively large wings, are often carried far above the snow line; they were seen at 5900 m. on Chimborazo by Humboldt, and are recorded from 6300 m. in the Himalayas. Some Lepidoptera, like the satyrid *Maniola glacialis*, are stenozonal and restricted to the snow border.[20] *Bombyx alpica* is so exactly adapted to the alpine environment that attempts to bring up the larvae or to transform the pupae at low altitudes have failed. The total number of high-mountain species is small. Of 785 species of Lepidoptera in the Tirol in Heller's lists,[21] more than half are Microlepidoptera, and only 271 (55 out of 122 butterflies) are truly alpine.

Beetles of the alpine zone are much less conspicuous than the butterflies. They are for the most part concealed under stones, in excrement, in the earth, or in blossoms. Most of them are small and inconspicuous forms, likely to pass unnoticed. It is accordingly surprising to find that the highland of Tirol has about the same number of species of beetles as of Lepidoptera. In the whole of Tirol about 4000

species of beetles were known by 1854, of which 783 occurred in the mountains, and of these 272 were typical alpine forms. This latter series is composed mainly of staphylinids, carabids, weevils, and chrysomelids. Many beetles such as the small carabids of the genus *Nebria* develop close to the snow line.

Hymenoptera are few in the alpine zone. Ants and wasps are relatively poorly represented. Sawflies and parasitic forms, which find more abundant food supplies, are better represented. Bees, on account of the large number of bumblebees, are relatively the best represented of the hymenopterous families. According to Heller, 24 of the 26 Tirolese species of bumblebees reach the alpine zone, and some of these range to the snow line. The predominance of bumblebees appears to be correlated with their adaptation to low temperatures by means of the dense hairy covering of their bodies (cf. pp. 471 and 612).

Collembola range into the snow zone itself. The best-known form, the glacier flea, *Isotoma saltans,* ranges up to 3800 m. in the Alps. Thirty-two of the 95 species of Collembola known from Switzerland occur in the snow zone. Many species are ubiquitous widespread forms such as *Entomobrya nivalis* and *Isotomurus palustris.* Others, like *Isotoma saltans* and *I. westerlundi,* are stenozonal and confined to snow and ice. The latter are black or dark blue, and are consequently quickly warmed by the sun's rays. At night they are frozen rigid and freeze fast to snow and névé.[20] They feed on the pollen of conifers, which blows into the alpine and snow zones. Their numbers may be countless, so that snow and ice are blackened by them. A few other extremely resistant organisms occur with the Collembola. The "red snow" of the Aar glacier (colored by algae) contains also a tardigrade and the rotifer *Philodina roseola.*[37] Just as the reindeer is preyed on by the wolf, and the baboon by the leopard, minute predators are found feeding on snow-zone Collembola, mostly mites of the families Bdellidae, Trombidiidae, and Gamasidae.

Mountaintops, especially in the tropics, may swarm with flying insects apparently carried by the winds, since they neither develop there nor feed there as adults. Arachnids are abundant in the highlands, especially spiders, harvestmen, and mites. Hingston found an attid spider at 22,000 ft. (6710 m.) on Mount Everest.[36]

The snails of the alpine zone, like the insects, consist of a majority of widespread forms and a minority of alpine species. Of 90 forms in the alpine zone of the Tirol, 24 are alpine-limited. Moisture- and cold-tolerant forms predominate, and bush and tree snails are absent.

The stenothermal cold-tolerant species of the genus *Vitrina* are widespread in the mountains of the Old and New Worlds, ranging up to 3000 m. in the Alps and to 4400 m. on Kilimanjaro.[52] Rock snails of the genera *Clausilia* and *Campylaea* are abundant. Reduction in size of the shell is frequent with increasing altitude of the habitat of the specimens.[48] The snow-zone *Vitrina annularis* and *V. nivalis* appear to be dwarf forms of *V. pellucida* and *V. diaphana*.[20] Snails of the same species are about twice as large at 2800 m. near Chini, in Tibet, as at 4000 m. near Spiti.[47]

The presence of amphibians at high altitudes depends on the presence of sufficient moisture and on their adjustment to low temperatures. In the higher parts of Tibet, where snails are extremely scarce on account of the dryness of the climate, frogs and salamanders are absent,[57] though both range to great altitudes in eastern Tibet and western Szechwan.[26] In the humid Paramo zone (alpine zone) of the Andes, frogs of the genus *Telmatobius* are abundant to the snow line at 4550 m.[39] The distribution of this genus seems to be definitely cold-limited. It is found everywhere in the Andes from the equator southward, descending in streams to about 6000 feet, as far as the water remains cold. In Chile its species appear at lower levels. *Bufo spinulosus* is likewise found at the Paramo level, its strings of eggs often found in streams flowing beneath a film of ice. *Telmatobius* in high-altitude lakes (e.g., *T. culeus* in Lake Titicaca) tends to forms with folds of loose skin, which are interpreted as an accessory breathing apparatus. Still other frogs of high-altitude lakes in Peru, like Lake Junin (4100 m.) are large forms with conspicuously flattened bodies (*Batrachophrynus*). The highest known occurrence of an amphibian is that of the green toad, *Bufo viridis*, at 5000 m. in the Himalayas. In the Alps the altitudes reached by frogs and toads depend on the length of their larval life, corresponding to the period during which the breeding pools are free from ice, which decreases with altitude. This is shown in the table[56] given in the footnote.*

Rana temporaria has no external adaptations to life at these high altitudes. It has a relatively larger heart than *Rana esculenta*, which

*

Species	Length of Larval Life, days	Altitude Reached, meters
Rana temporaria	85–95	2500–2600
Hyla arborea	80–98	2200
Bufo bufo	110–120	2000–2100
Alytes obstetricans	120–130	1500–1650
Bombina bombina	124–134	1200–1500

is confined to the warmer lowlands, and this may give it an advantage in increased metabolism and may tend to save it from fatal freezing, since frogs recover from freezing if the heart itself is not frozen. The newt *Triturus alpestris* ranges to 2500 m., and the viviparous *Salamandra atra* ranges up to 3000 m. and does not occur below 850 m. The duration of development in S. *atra* is two years at lower levels and probably three in the alpine zone.[55] In the Himalayas and western Szechwan, the curious pelobatid frog *Aelurophryne mammata* ranges to an altitude of 4500 m.

Reptiles are so characteristically stenothermal warmth-positive animals that the low temperatures of the alpine zone exclude most of them. In the Alps only three species reach the alpine zone: the viviparous lizard to 3000 m., the common viper to 2750 m., and the blindworm to only 2000 m. The grass snake *Natrix natrix* ranges up to 1650 m., but this is below timber line. The three alpine species, belonging to very diverse groups, are all viviparous, and this is the characteristic that makes possible their entry into the cold alpine zone. There would not be enough heat to bring reptilian eggs to complete development and hatching, but the viviparous female lizard or snake is able to keep the sun. The same three viviparous species are the only reptiles found in Scotland, though there are egg-laying forms in England. The highland chameleons of Central Africa, ranging up to 3200 m.,[49] are viviparous. The common African skink *Mabuya varia*, also viviparous, ranges up to 4000 m. on Kilimanjaro. The lizards of the genus *Phrynocephalus* in central Asia are oviparous at low altitudes * and viviparous at higher levels. †[57] The genus of iguanid lizards *Sceloporus* includes both ovoviviparous and oviparous species in Mexico. All of the species found above 10,000 feet in the mountains are viviparous, while most of the species in the tropical zone are oviparous. In Chile certain iguanids, ‡ ranging to 3000 m., are also viviparous.[7] More lizards than snakes range into the alpine zone.

Shortening of the limbs appears to characterize some of the skinks (*Leiolopisma*) in the mountains of western China, and great reduction or disappearance of the auditory apparatus is frequent in both frogs and lizards of the same region.

Homoiothermal animals are much more independent of the temperature limitations of high mountains than are cold-bloods, but are

* *P. forsythi* and *P. axillaris.*

† *P. erythrurus* and *P. theobaldi.*

‡ *Liolaemus bürgeri* and *Phymaturus palluma.*

still limited by oxygen and food requirements. It is astonishing with what scant food alpine mammals are able to live—the powerful yak, for example, which survives on pasture in which cattle would starve, seems to prefer hard and dry grass and eats lichens and moss. Many mammals of high altitudes are more sensitive to heat in summer than to cold in winter. Food scarcity and severe weather can be avoided by migration, and alpine mammals make regular seasonal migrations upward and downward. The marmot of the Alps moves downward to hibernate at the timber line. Areas with much snow and unusually snowy seasons increase these downward migrations.[32] The increase of size in the colder zones, in accordance with the Bergmann Rule, is a familiar phenomenon in the alpine zone. Thus in the Alps the wood mouse (*Apodemus sylvaticus*) and the meadow mice * are larger in the alpine zone than in the valleys.[17] The short-eared and compact Microtinae range to greater heights than the Muridae. The alpine shrews † are among the largest forms of their groups.

Reduced competition in the alpine zone may be related to the fact that a considerable number of mammals enter this treeless zone; many of them are relatively primitive. Most truly alpine mammals are herbivores. The predaceous mammals are mostly euryzonal forms that range into the alpine zone only when there is a sufficient food supply to tempt them. The snow leopard seems to be exceptional in this respect, being somewhat more closely confined to the high levels in central Asia. The herbivores include rodents, ruminants, and hyraces. Some of the more northern mustelids in North America, such as the wolverine, range southward in the Rocky Mountains, where they are confined to the alpine zone.

The smaller alpine rodents include numerous euryzonal forms, but some, such as *Microtus nivalis* of the Alps, are stenozonal and range to 3500 m., the highest altitude reached by mammals in Europe. The larger forms, like the marmots, range to 3000 m. in the Alps and central Asia. The chinchillas and their allies (*Lagidium*) in the Andes are abundant at 3000 m., and range to 5000 m.

Ruminants include a wide variety of forms, but principally sheep, goats, and (in the Old World) antelopes. The yak of central Asia is the only bovid of high altitudes, and the musk deer of the same region represents an isolated group. Wild sheep and goats seem to be almost entirely mountain animals, sure-footed and capable of extraor-

* *Evotomys glareolus nageri* and *Microtus arvalis.*

† *Sorex alpinus* and *Crossopus fodiens.*

dinary leaps. The goat-antelopes are characteristic, mostly stockily built and short-necked forms, which are usually associated as the subfamily Rupicaprinae. The chamois (*Rupicapra*) of the Pyrenees, Alps, and Caucasus is the most familiar European form. The Rocky Mountain goat (*Oreamnos*) represents the group in North America. Central Asia, with serow (*Capricornis*), goral (*Nemorhaedus*), and takin (*Budorcas*), and the orongo (*Pantholops*), which is a true antelope, exhibits a wide variety of forms. Goats, sheep, and antelopes are entirely absent from South America, where their place is filled in the Andean alpine zone by the camelid llamas, alpacas, vicuñas, and guanacos; the last extends to sea level in Patagonia. There are no corresponding montane antelopes in Africa.

Insectivorous birds are relatively few in the alpine zone on account of the scarcity of their normal food. Ground birds are perhaps best represented. The number of true migratory birds (distinguished from those with local vertical migration) is small, their proportion in the Alps being four to three at low levels, one to one in intermediate altitudes, one to three in the lower portion of the alpine zone, and only one to five as the snow zone is approached.[50] A considerable series in the Old World represents very widespread forms, with local races in central Asia, the Alps, and the North African mountains.

Many features of animal distribution in mountains are radically different in the western hemisphere, with its north-to-south mountain ranges, from those that obtain in Eurasia, where the general trends of the high mountains are east and west. The importance of this difference of direction for the dispersal of animals is discussed in Chapter 5.

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25. *The Animal Life of Polar Regions*

ENVIRONMENTAL CONDITIONS OF POLAR REGIONS EXHIBIT MANY SIMILARities to those of high mountains. Daily and annual temperature means become steadily lower as one ascends mountains or approaches the poles. With lowered temperature, the greater proportion of the precipitation is stored as snow, whose accumulation gives rise to mighty glaciers. Abundant ground moisture is provided in places freed from snow by sun and wind. Long winters are followed by short summers. Not until the end of May or the beginning of June do the great quantities of snow disappear from level ground, and the storms precursing winter begin in August. Eternal snow covers even low elevations, and sometimes vast areas, like the inland plateau of Greenland. Glaciers reach sea level.

But where the sun is not impeded by fog and where the snow has been blown thin by winds, the ground is quickly freed of its icy mantle and is warmed, together with the lowermost layers of air, to several times the temperature of the air above. Favorable conditions are thus produced for small poikilothermal animals, particularly in regions with southern exposure and with sufficient slope to allow the ice water to drain away as melted. Regions lacking such drainage or with northern exposures present much less favorable living conditions. At Bel-Sund, Spitzbergen, on the seventh of July, when the ground was frozen below 30 to 35 cm., and the air temperature at the height of 1 m. was +4.7°, the temperature just above the low plants was +15.5°. The warm air flows upward on slopes and assists in melting the snow; slopes with green turf and flowering plants develop in hills up to heights of more than 300 m., and these enable animal life to gain a foothold. Plants with deeper roots, and especially trees, are necessarily wanting in the circumpolar tundra on account of the frozen sub-

soil. The tundra is the treeless zone north of the line (or zone) of permanently frozen subsoil, in arctic America and Eurasia, with only an obscure counterpart on antarctic islands, Antarctica itself being essentially ice-bound the year around. The tundra vegetation is characterized by sphagnum moss in hollows, with low herbaceous flowering plants on higher terrain, and an abundance of lichens.

Environmental differences between the high mountains and the tundra consist in reduced pressure at high altitudes and in the great annual difference in the distribution of sunlight. The long midsummer days in the polar regions enable animals to search for food without interruption. Many birds and insects need little sleep or rest. The domestic fowl requires only three hours, and ants have been observed to work by moonlight.[5] Petrels in South Georgia may be active during the entire 24 hours; ducks are active day and night on Lake Myvatn in Iceland. Bumblebees, among the insects in the subarctic, continue to work without regular rest.[8] This amounts to a great increase in the effective working and feeding time, in the short summer. The long day also favors the growth of vegetation. Grass springs up, and many plants are able to bloom and ripen seed in spite of the short season; this is important for polar animal life.

Antarctic life

The Antarctic, with its isolated land mass and high mountains, affords an extreme contrast with the Arctic. The winters are less cold, but the summers less warm than in the Arctic. The low annual temperature in itself does not prevent the development of plant and animal life in Antarctica, if only the distribution of heat is such that the summers are sufficiently warm. On Seymour Island, for example, at 64° S. latitude, about the latitude of Drontheim in Norway, the warmest month (January) has a mean temperature of −0.9°, and that of the three summer months is −2.15°. In the Antarctic the summer temperature remains almost constantly below the minimum for the development of higher plants. There are consequently only two flowering plants, a grass and a *Colobanthus,* on the continent of Antarctica and its near-by islands, and only a few species of mosses and algae maintain a precarious existence, whereas some 400 species of flowering plants grow north of the Arctic Circle;[24] even on west Greenland, 600 miles north of the Arctic Circle, Ekblaw reported 120 species of flowering plants including chickweed and dandelion. The subantarctic South Orkney Islands at 61° S. have no flowering plants, although a hundred species bloom in Spitzbergen in summer

at 79° N. Land vertebrates are absent in Antarctica; birds and mammals present are usually directly dependent on the wealth of life in the sea. The dependence may be indirect, as when the skua preys on the eggs and chicks in penguin rookeries. Invertebrate life in the Antarctic is also surprisingly poor, and there is almost no land fauna away from the penguin rookeries where one may find minute springtails, a wingless chironomid fly, tardigrades, mites, a few rotifers, and two or three protozoans. They are active for but a few days at most during the year and can exist for months, perhaps for years, in a frozen state.[24] The only widely distributed species of antarctic insects are parasites on seals.[7]

Arctic land life

The land fauna, independent of marine life, is far from rich in the Arctic. The number of species and of individuals decrease to the northward as they do with approach to the snow-covered zone in the mountains. Relatively few species are able to survive the rigid selection by the severe environmental conditions. The composition of the fauna that survives this selection exhibits a similarity with that of high mountains in the groups represented. The arctic fauna is composed in large part of widely distributed (euryzonal) forms that range northward from more temperate latitudes, with a smaller element of local (stenozonal) species absent to the south. Thus of 565 arctic Hymenoptera, only 86 species are confined to the North Polar Zone.

Many arctic animals range to the alpine zones of high mountains without specific difference or are found to have representative forms on mountains in lower latitudes. Examples include butterflies like *Lycaena orbitulus,* which occurs in Labrador, arctic America, and Lapland, and reappears in the Pyrenees, Alps, and in the mountains of central Asia, though wholly absent in the intervening areas; breeding birds, like the arctic ptarmigan, with related forms in the Alps and in the high Rockies; and the arctic hare, *Lepus timidus,* which is closely related to *Lepus varronis* of the Alps. Such distributions are understandable when the alpine forms are interpreted as glacial relicts. Some such animals are widespread and range through the intervening lowlands, like the collembolan *Entomobrya nivalis,* the tardigrade *Macrobiotus macronyx,* or the snail *Euconulus fulvus.* For migratory birds the lowlands obviously do not constitute a barrier.

Arctic insects

Not all the orders of insects are represented in the Arctic. The Thysanura are absent, as are the panorpids. Others, like the mayflies, forficulids, and neuropterans (in a wide sense) are, in general, rare. In the enumeration of the known species in the *Fauna Arctica* in 1902, the number of species of insects in arctic Scandinavia was 2596, 437 in Greenland, 326 in Iceland, 208 in Nova Zembla and Waigach, and 94 in Spitzbergen and the Bear Islands. Of Hymenoptera 380 species are known from Scandinavia north of 65°, 66 in Greenland north of 60°, 31 in Nova Zembla (71°–76°), and 15 in Spitzbergen (76°–81°).[8,11] The proportion of species of the separate orders in the Arctic is quite different from that in the world as a whole. As in high mountains, Diptera predominate, and during the short summer season mosquitoes are a veritable plague; they are followed in importance by Hymenoptera, Coleoptera, Collembola, and Lepidoptera. The proportions of species for the orders are as follows:

	Diptera	Hymenoptera	Coleoptera	Collembola	Lepidoptera
The Earth	11.4%	14.3%	44.9%	1.2%	15.6%
Greenland	43.0	15.1	9.3	3.2	10.5
Nova Zembla	47.4	27.0	9.3	8.8	5.8
Spitzbergen	70.0	18.6	0.0	7.2	2.1

The type of food available as well as the resistance to cold of the various groups in both adult and immature stages govern the composition of the fauna. Insects that feed on green plants disappear to the northward much more rapidly than those dependent on plant remains or on animal food. The separate orders afford a variety of further observations.

Springtails (Collembola) occur on snow and ice, just as they do in the high mountains. The snow flea of Spitzbergen, *Isotoma nivalis*, is only half as large as the alpine *I. saltans*, but occurs in equal numbers, forming black aggregations to the extent of a square foot. A series of cold-resistant forms, including infusorians, rotifers, nematodes, and tardigrades,[25,28] is associated with *Isotoma* in this habitat. Eight species of arctic-alpine collembolans are known.[10]

Grasshoppers are represented by only a restricted number of forms that range into the arctic from the south. A few Corrodentia and Dermaptera reach Greenland. Homoptera are represented by a few species of aphids. A few Heteroptera, such as the shore bug *Acanthia* and the resistant lygaeid genus *Nysius*, are also found in the snow zone in the Alps.[4] The beetle fauna is notably poor. There are arctic-

alpine forms such as the dung beetles, among which 10 of the 12 species in arctic Norway live also in the Alps.[20]

The relation between montane and arctic butterflies is especially noteworthy. Many genera * are represented in the Arctic and in high mountains as well. Hawk moths and bombycids are infrequent in both, while noctuids and geometrids have common species and genera. The same is true of Microlepidoptera. This similarity applies to the mountains of Eurasia and North America, and extends even to the southern hemisphere in the Andes.[26] In general, small species are characteristic of the polar region. The larvae are usually omnivorous, feeding even on the resistant grasses and shrubs. Their period of growth often extends over two years, as in high mountains. The small arctic form of the widespread *Vanessa urticae* can be produced experimentally by subjecting pupae of the same species from temperate latitudes to cold. Endemic forms, confined to the arctic zone, are few.

Among Hymenoptera, the Tenthredinidae and Ichneumonidae (in the Linnaean sense) are the best-represented families. Ants are represented by only a few species of the genus *Lasius*. Among bees, the bumblebees predominate, especially in the extreme north. Their plump bodies with small surface relative to size, and dense hairy covering, conserve the heat generated by the rapid vibration of the wings. Bumblebees may accordingly be active in cool weather when other insects are unable to fly. They become larger and more rough-haired to the northward, as they do with increasing altitudes in mountains. *Bombus consobrinus* of arctic Norway is larger than the largest forms of the lowlands (*B. terrestris* and *B. hortorum*), though shorter haired; *B. kirbyellus*, which reaches 77½° N. in west Greenland, is still larger, broader, and more hairy; *B. hyperboreus*, which occurs everywhere in the Arctic, is the largest and hairiest species of all. The larger species emerge from hibernation as early as the first of June; the smaller do not appear until the middle of July.[8] As these creatures continue their work during the bright summer nights, they accumulate a food supply sufficient to ensure the development of their larvae in a single season.

Other poikilotherms

The number of species of spiders diminishes greatly to the northward. There are 219 species in Lapland, 46 in Greenland, and only 29 in the arctic islands.

* *Pieris, Colias, Polyommatus, Lycaena, Maniola, Oeneis, Vanessa, Argynnis, Melitaea,* and *Syrichthys.*

The land and fresh-water snails of the Arctic are all very small. They occur principally at the borders of springs. In Norway, favored by the Gulf Stream, 50 species range beyond the tree limit. Twenty-four species have been found in Iceland, and 9 in Greenland. These northern forms are principally widespread species.* *Helix* (*Acanthinula*) *harpa,* which occurs in northern Scandinavia, Kamchatka, and Canada, is known from a single locality in the Alps, at 2000 m. altitude.

As in high mountains, reptiles and amphibians are few in the Arctic. In Eurasia the frogs *Rana temporaria* and *Rana arvalis* range northward beyond the Arctic Circle. *Rana sylvatica* (the American representative of the Old World *temporaria*) is found in Alas[1]a, at Great Bear Lake, and in Labrador. The swamp tree frog of the American Great Plains, *Pseudacris nigrita,* also reaches the Arctic Circle at Great Bear Lake. A single species of salamander, *Hynobius keyserlingii,* ranges north of the Arctic Circle at Verkhoyansk in Siberia. No reptile reaches the Arctic Zone in North America; in Europe the viviparous lizard, *Lacerta vivipara,* another lizard, the blindworm *Anguis fragilis,* and the common European viper, *Vipera berus,* are found at least as far north as the Arctic Circle.[30] In the frogs a north-south gradient in leg length is discernible, the northernmost populations being conspicuously the most short-legged.[29] The three most northern reptilian types are all viviparous, and thus share the advantage of being able to follow the sun to maintain a higher temperature for the developing young (cf. Chapter 24). None of these species occurs on the arctic islands. Iceland appears to have had frogs (presumably introduced) until the severe winter of 1829–1830 exterminated them.[21]

Arctic mammals and birds

Arctic conditions are radically different for warm-blooded animals. Their uniform body temperature makes them independent of the temperature of the environment as long as they can maintain it. The maintenance of their body temperature becomes especially difficult during the low temperature of polar winter. All warm-blooded animals of the polar areas have developed some means of conserving body heat. Insulation by means of thick fur or feathers, effective on account of the enclosed air, is general. Small forms, such as arctic fox, hare, and lemming, have a silky fur with a woolly undercoat, and this affords them sufficient protection since they can avoid severe

* *Euconulus fulvus, Cionella lubrica, Vitrina diaphana,* and a few Pupidae.

storms by retreating into crevices or into the snow itself. Reindeer and musk oxen, however, require further protection. The long hairs of the reindeer are thicker at the end than at the root, and form an almost airtight coat.[3,23] The musk ox has a fleece of 60–80 cm. length which hangs down over the woolly undercoat. Many polar resident birds have the tarsi and the feet feathered, as in the snowy owl (*Nyctea nyctea*), and in the ptarmigan (*Lagopus*) even the soles are feathered. Arctic hare, fox, and bear, similarly have the soles furred. In spring there is molting of plumage or shedding of hair so that a less heavy covering is worn in summer; in the barren-ground caribou, the summer coat is not fully developed until September.

An excellent protection against loss of heat may be provided by a thick layer of fat beneath the skin, which at the same time affords a reserve for the winter fasts. The arctic hare is very fat at the beginning of winter, though its European relative *Lepus europaeus* rarely shows a trace of fat. Such a storing of reserves depends primarily on favorable food conditions in summer, and is the more essential since the nutrition requirements are increased by low temperature.* Results obtained independently by several workers under a variety of conditions indicate that the food consumption of 12 species of birds tested separately shows a crude average ratio of 3:2 for winter or relatively low temperature as compared with that for summer, or for approximate summer temperatures even with day length equalized.[12,17,31] In winter the external food supply is scanty. Where the covering of snow is blown thin by the winds, herbivores dig for lichens and moss and some grasses and herbs. The ptarmigan eat berries and leaves of species of Vaccinium. These supplies are supplemented by the fat layer, which disappears completely before spring.

The occasional scarcity of food, combined with increased needs, changes many northern animals, especially predators, into omnivores. The snowy owl in time of need eats carrion and fish. Gulls feed on the remnants of the meals of the arctic fox. The fulmar, *Fulmarus glacialis*, feeds on plankton, and plant materials have been found in stomachs of this species. The purple sandpiper, *Erolia maritima*, of Spitzbergen may occasionally resort to a plant diet. Many birds normally eat the most available foods. When their accustomed food is wanting or scarce, they feed on varied items that normally would not be eaten. Birds at times learn to accept new kinds of food that formerly were

* Curiously enough, the fat layer of male reindeer, which may be 3 to 5 cm. thick beneath the skin, appears to be an energy store for the autumn breeding season. It is entirely used up before the onset of winter proper.[15]

passed by (Cottam, Clarence, *in lit.*). Such euryphagy is clearly one of the factors that enables birds to flourish in polar regions. The polar bear eats fishes and birds' eggs and even plant food when seals are unavailable. The arctic fox is still more completely omnivorous and feeds on mollusks and other sea food. Even the reindeer eats algae from the coast and occasionally takes a lemming.[23] Some mammals lay in food supplies for winter. The lemmings dig out hollows under stones in which they store rootlets, and when there is a surplus the arctic fox is said to store ptarmigan in ice crevices.

The tundra in many places is riddled with the holes of the true lemming (*Lemmus*) and of the collared lemmings (*Dicrostonyx*), and these small creatures are conspicuous in the summer life of the Arctic. During the summer, with the activity of rabbits, they pop in and out of their holes. The nests are made in grass and moss, and young can be found as late as September. A full-grown lemming is about 6 inches long from nose to the tip of the short rat-like tail. Lemmings are key industry animals, and as such their well-established but unexplained cycles of abundance, with greatest numbers every three or four years, greatly affect the numbers of their associates, including particularly northern foxes, white, red, cross, and silver, and the snowy owl.

The lemming of Lapland and the Scandinavian mountains is *Lemmus lemmus,* which is famous for cyclic spectacular emigrations. Another species of *Lemmus* ranges across arctic Eurasia from the White Sea to Behring Strait and is in turn replaced by the closely similar but distinct *L. trimucronatus* that extends from Alaska to Hudson Bay. The lemmings *Lemmus* and *Dicrostonyx* live nearly or quite together in most polar lands. In Scandinavia only *Lemmus* occurs, whereas only *Dicrostonyx* has been found in Greenland and the Quebec peninsula. *Lemmus* is gaily colored in rich browns and blacks throughout the year; in contrast *Dicrostonyx* is grayish in summer and white in winter. Canadian lemmings do not usually exhibit the impressive emigrations shown by those in Norwegian mountains, though they have been seen emigrating on a large scale near the peak of their abundance.[6, 9]

Reduction of surface is an important means of heat conservation in arctic animals. This may take place by development of a compact form, with reduction of the appendages, especially the ears and tail (as noted in Allen's Rule), or by increase in size in accordance with the Bergmann Rule (see Chapter 20). The musk ox is a typical example of this type of body form. Its legs are so short that it stands only 1.1 m. high, though 2.5 m. long. The neck is thick, the tail only

7 cm. long, and the external ears almost entirely concealed in the furry coat.

Warm-blooded animals of polar regions contrast further with the poikilothermal forms in their pale or pure white coloration. The poikilothermal forms are almost all dark, and thus absorb the greatest possible amount of heat during the brief season of their activity. The white coloration of the homoiotherms radiates less heat than the dark, and prevention of heat loss is evidently of greater importance to them than absorption of the relatively small amounts of heat received from the sun.

The earlier opinion, that the white coloration of polar animals functions as a cryptic coloration, which makes both prey and predators less easily visible on the snowy landscape, need not be entirely rejected. The ptarmigan, for example, keep to the remaining snow patches in spring until they lose their white winter plumage.[14] White coloration in birds appears in the Antarctic, where land mammals are absent, and in the great albatross of antarctic seas, which appears to have no effective enemies.[33] White coloration is more frequent towards both poles.

Every means of heat conservation for homoiothermal animals in polar regions is of importance, since they depend directly on heat of metabolism during the greater part of the year, and only secondarily on radiant heat from the sun. White animals are numerous in the polar regions and relatively infrequent in the tropics. Ptarmigan, snowy owl, arctic hare, arctic fox, and polar bear are completely white. The Greenland reindeer and the Greenland falcon are very light colored. The number of white wolves increases to the northward in North America. The lemmings of the genus *Dicrostonyx* (but not *Lemmus*) turn white in winter, as does the large weasel whose fur is the ermine of the fur trade. It should be remembered that the change of coat color from brown to white in the varying hare, *Lepus americanus,* can be brought about even at mid-summer temperatures by shortening the lighted part of the day-night cycle.[22] The snow bunting in winter plumage is entirely white beneath and rust brown above. The Greenland redpoll, though only a summer resident, is the palest of its group (cf. p. 456).

Hibernation of warm-blooded animals (cf. p. 488) is scarcely possible in the arctic winter except under special circumstances, and these are by no means well understood. Thus the ground squirrel *Citellus parryi parryi* occurs in the Mackenzie River delta, far within the limits of the permanently frozen subsoil as ordinarily defined.

Since the wood frog (*Rana sylvatica*) also occurs in this area, there may be special temperature conditions, perhaps resulting from the great flow of water. The black bear of this region is said to hibernate from October to mid-April.[28a] Deep caves do not serve as warmer refuges, since the temperature in the depths is the mean annual temperature, and this is below 0°. The earth is frozen year in and year out below a depth of 30 to 40 cm. In the extreme north, most warm-blooded animals that can do so, migrate. Even the residents such as the snow bunting, falcon, and raven give way before the deep ice and snow, and move to somewhat more southern regions and to the coasts of open seas. The barren-ground caribou of the mainland of America and of Greenland migrates southward in vast herds. The Spitzbergen reindeer does not migrate. Arctic hare and musk oxen maintain their stations. The ptarmigan digs tunnels in the snow, where it finds both shelter and food.[19] Smaller mammals take refuge from storms in rock crevices or in the snow. The reindeer and musk oxen, which cannot conceal themselves in this way, gravitate to quiet localities and crowd tightly together. The exhaled and transpired moisture of the herd forms a cloud above them, beneath which the warmed air is retained as if in a closed room.

The arctic avifauna is poor in land birds, though marine birds may be abundant. All the smaller forms are migratory, as are many larger ones, such as swans and geese. The long summer days enable them to maintain a nearly constant search for food, and bring up their brood in a relatively short time. Passerine birds in North Lapland forage for 19 hours, and the snow bunting in Greenland may be active for 22 hours.[27,32] Margaret Morse Nice informs us that the summer daytime activity of the song sparrow in Ohio (lat. 40° N.) may be set at 16 hours. The only genuinely resident bird in the Arctic is the ptarmigan, which extends northward of the 84th parallel. At 82° 30′ N. latitude, in Grinnell Land, only the snowy owl, snow bunting, and raven are to be found nesting, in addition to sea birds. In the Antarctic all the birds depend on the sea, and strictly speaking there are no land birds.

In Greenland and Spitzbergen, and probably in other parts of the Arctic, certain species of birds fail to breed about every four years, or at more irregular intervals. The reasons seem to lie in failure of food supplies or in unfavorable weather conditions at the beginning of the necessarily short breeding season, or in a combination of factors. The eider ducks, among such non-breeders, are near the extreme northern limit of their breeding ground. Red-throated divers in

North East Land (Spitzbergen) were apparently breeding in normal numbers in a season when only a small percentage of eider ducks were nesting.[16] In northeast Greenland the several species of resident birds that depend on the lemming for food may fail to breed for one or more successive seasons during the periodic low level in the lemming population cycle.[2]

The number of land mammals that survive the pessimum of environmental conditions in the arctic is very limited. The richest fauna appears to be that of northeast Greenland, where there are 7 species in addition to the polar bear. They are hare and lemming, musk ox, and reindeer, ermine, wolf, and fox. On the islands of arctic Eurasia the number of species of mammals is very small, with only 5 on Nova Zembla and 3 on Spitzbergen. The arctic fox is found on the northernmost land reached by man.[2,3] It spreads from island to island by means of ice floes, like the polar bear.

The species in Greenland and the arctic islands of America differ in part from those of the Old World. The caribou corresponds to the reindeer, the hare is *Lepus arcticus*, distinct from the Eurasian *L. timidus*, and the lemming *Dicrostonyx hudsonius* replaces *D. torquatus*. The musk ox is now wholly confined to eastern arctic America and Greenland, though it ranged over all central Europe even in postglacial time and is known to have been exterminated in Alaska within the memory of man. The last stronghold of this species is in eastern Greenland, where some 10,000 were estimated to be still living in 1934.[13] In 1935 members of an airplane expedition counted 180 musk oxen in the Thelon Game Sanctuary of 15,000 sq. miles located northeast of Great Slave Lake in Canada. A few other scattered bands and individuals were living still farther north. Under protection the species appears to be temporarily secure in this area.

Thirty-one musk oxen were introduced from East Greenland to Nunivak Island in Behring Sea north of the mouth of the Yukon River in 1935 and 1936. An inspection reported in 1942 showed the herd was in excellent condition and had increased to 90 animals. Nunivak Island contains about a million acres of good arctic grazing land, and predators such as bears and wolves are reported to be absent.[1]

Arctic boundaries

Opinions differ concerning the zoögeographic delimitation of the arctic region. The Arctic Circle is an unsatisfactory limit, for it cuts through very diverse regions. Timberline and permanently frozen

subsoil offer fairly satisfactory limits, as in high mountains. Kiaer [18] adopts the annual isotherm of 0°, which extends the region southward to the 51st parallel of north latitude in America. Friese,[8] however, suggests that this limit be set at −5° in North America on account of the continental climate, with relatively high summer temperatures. For our purposes, an exact delimitation is not required. All the islands of the Arctic Ocean, with the exception of Iceland (which is forested), belong plainly to an arctic life zone. A mixture of faunae takes place on the arctic borders of the continents, which makes exact demarcation impossible. The intimate relation between faunal composition and climate makes it self-evident that a sharply defined faunal boundary will be found only where natural barriers, such as coast lines and mountain ranges, produce well-defined climatic limits.

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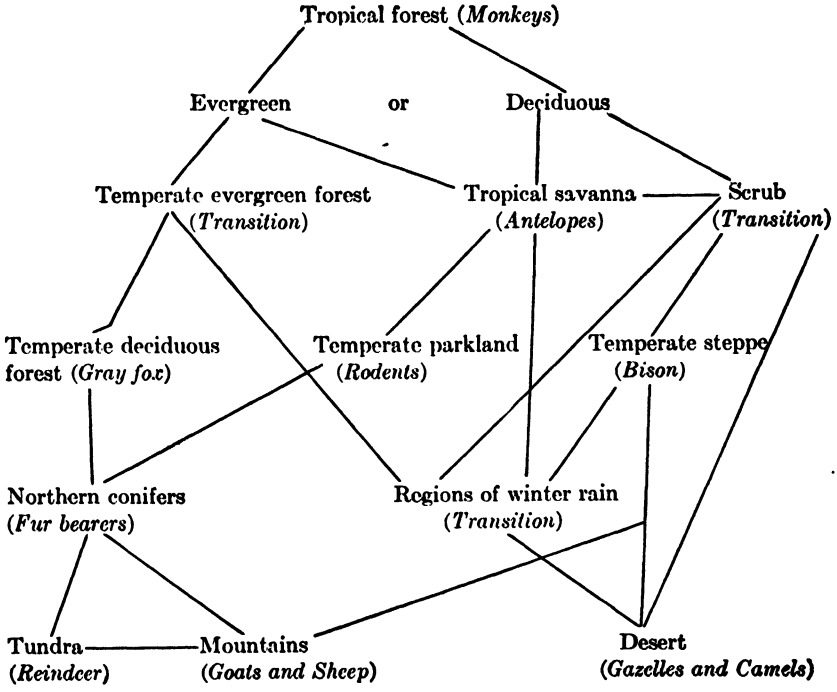
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26. *Island Communities*

THE GEOGRAPHIC ANIMAL FORMATIONS OF THE LARGER LAND MASSES, together with some of their interrelations and an indication of typical mammals, may be summarized as follows:



All these have been discussed more or less, although the transition areas have received only incidental attention in chapters devoted to related formations. The communities found on islands do not fit naturally into this ecological classification. They are influenced, more than

any of the above, by local conditions. Island life particularly depends on distance from the nearest continental land mass and on the length of time since connections existed, if ever, as well as on such ecological factors as climate and soil and the resulting types of vegetation.

Such special environmental conditions are not at all equally developed on all islands or archipelagoes, which may in fact be arranged in a series, from islands whose faunae are scarcely different from those of the adjacent continent to groups in which insular characteristics are especially pronounced. These two extremes are recognized in the grouping of islands as *continental*, i.e., islands that have been connected with the mainland, and *oceanic*, those that have never had a land connection.[32,37] Continental islands are for the most part near some continent, which they resemble in geological structure, including similar sedimentary deposits. The sea separating them from the continent is usually shallow, rarely deeper than 1800 m., and usually much shallower. Oceanic islands are of volcanic or, secondarily, of coralline origin, are often far from the nearest continental mainland, and are usually separated from it by greater depths. Both continental and oceanic islands may be classified according to their age.

The different mode of origin of continental and oceanic islands naturally has an important effect on their faunal character. A continental island first received its fauna from the mainland and, in general, if the island is not too small in area, island and mainland will be occupied by much the same biota. On ancient continental islands, some animal groups may have become extinct; or forms that have become extinct on the mainland on account of competition with more modern species may be preserved in the insular habitat; others may have reached either mainland or island without being distributed over both. An oceanic island, however, must have originally been without air-breathing animals, and its land fauna must be composed of animals that have been able to cross the ocean, either by active flight or swimming, or by some means of passive dispersal (see Chapter 5). The capacity for such dispersal varies for the different groups of animals. Animals incapable of flight or other aerial transport, and to which sea water is fatal at all stages of development, are excluded from oceanic islands. Land turbellarians, many fresh-water forms, and amphibians tend to be so excluded. Land mammals do not ordinarily survive long journeys on driftwood and are also characteristically wanting on oceanic islands. If introduced they may flourish there, like the rabbits of Kerguelen or the cattle of New Amsterdam, but they rarely reach remote islands without the intervention of man. Animals

that have thus accumulated on oceanic islands have reached these havens accidentally, and neighboring islands, on account of the rarity of such transportation, may have radically different animal life. Oceanic island faunae appear to be chance assemblages, with some animal groups conspicuously absent, and a haphazard composition as compared with the more ordered faunae of continental islands.

The decision as to whether an island is to be regarded as continental or as oceanic is not always easy. The British Isles, Japan, and the Sunda Islands are unquestionably continental; Madagascar is probably also a continental island; St. Paul, New Amsterdam, the Cocos or Keeling Islands, and the more familiar Azores, Bermudas, and the Hawaiian Islands, are as unquestionably oceanic. The Galapagos Islands are cited by Darwin, Wallace, and many others as typical oceanic islands, and we agree with them. Other investigators have referred to such islands as the last remnants of continental land masses.[2,33] New Zealand is regarded as continental by Wallace,[37] but some geologists, like Wilkens, think such connection improbable. In such disagreements the argument rests heavily on basic geology (see Chapter 7), and more lightly on the composition of the insular biota. In ancient islands the differences between the two types of fauna are much erased; since continental islands may receive transported animals, and their faunal relations may be obscured by extinction, the interpretation of their faunae offers much difficulty. Amphibians are present in the Fiji Islands; they are absent in the presumably continental New Caledonia. In such historic problems, the difficulties increase with increasing geological age, and the two categories of islands are not emphasized in the present chapter, though it is necessary to return to them repeatedly in the illustration of the two extreme types of faunal composition.

The special character of insular faunae rests on the conditions common to all islands--isolation, modified competition, space restriction, and special insular climates.

Isolation

The most important and effective of these factors is that of isolation, which term is in fact derived from "isola" (=islands). The sea as a barrier makes access to any island impossible to numerous animals. Not all, however, are excluded. Flying animals of all sorts reach islands, favored sometimes by prevailing winds. Animals that swim well and tolerate salt water, such as crocodiles, or snakes, such as the European water snake, may reach islands that are not too distant.

Others are transported on driftwood, to which they have attached themselves (snails, for example) or in which they live as larvae or pupae, or they are carried as eggs in the earth transported by tree roots. Small forms, even minute snails, may be transported above the water by winds, especially by hurricanes or typhoons,[6] and, once a successful landfall is made, they may undergo extensive adaptive radiation and occupy niches quite different from those in which relatives thrive elsewhere.[12, 20]

Ease of transport explains the predominance on many islands of weevils, whose larvae frequently live in wood. In New Zealand 737 species out of 2787 species of beetles are weevils; in the Mariana Islands they predominate; in Madeira there are 80 out of 482 forms; in St. Helena 31 of 60 endemic forms are weevils; in the Falkland Islands there are 16 out of 35; and 5 out of 9 on Kerguelen.[15] This is further illustrated by the distribution of the weevils of the genus *Proterhinus*, whose normal larval habit is to bore in dead wood or dead bark. This genus was described from Hawaii, where 164 endemic species exist, together with 17 other endemic forms of subspecific rank. The genus was long considered to be restricted to the Hawaiian Islands, but new species have since been found widely distributed through Pacific islands, including the well-isolated Marquesas. All Hawaiian species of *Proterhinus* are flightless, but the Samoan species, which also lives in the Fiji Islands, is fully winged. The family * has two known species in New Zealand and one in the Canary Islands in the Atlantic Ocean. Such groups, with representatives on certain archipelagoes in two well-separated oceans, may represent ancient forms that have persisted and evolved in insular isolation during long periods of time, although their continental ancestors meantime have become extinct.[38] They also plainly reflect erratic dispersal with secondary speciation.

Amphibians and most land mammals are unable to cross oceans unless they are accidentally transported or are introduced by man. The absence of mammals is especially notable in small islands, but even New Zealand has no native mammals other than bats. The absence of amphibians and mammals is readily explainable, but why snakes, which should be equally as aquatic as lizards, are so generally absent, is less obvious.

Stenohaline fresh-water animals have especial difficulty in reaching islands, and they may be poorly represented even on undoubtedly continental islands, since they are exposed to extinction and cannot

* Formerly Proterhinidae, now Aglycyderidae.

be readily replaced. Poverty in fresh-water snails and complete absence of fresh-water bivalves are characteristic of islands. (The larger East Indian islands, to be sure, have fresh-water snails, ampularids and viviparids for example, in Celebes.) Neritidae, immigrants from the sea, replace them.[26] Aquatic insects are also entirely absent on most small islands. A single water beetle is recorded from the Azores. The Hawaiian Islands have few aquatic insects, no caddisflies, for example, and only 4 species of water beetles and 2 aquatic Hemiptera. Dragonflies are widespread in islands on account of their great powers of flight.

Many islands, similarly, have few fresh-water fishes, or these may be entirely absent. Large islands close to the continents, with large and permanent river systems, such as Borneo, may be rich in fishes. Celebes, however, has only 3 species, and the poverty of the Pacific islands in this respect is notable. Even the large island of Madagascar has an impoverished fauna of true fresh-water fishes: 2 silurids, 2 cyprinodonts, 1 atherinid, 4 cichlids, and 7 gobies, the last undoubtedly recent immigrants from the sea.[3]

A considerable number of marine fishes enter fresh water, and such forms constitute the main part of insular fish faunae. Presence of relatively large amounts of dissolved calcium facilitates such invasions by marine forms.[4] Some fishes are able to enter fresh water directly; others are represented by closely allied forms in the fresh-water habitat.* The species of *Galaxias*, widespread in the southern hemisphere, belong in this category, since they have marine relatives, and one species at least, *G. attenuatus* of New Zealand, descends to the sea to breed. San Thomé in the Gulf of Guinea, with numerous rivers, has only 2 species of fresh-water fishes, both gobies and hence undoubtedly derived from the sea.[10] Even the blind cave fishes of Cuba belong to the marine family Brotulidae.[18] In accordance with its habit of spawning in the sea, the common eel and its allies are widely present on islands. It is the only fresh-water fish in the Azores, Madeiras, and in Sardinia.

Effects of isolation appear in the independent further development of the insular populations separated from the parent stock. Mutations in the island stock may become fixed, whereas in the parent stock they may well be swamped by crossing. Islands accordingly will have more endemic forms the more effectively and the longer they have been separated from the nearest inhabited area. The length of time

* Gobiidae, Percidae, Mugilidae, and Poeciliidae afford examples.

through which isolation has continued is the principal factor, and it makes little difference whether the island is of oceanic or continental origin. Ancient continental as well as ancient oceanic islands are contrasted with youthful islands by their great number of endemic species, genera, and even families. In the British Isles a divergence of the mammals and birds from those of central Europe is discoverable only by detailed study. In Madagascar, on the other hand, all the non-flying members of these classes, except the species of *Potamochoerus, Hippopotamus, Crocidura,* and *Fossa,* belong to genera or even families unknown elsewhere.[22] The fauna of Krakatoa, which has been entirely acquired since 1887, does not have a single endemic form, while on the Canary Islands 133 out of 167 land mollusks are endemic, with a somewhat smaller proportion of endemism in insects.*

The proportion of endemic species to the total increases with distance from the mainland, with the age of the islands, and probably with other factors. The Azores, for example, were known in 1946 to have about 300 species of beetles, of which 35 are endemic.[28] By contrast, the Hawaiian Islands, 3000 km. from the nearest continent, have about 1060 species of endemic land snails and 1, or perhaps 3, indigenous forms that also live naturally elsewhere. Over 5000 species of insects were recorded by 1948; many others were known, but undetermined and "untold numbers of new species have yet to be collected from their mountain haunts." Of the insects known, 3722, approximately 74 per cent, are endemic, apparently speciating from 233 to 254 original arrivals. The more than 1600 species of beetles show a somewhat greater percentage of endemicity. The Hawaiian fauna has a strong tendency toward uni-insularity, with about 98 per cent of the ground beetles (Carabidae) confined to single islands. More than 90 per cent of Hawaiian insects have Pacific affinities.

The land and shore birds of Hawaii contain 70 endemic forms, of which an ancestral drepanid (a single arrival) gave rise to 42. This was the only bird immigrant to have speciated extensively in the islands. The balance of opinion concerning drepanid origin seems to lean toward their having come from America. The interested student is referred to Zimmerman[38] for a broad analysis of these and other phases of ecological zoögeography and of historical biogeography of the Hawaiian Islands. See also the introductory essay in the older *Fauna Hawaiiensis.*[31]

* The distribution of land mollusks is thought by many students to require land bridges and to indicate that even the oceanic islands of the Pacific are vestiges of a former continent (see Chapter 7).

The relation between speciation and insular isolation is well shown by the 201 species of island-inhabiting land planarians known up to 1899, of which no less than 186 are confined each to a single island.[9] The island-inhabiting cassowaries are split into 20 subspecies by Rothschild, while the continental ratite birds are much less diversified—the ostriches in 4, the rheas in 4, and the emus in only 3, subspecies. The development of subspecies by insular isolation is still further emphasized by comparison of an archipelago with a near-by mainland area. The Philippines, for example, in 1898 had 1079 species of land snails (without enumerating subspecies), whereas there were only 618 species in Indo-China and Siam.[5, 30] The West Indies have 64 amphibians and 261 reptiles, as compared with 26 amphibians and 83 reptiles on Celebes, which has about an equal area.

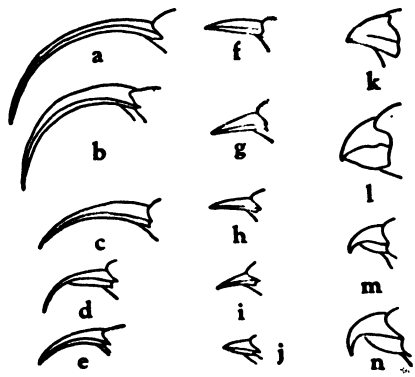


FIG. 137. The beaks of drepanid birds exhibit their remarkable evolutionary diversification into food habit types on the Hawaiian Islands. *Loxops* (*i*) is thought to be nearest the ancestral type. *a*, *Hemignathus* (feeding on insects and nectar); *b* and *c*, Drepanis (nectar); *d*, *Heterorhynchus* (insects and spiders); *e*, *Vestiaria* (nectar); *f*, *Palmeria* (nectar); *g*, *Viridonia* (insects); *h*, *Himatione* (nectar); *i*, *Loxops* (mostly insects); *j*, *Ciridops* (palm fruits); *k*, *l*, *Loxiodes* (mostly seeds); *m*, *Psittirostra* (fruits and seeds); and *n*, *Pseudonestor* (wood-boring beetle larvae). From Zimmerman.

Isolation on islands affords effective protection against the entrance of competitors, and, with the relatively smaller number of forms on a single island, the struggle for existence is less severe. Forms that have succumbed to the struggle with more advanced types in mainland areas may accordingly survive on islands. The small operculate snail, *Craspedopoma azoricum*, persists in the Azores, while its only relatives are known from Tertiary deposits in Europe.[8] The helicid genus *Janulus*, of the continental Oligocene and Miocene, persists in Madeira.[35] Primitive forms of the most diverse groups of animals have been preserved in New Zealand. The Tasmanian wolf (*Thylacinus*) and the Tasmanian devil are only recently extinct in Australia, where they appear to have been displaced by the dingo, which did not reach Tasmania. Madagascar affords a further example; lemurs, civets, and primitive insectivores, in the ab-

sence of true monkeys and true cats, together with the paucity of ungulates, distinguish its fauna from that of Africa, from which it has been separated at least since mid-Tertiary time. Modern groups tend to be represented by their more primitive members.

The absence of native mammals, bats excepted, or their scarcity on islands, is especially favorable for bird life. The rather helpless pigeons increase in numbers in the Malay Archipelago to the eastward as the mammals decrease, and are strikingly developed in Polynesia, where no native mammals exist; the distinctive family Didunculidae is confined to two islands of Samoa. For the same reason, islands in the tropics, as well as in the arctic and antarctic, afford undisturbed nesting sites for great colonies of sea birds, which gather for their breeding season from wide areas.

Reduction of biotic pressure may be one of the factors that make possible unusual colorations among insular birds. In Iceland, albino ravens are abundant; and white ravens may even exceed the normal individuals in numbers in the Faeroes.[14,21] Albinism is frequent in land birds in New Zealand.[17] The evolution of birds of paradise in New Guinea and adjacent islands may be explained in part by the scarcity of predators. The absence of predaceous mammals, monkeys, and large birds of prey makes possible the frequent development of flightless birds in islands, which is (or was) so remarkable a phenomenon in New Zealand and islands near by, in the Mascarene Islands, and in some degree in various other localities. The parallelism in loss of power of flight is continued in a number of forms in the loss of coherence of the feathers, not only in the ratite birds but also in the extinct dodo, the ralline *Ocydromus* and *Cabalus* of the New Zealand area, and the kagu of New Caledonia.

Extreme development in size is to some extent characteristic of insular birds, correlated with flightlessness and perhaps with the consequent saving in energy expenditure. A great number of unusually large birds of diverse groups is known from the New Zealand region and from the Malagasy Islands, most of them recently extinct, and some, like the dodo and solitaire and the relatively gigantic Mauritian parrot, *Lophopsittacus mauritianus*,[23] known only from fragments or from drawings, since they became extinct within a few years of the discovery of their islands by Europeans.

Small mammals and small birds may exhibit larger average size on islands; thus the field mice, house mice, and wrens of sea-girt St. Kilda are larger than the corresponding forms on the "mainland" of Scotland.[34] Insular reptiles, especially tortoises and lizards, frequently

reach unusual size, but many of these are relicts rather than insular developments. The largest existing land turtles are confined to the Galapagos and to islands in the Indian Ocean. Fossil remains of equally large forms are known from continental deposits. The largest living lizard, *Varanus komodoensis,* is confined to Komodo, Rindja, and Flores Islands in the Dutch East Indies but seems plainly to be a remnant of a form once more widespread. The large scincid lizard of the Cape Verde Islands, *Mabuya coctaei,* and the large geckos and skinks of New Caledonia suggest that there may be correlation between insularity and large size in some animals, though not in all. It will be shown shortly that the opposite phenomenon, namely dwarfing, particularly among birds and mammals, is characteristic of island life.

Among other characteristics of oceanic island faunae related to their isolation is the fact that they are distinguished by having disproportionately developed taxonomic groups in which one or a few basic types have undergone adaptive radiation and come to make up large proportions of the population as compared with conditions that obtain on neighboring continents. When insects are considered, on islands there tends to be a dominance of small-sized forms, dull coloring, obscure habitats, erratic distributions with absence of many families, superfamilies, and even entire orders, and a sparse representation of fresh-water forms.

Insect groups that are typically reduced or absent in oceanic islands include stoneflies, caddisflies, mayflies, and scorpionflies, aquatic Hemiptera, and the cicadas, membracids, aphids, Cercopidae, and many groups of fulgorid bugs; most families of neuropterans, many beetles, such as the lamellicorn series; many families of flies; the suborder Symphyta (sawflies) from the Hymenoptera, and most families of aculeates. The absence of such groups is strong evidence against the existence of extensive land areas in the Pacific at any time in the past.

Space limitation

The limitation of available space in smaller islands is reflected in the composition and development of their faunae. Any animal requires a certain space to enable it to develop and live freely, and this space varies with the size, activity, and mode of feeding of the animal in question. For a springtail or mite, a moss-covered stone may suffice; a rock projecting from the ice of Greenland may support a gnat or a spider; a single plant is enough for a caterpillar, whereas sheep

require a considerable extent of meadow. The deer of Germany are distributed approximately in the proportion of one to every 10 to 15 hectares (25 to 40 acres) of forest. Roe deer and hares are unable to withstand confinement in zoölogical gardens, doubtless on account of restriction of their movements. Herbivores require less space than carnivores, the woodchuck, for example, less than the fox. The species naturally requires a much greater area than its individuals, since a minimum numerical strength is required to safeguard it from extermination, whether by fluctuations caused by the struggle for existence or by inbreeding. Small islands, consequently, can have only small mammals. The Balearic Islands have only mice, weasels, hedgehogs, and bats, and forms of equivalent size. The red deer declines in forests of too small an area. The island of Bali, with about 5000 sq. km., seems to be the smallest area that will support a population of tigers.

Other conditions being equal, an insular area must accordingly have a smaller fauna than an equal or even much smaller area on the mainland. Even when the area is large enough for individuals of a species of given size, it may not suffice for the breeding and other necessary activities of the species. The botanical gardens at Bonn harbor about 43 species of nesting birds, on an area of 8.8 hectares; the central cemetery of Hamburg at Ohlsdorf has about an equal number, and the Seeburg estate at Langensalza has no less than 61 breeding species in an area less than 1 sq. km. The Azores, with an area of 2388 sq. km., have less than 30 breeding species; the Comoro Islands, with 1972 sq. km., about 53 species; the Bermudas, with 50 sq. km., only 13. Continental islands exhibit the same relations. Germany has about 90 species of mammals, Scandinavia 60, Britain 40, Iceland only 22 (see p. 159). Although the number of species is small, the number of individuals may be large. There were vast numbers of birds on the Azores at the time of their first settlement, and it is reported that pigeons settled on the hands, shoulders, and heads of the colonists.[36] The fact that many insular species have relatively few individuals, as is the case with the nestorine parrots of the islands near New Zealand, the extinct starling *Fregilupus varius* on Bourbon, or the flycatcher *Monarches dimidiata* on Rarotonga, is not necessarily due to insularity.

The dwarfing of both mammals and birds is a peculiarity of insular faunae, probably referrable to correlation with limitation of space. This is in strange contrast with the converse phenomenon of giantism also found in insular birds and lizards. The birds of Corsica and

Sardinia are mostly smaller than the directly related forms on the mainland. The birds of the Canary Islands are likewise frequently smaller than the related species in Europe. Among many complicating factors, the Bergmann Rule must be remembered in this connection. Decline in size in mammals on islands seems to be well established.[15] Island races of ponies are notably numerous on the Shetlands, Iceland, Oeland, the islands of Brittany, Sardinia, and Corsica, the Cape Verde Islands, Timor, Bali, Sumba, and the Japanese Islands. The large English horses introduced from Australia to the South Sea Islands become small after a few generations. Deer become dwarfed on islands, as in those introduced into Cuba,[25] the small insular race of the water deer on Bawean (*Cervus equinus kuhlii*), or the sika deer of Japan, which reaches a height of only 813 mm. at the withers as compared with 1117 mm. of the continental form.[29] The small buffalo of Mindoro in the Philippines (*Bubalus mindorensis*) and the still smaller dwarf buffalo of Celebes (*Anoa depressicornis*) represent the water buffaloes of the mainland. The gray fox of Catalina Island does not reach the size of the mainland form in California. The mammals of Sardinia,[19] equally with those of Mexiana Island [16] in the mouths of the Amazon, are uniformly smaller than the same species on the adjacent mainland. The average human stature on Sardinia, 1619 mm., is smaller than the average for Italy of 1645 mm.

Insular forms are especially liable to extermination. Primitive animals, forms whose vitality has diminished and those which have become modified as the result of the absence of enemies, are especially exposed to destruction by introduced forms. The ant, *Pheidole megacephala*, introduced in Hawaii, has destroyed the endemic forms in extensive forest areas. Feral dogs and cats are exceedingly destructive on islands where there were originally no predaceous mammals; the toothed pigeon, *Didunculus*, of Samoa, has been forced to adopt arboreal habits. The Lord Howe Islands were made a bird reservation in 1879, but a plague of house rats has defeated the hope of preserving the endemic birds.[24] More than 50 species have become extinct in New Zealand in the past 700 years, and there are 36 recently extinct forms known from the Mascarene islands.[23]

Special insular climates

The effect of insular climates on the composition of their faunae remains to be considered. The relative humidity is high, especially on small islands. Constant humidity together with relatively great extent of coast line, favors land crustaceans, especially amphipods and

decapods. Most of the land-inhabiting *Orchestia* (Amphipoda) occur on islands, *O. chevreuxi* on the Azores, *O. bottae* on Cyprus, and *O. sylvicola* in New Zealand, for example. *Talitrus platycheles* occurs in the interior of Minorca; other species of the same genus in Rodriguez and in Tasmania.[11] Small tropical islands have great numbers of hermit crabs and land crabs. On the Cocos or Keeling islands there are no less than 16 species of land crabs, and 7 hermit crabs which

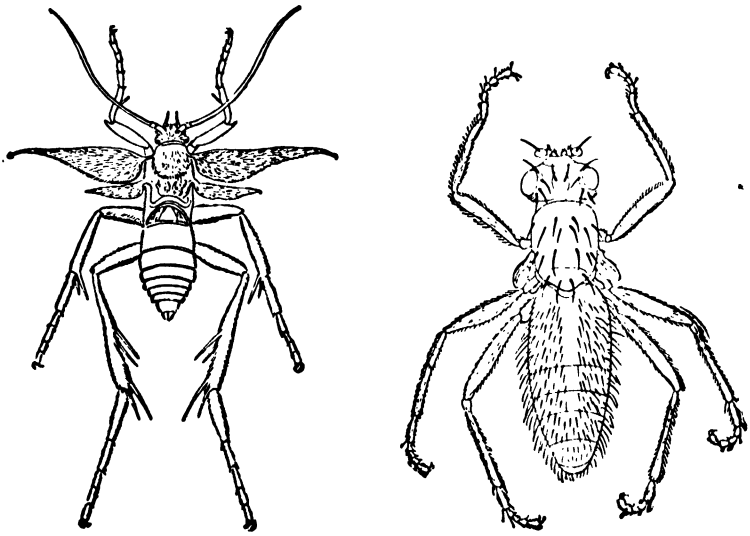


FIG. 138. Insects with vestigial wings from Kerguelen. *a*, moth, *Pringleopsis kerguelensis*, × 2; *b*, fly, *Apetenus litoralis*, × 9. After Enderlein.

have adapted themselves to land life. The cocoanut crab *Birgus latro* is widespread in the Pacific islands. Many of these land crustaceans may range far from the seacoast and to the tops of mountains.[27] Hermit crabs may adopt the shells of large land snails (*Bulimus, Helix*), as on Fernando Po and in the Solomon Islands.[13]

Strong winds on small level islands subject the fauna to severe selection, for small animals that cannot find refuge will be blown into the sea. This factor especially affects insects and certain birds with weak flight, and is the more effective the smaller the islands and the more stormy the area in which they lie.

Flightlessness, in general, is more frequent in insular insects than in those on the continents (Fig. 138). The small number of flying insects explains the absence of insectivorous animals such as swallows, swifts, flycatchers, and the smaller bats. Thus there are only two bats in New Zealand, and one of these, *Mystacina tuberculata*, catches

insects by climbing about on tree trunks and branches as well as by capturing them in the air.[7] Fruit bats are not uncommon on the islands of the western Pacific. It is interesting that a number of insular bats have taken to fish eating. Such forms cross straits and wide stretches of ocean, and fail to form local races on islands. Thus *Noctilio leporinus*[1] ranges widely in the West Indies.

Water birds tend to have a separate community for an area of 200 miles or more in radius about an oceanic island or archipelago. Marine fishes also form more or less characteristic island littoral communities, the composition of which is strongly affected by the prevailing currents, and the numbers present depend on the amount of nutrient material washed in from the land. The coral reef fishes of the Hawaiian Islands are mostly distinct species of genera that range through Polynesia from the East Indian seas. Small desert islands in the Atlantic have noticeably fewer marine fishes along their shores than do islands with fertile soil that lie in regions with good rainfall.

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27. *Subterranean Animal Life*

THE ENVIRONMENT TO WHICH ANIMALS OF SUBTERRANEAN SPACES ARE exposed is highly peculiar and does not fit into the schematic summary of animal communities given at the opening of the preceding chapter. Such spaces include not only caves with their waters, but also crevices and holes in rock, mine galleries, cellars, catacombs, aqueducts, ground waters, and deep springs. It is from these varied sources, some of them inaccessible to investigation, that the faunae of the larger caves are in some measure derived. Limestone mountains, especially like the Karst or Alb of Europe or like the Ozarks in North America, are riddled with cavities and channels, in which run a whole system of small and large watercourses, which may finally emerge as large springs. These spaces harbor a fauna characterized by a number of parallel or convergent adaptations and correlations that fit their peculiar habitat. The continuing and even increasing interest in cave faunae is reflected in the useful summary "Animalium cavernarum catalogus." [36]

Cave animals are not all equally bound to a subterranean life. They may be divided into three groups: exclusively subterranean forms, confined to such situations, and found elsewhere only when carried out by accident or force, so-called troglobic forms; occasional cave inhabitants, which also occur on the surface, but are regularly to be found in caves; and accidental cave dwellers.

Examples of the accidental appearance of the first group at the surface are the occurrence of the olm (*Proteus*) in the Zirknitz Lake, or the appearance of the cave amphipod *Niphargus* [33] or the cave snail *Lartetia* [18] in springs. The second group is a varied one; many are widespread forms, "ubiquists," that also enter caves; thus the five most common European cave copepods * are among the most widely

* *Cyclops viridis, strenuus, serrulatus, fimbriatus,* and *bicuspidatus.*

distributed species of the genus, and occur also in the depths of lakes.[32] Other forms able to live both above and below ground may be much more abundant in caves than elsewhere, like the mite *Linopodes longipes,* the opilionid *Nemastoma lugubre,* and the springtail *Macrotoma viridescens.*[2] Such forms exhibit a transition toward confinement to cave life. Other species may be rare in caves, like the planarian *Pl. montenegrina,* which is everywhere found in brooks and more rarely in subterranean waters. In some species certain individuals live constantly in caves, whereas others do so only part of the time, e.g., the salamander *Hydromantes fuscus.* Others use caves as winter quarters, like the Lepidoptera *Triphosa dubitata* and *Scoliopteryx libatrix.*[1,36] Some species use caves merely as a retreat, like bats, while the oilbird *Steatornis* in Trinidad, though seeking its food outside, nests in caves. The accidental cave inhabitants are merely those that fall in or wander in and are able to maintain themselves.



FIG. 139. A springtail from the Adelsberg Cave, *Aphorura stillicidii,* ×20. After Absolon.

Cave animals are both terrestrial and aquatic. They belong to varied groups—a number of turbellarians, several chaetopod worms, such as the oligochaet *Haplotaxis gordioides,* and even a leech, *Dina absoloni.*[24] There is a large variety of snails. The majority of cave animals, however, are arthropods, including aquatic crustaceans and terrestrial insects and arachnids. Besides entomostracans, cave crustaceans include amphipods, isopods, and decapods. Among insects the springtails predominate (Fig. 139), together with beetles, the other orders being only sparingly represented. Among arachnids, mites and true spiders are most numerous, with pseudoscorpions and phalangids also present. Vertebrates are represented by fishes and salamanders. Coelenterates bryozoans, tardigrades, and lamellibranchs are thus far unknown in caves; insects that depend on green plants for food are excluded; and reptiles, birds, and mammals have not developed true cave forms, although snakes are occasionally found, and *Steatornis* almost qualifies as a cave bird.

Cave faunae originated on the surface, and many forms were already adapted to moist, cool, and dark habitat conditions before entering caves. All triclad turbellarians are negative to light and live beneath stones or in similarly dark places during the day. The

terrestrial beetles *Trechus* live concealed under stones and in similar places, especially in forests in the mountains; Jeannel says, in his monograph on the distribution of American species, that, in entering caves, they have not essentially changed their habitat.[23] Springtails



FIG. 140. Cave amphipod, *Stygodytes balcanicus*, from subterranean waters of Herzegovina. Length 5 cm. After Absolon.

and mites are everywhere photonegative and are often blind even when not subterranean in habits. The fishes of the family Amblyopsidae (to which certain cave fishes belong) that live in surface waters are negative to light and conceal themselves under stones.[16] Entry into the cave habitat was made in various ways. Some forms were carried in by water; others, working their way against the current, found caves at the source. Terrestrial animals wandered in at cave mouths, but also entered by way of cracks and rock clefts. The cave of Šošůvka in Moravia, which was until recently without an open-

ing, contains only 9 species, 5 springtails and 4 mites, all extremely minute forms. Open caves in the same region have a richer fauna; the Sloup cave harbors more than 50 species, and the cave of Vypustek, about 30.[2]

From the extent of their transformation, conclusions have been attempted as to the length of time elapsed since the entry of certain animals into caves. Thus Komarek [26] distinguishes younger and older cave forms among planarians. The younger, *Pl. anophthalma* and *Pl. montenegrina,* are races of *Planaria alpina,* which is a stenothermal animal of cold habitat and could have reached the Balkan Peninsula only during the glacial period, so that the date of entry of its derivatives into caves is placed as postglacial. *Soroccelopsis decemoculata,* and the "land triclad" *Geopaludicola absoloni* seem to have been longer in the cave habitat, as planarians of their type are otherwise unknown. *Dendrocoelum subterraneum* is also reckoned as one of the older entrants. Data for valid conclusions of this nature are inadequate.

The cave environment

Deep within caves the habitat conditions are remarkably uniform. Uniform darkness, uniform high humidity, temperature with slight variation, near the annual mean of the locality, and almost complete absence of air currents characterize the cave environment. Rain, snow, and heat are unknown in caves.

The absence of light in the subterranean spaces is the most important feature of this environment to its animal population. It is even more complete than in the abyssal ocean, where light-producing animals exist in considerable numbers, whereas only very few bioluminescent cave animals are known.[31] The best known of these is the New Zealand "glow worm." The roofs of large and small caves in New Zealand (at least throughout the North Island) are seen to be studded with innumerable greenish-blue lights. These are produced by sharply defined light organs near the posterior ends of the bodies of the larvae of *Arachnocampa luminosa,* a mycetophilid dipteron. The larva has further remarkable peculiarities, in that it lives in a gelatinous case, within which it moves freely back and forth, and it suspends spider-web-like threads from its case to ensnare midges rising from the mud banks of streams flowing through the caves. The suspended threads may dangle to a length of two feet; they are ordinarily six to eight inches in length. When the larva detects the disturbance produced by a trapped midge, it is said to draw up the thread and devour

its prey.[6,12] Animals in the depths of fresh-water lakes are less completely cut off from light, as they are able to swim up to the lighted layers. The effect of total darkness is manifested in various ways.

The absence of green plants is fundamentally important. From this it follows that the food of cave animals must come from without, except as the roots of surface plants may reach these depths. This food supply is of varied character. An important element is plant débris, wood, leaves, etc., on which molds and other fungi are able to grow, as they may also on bat excreta. More than 10 species of such plants without chlorophyll have been found in the Karst caves. These support fungus-eating beetles * and snails. Caves with a down slope at the entrance are in consequence much richer in life than those in which the entrance rises from the opening, since the entry of débris is thus facilitated. An entering stream of water brings in food materials. Bat guano, sometimes present in enormous amounts, affords a food supply to springtails and mites. Finally, dissolved and colloidal food substances of plant origin are carried in by ground water. Springtails † and mites occur in incredible numbers in the recently wholly closed Šošůvka Cave in Moravia.[2] Many stalactites and stalagmites are literally covered with these animals. Springtails gather at the moist places to feed on colloidal substances carried in by seepage, especially around the cup-shaped depressions on stalagmites.

The size and number of inhabitants afford a measure of the amount of food available in a cave. The food supply is in general small, and cave life is correspondingly scanty and made up of small forms. The cave snails, especially the plant feeders, are mostly tiny, measuring only a few millimeters in length. Only a few predaceous pulmonates in the Balkan caves can be said to reach a moderate size.[35] Springtails and mites are almost entirely minute animals. Cave beetles may also be small; the species of *Trechus,* for example, measure 4 to 6 mm. Aquatic forms become somewhat larger, though they too are small on the average. Most cave fishes reach no more than 50 to 60 mm. in length; only *Amblyopsis spelaeus* is larger, and it may reach 135 mm. The olm (*Proteus anguineus*) is a giant among cave forms, with a length of 250 to 285 mm. Occasional cave arthropods, however, grow to an unusual size, larger than that of their relatives. Thus the giant amphipods in the Balkan caves (Fig. 140) exceed 50 mm. in length; the springtails, *Aphorura gigantea* and *Tetrodontaphorus gigas,*

* The so-called cave silphids, *Adelops, Orycus, Leptoderes,* etc.

† *Dicyrtoma, Heteromurus,* and *Anurophorus.*

and the common cave amphipod *Niphargus* may reach a length of 30 mm.

Some caves seem to be rich in food, to judge from the amount of their animal life. The abundance of springtails in the Šošůvka Cave has been mentioned. Viré took about 10,000 specimens of *Niphargus* and 50,000 of *Bithynella* in one set of caves in southern France. The snail *Carychium* is very abundant on wet wood in Mammoth Cave.[8]

Plant and detritus feeders serve as food for predaceous animals, which are of course much less numerous. Spiders, pseudoscorpions, and mites fill this rôle. Tiny mites, such as *Pygmophorus,* may be seen carrying off springtails (*Lepidocyrtus*) ten times their size and spiders (*Porrhoma*) fifteen times as large as themselves.[2] A number of cave snails in the Balkans are predaceous, as inferred from their radula.[35] Cave Orthoptera are also predaceous. The decapods (shrimps and crayfish) are doubtless dependent on animal food. Cave vertebrates are all carnivorous; the olm feeds on amphipods, *Hydromantes* on insects.

Lack of pigmentation

The white or colorless character of many cave animals is associated in some way with darkness. Examples are to be seen in the cave planarians, the leech *Dina absoloni,* many crustaceans,* many springtails, cave snails, blind fish like *Amblyopsis* of the Mississippi region and *Lucifuga* of Cuba, and the olm. Such colorlessness is not absolute, even among cave forms; the cave fishes *Typhlichthys* and *Troglichthys* have traces of pattern, and most cave spiders are more or less dark. Cave beetles are all pigmented, though they may be paler than their relatives above ground. The transitions in coloration may be seen in the fishes of the family Amblyopsidae.[13] Of the three species of *Chologaster, C. cornutus* lives in surface waters in Florida, *C. papilliferus* lives in springs under stones, and *C. agassizii* is a cave fish, in the Mammoth Cave of Kentucky. *Typhlichthys subterraneous* and *Amblyopsis spelaeus* are also confined to cave waters. Among the species of *Chologaster,* the coloration becomes paler from *cornutus* to *agassizii; Typhlichthys* is cream-colored and shows abundant pigmentation; *Amblyopsis* is colorless; the blood and liver show through the body, and a little yellow pigment is retained only at the fin bases and on the head. In other groups, the coloration seems to be lost more

* *Niphargus* and *Asellus cavaticus, Palaemonetes antrorum,* and *Cambarus pellucidus.*

rapidly. The brook amphipod *Gammarus pulex* in the caves in the Harz is colorless, and *Planaria montenegrina,* widespread in the brooks of the Balkans, has a wholly milk-white coloration in the Golubnjaka Cave in central Dalmatia.[26]

Experiments show that color disappears under the influence of darkness. Viré kept *Gammarus fluviatilis* in aquaria in the Paris catacombs. They began to lose color after six months, and the pigment finally disappeared entirely. On the other hand, the cave amphipod *Niphargus,* maintained in the light, develops pigment spots in less than two months, and *Proteus* in the light acquires a dark violet-brown coloration. The ability to form pigment has thus been retained through uncounted generations of subterranean life. Absolon [2] states that even short exposure to light is deadly to a number of subterranean springtails and mites. Whether this results from the chemical action of light or in part also from heat rays was not determined.

Sense organs of cave animals

Degeneration of eyes, optic nerves, and optic ganglia is widespread among cave animals. Many cave turbellarians have no external eyes. In *Planaria montenegrina* from caves, the eyes seem reduced in comparison with specimens from without. The dark planarian, *Pl. vitta,* still has eyes. The leech *Dina absoloni* is without pigmented eyes. In many cave snails, especially in *Lartetia,* the eyes are reduced. The cave crustaceans *Niphargus, Asellus,* and *Cambarus* have reduced eyes. Numerous cave beetles * are eyeless. The olm and the American cave salamanders *Typhlotriton* and *Typhlomolge* have much-reduced eyes. Cave springtails may be eyed or eyeless, like those of the surface. The same is true of mites, but the gamasid mites of caves are uniformly without eyes. The beetle *Machaerites mariae* is found with or without eyes according to the distance at which it lives from the cave entrance.[31] The species of *Chologaster* have perfect eyes, but they become smaller with increased fixity of cave life. In the fishes *Amblyopsis, Typhlichthys,* and *Troglichthys,* the eyes are reduced in size, the lens is minute, and the retina more or less vestigial, little pigmented or unpigmented (Fig. 141).[14]

The question has been raised as to whether the eyes were not already on the road to reduction before these animals took to subterranean life. This is pertinent among such forms as the springtails or mites, but does not apply to animals like the beetle *Machaerites mariae*

* *Trechus* (*Anophthalmus*), *Caulomorphus, Bathyscia,* and *Orostygia.*

or *Planaria montenegrina.* Kammerer's experiment [25] on the olm, in which he found that larvae maintained in red light would produce adults with well-developed eyes, also speaks against it. The larvae of the cave salamander *Typhlotriton spelaeus,* which develop in waters outside the caves, have functional eyes. These degenerate in the course of normal metamorphosis, which takes place in the completely

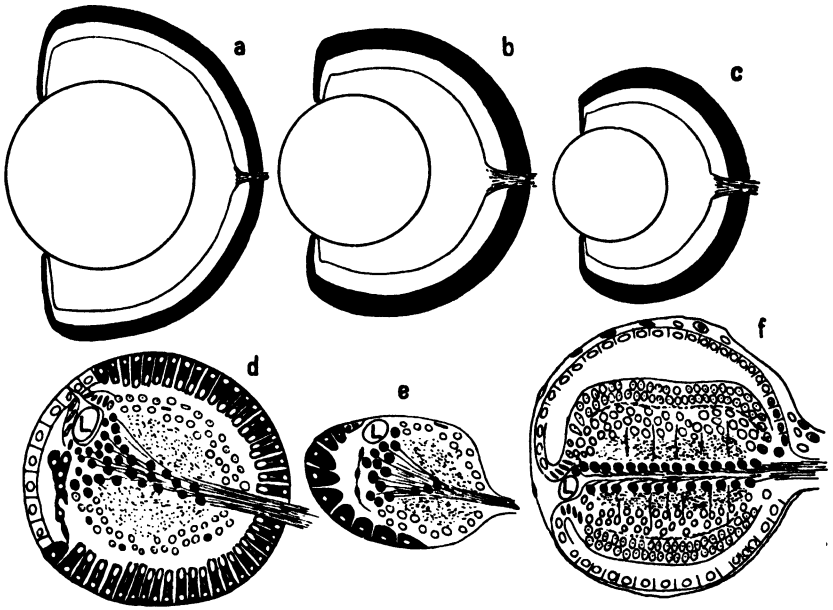


FIG. 141. Degeneration of the eyes of American cave fishes: *a-c,* eyes of *Chologaster cornutus, C. papilliferus,* and *C. agassizii,* × 40; *d-f,* vestigial eyes of *Amblyopsis spelaeus, Troglichthys rosae,* and *Typhlichthys subterraneus.* L is the lens. × 200. After Eigenmann.

dark caves; but larvae kept in the light will produce adults with functional eyes.[28] Viré's experiment with *Gammarus fluviatilis* produced no reduction of eyes after a year. Obviously, animals react differently to darkness, both with respect to loss of pigment and reduction of eyes. Any conclusion as to the relative length of cave life of a species on this basis is consequently untrustworthy, except perhaps in respect to series of closely related forms, like the blindfishes. The eyeless characin, *Anoptichthys jordani,* of Cueva Chica in San Luis Potosí, Mexico, has been shown by Breder [7] to be connected by intermediate stages of eye reduction with the fishes of the adjacent surface waters.[3]

The loss of eyes in cave animals, as in the deep sea, may be ac-

companied by compensating strengthening of other sense organs. Many insects, myriapods, and arachnids of the cave world have legs and antennae of notable length, often set thickly with tactile hairs. The locustids of caves have remarkably long antennae; *Phalangopsis angulata,* with a body length of only 9 mm., has antennae 48 mm.

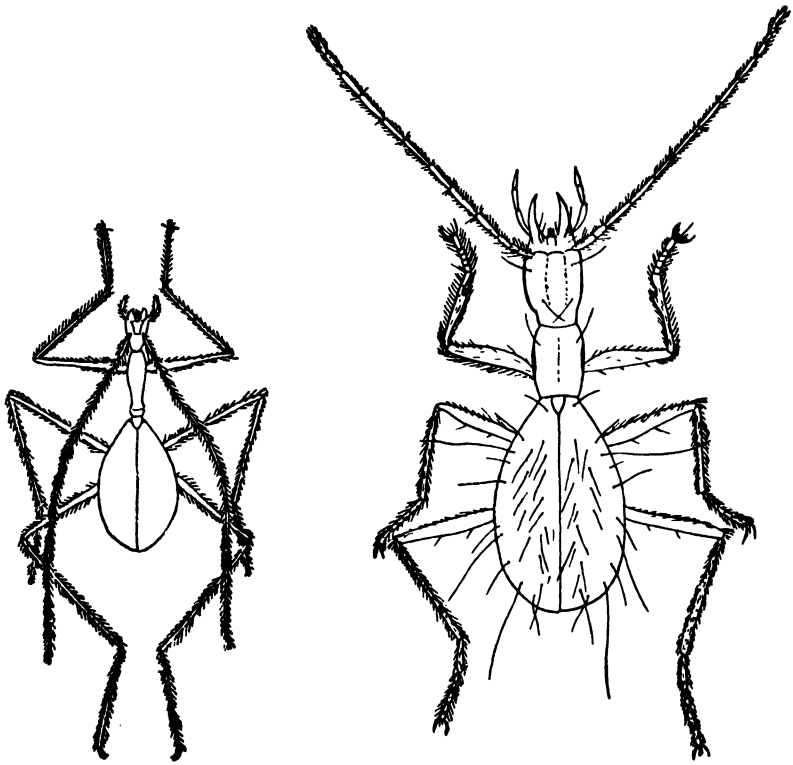


FIG. 142. Cave beetles from caves in Herzegovina. Left, *Anthroerpon apfelbecki;* right, *Scotoplanetes arenstorffianus.* After Absolon.

long.[5] Many cave beetles, spiders, and mites have unusually long appendages. Other beetles bear tactile hairs scattered over the whole body (Fig. 142). The cave beetle *Antisphodrus navarricus,* which is indifferent to light, is extremely sensitive to slight air currents.[20] Cave crustaceans also have notably elongated antennae. In *Stygodytes* (Fig. 140) they are longer than the body, and in the cave *Cambarus* they are longer than in the surface forms of the same genus.[19]

The organs of chemical sense are also more highly developed in many cave animals than in their relatives above ground. The "sense

bulbs" of the cave isopod *Asellus cavaticus* are larger than in the common *Asellus* and have been shown to have greater sensitivity.[27] The isopod *Caecidotea* is much more sensitive to mechanical stimulation than is its epigeal relative *Asellus communis.* It is less sensitive to light and shows superior discrimination as regards food.[4] In Viré's experiments with *Gammarus,*[19] a notable hypertrophy of the chemical sense organs appeared after a few months below ground. Two hyaline bulbs occur on each antenna of a blind gammarid from a cave in Montenegro, instead of the single one of the brook amphipod.[29] Observation shows that cave animals move with as much certainty as if they could see. Springtails, for example, often leap at the right moment to escape from attacking mites.[2]

Humidity and temperature

The constant moisture of most caves, which removes all danger of drying out, is of especial importance to cave animals. In Algeria entirely dry caves lack animals, while moist ones are well inhabited. The skin of cave insects and their larvae is much thinner than in their epigean relatives.[30] The snails of caves have thin shells, as in humid regions. The cave salamander *Hydromantes fuscus* of southern Europe can remain active in the humid air of caves and crevices in summer, while its fellows outside caves are forced to find hiding places in the ground. *Typhlotriton spelaeus* in North America is at home both in and out of the water.[15] Small drip-pools in caves are inhabited by amphipods, from which it may be concluded that they are able to pass from pool to pool. The remarkable air-breathing turbellarian *Geopaludicola,* secured in central Dalmatia, differs in structure from all other land planarians and resembles the aquatic triclads.[26] This appears to be an example of change from aquatic to air-breathing life made possible by the humid cave environment. Cave animals sometimes retain vestigial habits that have only historical significance. Thus land isopods are positively thigmotropic and, by living under stones, escape from light to which they are negative and from many epigean enemies, and also find optimal moisture relations. The habit is retained by cave dwellers although the thigmotropic reaction has little, and at times probably none, of its epigean value.

Caves are well suited to stenothermal animals, and investigation has shown that many cave animals are more than usually sensitive to raised temperatures. The turbellarian *Dendrocoelum cavaticum* disintegrates when one attempts to transport it on a warm day in a flask of water,[17] and *Niphargus* dies at 20°, while *Gammarus* can withstand

a further rise of 10°.[19] Uniformity of temperature has the same effect as in the tropical rain-forest in that periodicity of breeding season disappears in many forms. Among the Cuban blind cave fishes, *Lucifuga* and *Stygicola,* pregnant females are to be found throughout the year, and the same is true of the similarly viviparous *Amblyopsis* of Mammoth Cave.[18] Some cave forms have a definite breeding season; *Lartetia* lays eggs in February, and *Cambarus* breeds in the fall.

The presence or absence of air currents in caves seems to be of importance to the development of their peculiar population, as air currents tend to upset the uniformity of humidity and of temperature. Caves with air currents do not have a true cave fauna.[20]

Isolation in caves

Isolation is an important factor in the development of cave faunae; it may be even more effective in separating small areas than it is on islands. Though there may be more connections between caves in limestone regions than are apparent, such systems of caves are well isolated, and isolation explains their faunistic peculiarity. The cave faunae of Moravia exhibit a great preponderance of springtails and mites, which together make up more than four-fifths of the fauna, whereas the caves of the Karst are characterized by pseudoscorpions, blind beetles, and the olm. The cave fauna of the Swabian Jura, as contrasted with the French Jura, is characterized by the development of the genus *Lartetia.* The escarpment of the Edwards Plateau in Texas is sharply distinct in its blind salamander *Typhlomolge* from the Ozark cave region with *Typhlotriton.* Solution caves in Florida are found to have a distinctive blind white crayfish [21] and a third distinct American type of cave salamander, *Haideotriton.*[10] The great cave region of the central United States, in which Mammoth Cave lies, is characterized by absence of cave salamanders and the development of the cave fishes of the genus *Amblyopsis.* Similarities between the cave faunae of widely separate regions are attributable to the fact that only members of certain groups are able to adapt themselves to cave conditions and that such adaptation produces parallel structure and appearance.

The frequent appearance of endemic forms confined to single caves or to cave systems has already been discussed. It seems evident that this is not merely an appearance of rarity based on inadequate knowledge but represents an extreme of range and habitat restriction.

Isolation in caves, combined with the selection of the entrants

exercised by the peculiar conditions, removes many cave animals from the stress of the terrestrial struggle for existence. Snails are safe from their enemies; beetles have none except spiders and mites; amphipods have enemies only where fishes and salamanders exist. Thus, in addition to animals with close relatives above ground, cave faunae exhibit a considerable number of relicts whose terrestrial ancestors are extinct. Such relicts are the snails of the genus *Lartetia* in the Swabian Jura.* Two representatives of the primitive crustacean *Bathynella* are found in caves and springs in central Europe. These belong to the Palaeozoic group Syncarida, with representatives in surface waters in Australia and Tasmania.[11] The olm is such a relict. Another group of relicts is composed of forms with marine relatives, not represented in fresh waters except in caves; [9] to this group belong the small polychaete annelid *Troglochaetes beranecki*, .5 mm. in length, and the cave isopods *Cirolanides* and *Cruregens* (Anthuridae) from New Zealand. Other cave forms have been assumed by various investigators to be glacial relicts. Absolon supposes the springtails *Onychiurus sibiricus* and *Pseudosinella alba*, which are known from the Moravian caves and northern localities, to be such relicts. Geyer assumes that *Lartetia* was saved from the glacial refrigeration by its existence in caves, while its relatives on the surface became extinct.

The northern limit of the European troglobic fauna, and especially of its non-aquatic element, is shown by Holdhaus [22] to coincide in the main with the southern limits of glaciation. The American trechinid beetles of the genus *Pseudanophthalmus*, originally forest dwellers, were apparently killed by the Pleistocene glaciation except where they survived in caves near the southern border of the glaciated region.[23]

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28. *The Effect of Man on the Distribution of Other Animals*

PRIMITIVE MAN INTERFERED WITH THE CONDITIONS OF HIS ENVIRONMENT relatively little, yet even his activities affected animal distribution both locally and on a geographic scale. Civilized man changes his environment greatly and alters it, in so far as he is able, according to his needs and desires. He destroys many kinds of habitat and replaces them with others, in part with such as would never be formed without his aid and would be unable to maintain themselves without his constant intervention. At the same time, his measures alter the composition of biotic associations; he forces out some elements and introduces others. He cultivates plants, maintains domestic animals, destroys plants and animals harmful to his domestic races, and attracts some forms, which find favorable conditions of life in his neighborhood. He disposes of his wastes, sometimes intelligently, sometimes crudely, and in the latter case produces effects that are harmful even to himself and to the plants and animals he favors. Air pollution in cities and in the vicinity of industrial establishments such as smelters or paper mills, by smoke and waste gases, presumably affects man in more or less obscure ways. All these destructive and creative activities give rise to man-modified or man-dominated areas, with their specialized and distinctive associations. For an admirable study of this process the reader may be referred to Ritchie's *The Influence of Man on Animal Life in Scotland,* 1920.

The extent of change from "natural" to "artificial" is greatest in cities, where masonry and pavement may extend continuously for wide stretches. Most accounts of natural history of the regions about the great cities have been focussed on the wildlife before the advent of

the city, and they fail to recognize the city as a phenomenon in the natural history of man. The realization that cities are, after all, a natural expression of the activities of mankind, plus an account of the interrelations of man and the residual animal and plant life, makes *London's Natural History* by Fitter (1945) a uniquely interesting work.[5]

Deforestation

An early step in wooded countries consists in the clearing of land either for the lumber or to obtain soil free for the cultivation of grains. This tranformation has long been accomplished in Europe, where the period of land-clearing extended from the seventh to the thirteenth century; in North America it occupied the eighteenth and nineteenth centuries; the transformation of the well-forested states of Ohio and Indiana into savanna country practically within the nineteenth century is an outstanding example of the deforestation activities of man.

The area of virgin forest in territory now within continental boundaries of the United States was approximately 800,000,000 acres at the time Columbus came to America, and by the 1920's was less than 100,000,000 acres, according to estimates made available in 1931 by the U. S. Forest Service. Although timber is still being cut in this country to permit extension of farm areas, the amount of land formerly used for farming and allowed to revert to "forest land" is larger,[38] and our forested areas now show a slight net increase. Much "marginal land," where successful farming proves (after trial) to be impractical and where the maintenance of roads, mail service, and schools proves to be more than the area can support, now requires survey and "zoning" as forest, with relocation of the farming populations, or rather of the isolated farm families, concerned. Such "land-use surveys" are exemplified in Wisconsin's studies of her northern counties.[42]

When further need of agricultural land arises, the draining of swamps and marshes and the irrigation of arid districts is begun, or so-called dry farming is improved and extended. Open land, however acquired, is transformed into tilled fields, made fruitful by cultivation and fertilization, and uniformly planted with useful grains or other domestic plants. The growth of plants, which, as "weeds," compete with the cultivated ones, is more and more reduced by careful cleaning of the seed, plowing, cultivation, and the use of selective weed-killing chemicals. Fields with a uniform growth are the result. On account of being harvested at stated times, such fields are an unsuitable habitat for many animals. The composition of the plant

associations in grassland is influenced by the repeated cutting and by manuring; but even under these conditions wild prairie is closely represented by pastures and hay meadows. Special biotopes are more and more sacrificed to civilization.

In well-populated countries, continuous forest persists only in districts unsuited to agriculture, such as barren sands and the steep slopes of mountains or of stream valleys. Forests have been conserved in the remarkably extensive hunting preserves of Great Britain and Central Europe. In the United States state and national forests and national parks and monuments serve this function.

Uniformity of the vegetation over large areas is characteristic of civilized countries. This is especially true of cultivated fields, whether in field crops, such as small grains, or in cultivated rows, and whether in the temperate zone or in the tropics. To a smaller degree, the same is true of meadows and pastures. Such uniformity of food plants makes for uniformity of animal life. Each species of plant has a series of animal dependents, and these are more or less overlapping. The number of animals feeding in part or wholly upon various cultivated plants seems unduly large; more than 100 species of animals feed on sugar cane, more than 200 on corn, the same number on clover, and over 400 attack apple trees.

Nevertheless, the number of species among the inhabitants of such uniform environments is always less than that of more varied habitats. In compensation, certain species appear in great abundance of individuals in cultivated areas and in planted forests. This phenomenon is connected with the superabundance of food; succeeding generations find it unnecessary to emigrate. Pest outbreaks occur when weather conditions are favorable and mortality is low; *Phylloxera* appears in the vineyards of southern France; the Colorado potato beetle appears in potato fields, and the chinch bug *Blissus leucopterus* in grain fields, of the United States; and the gypsy moth *Lymantria monacha* and other insects in European pine plantations. A small number of species goes hand in hand with a great number of individuals in environments of this uniform type, as so often occurs elsewhere under partially adverse conditions.

The environmental formations produced under the influence of civilization are more or less analogous to primitive natural habitats, and they exhibit relations with the latter in their faunae. Cultivated land may be compared to steppe; it is, in fact, an artificial steppe and comprises the greater part of the area dominated by man. The settlements of the stone age in central Europe occupied only a few areas

of grassland. At that time the greater part of the area now under cultivation was forested. Still earlier, this region was natural parkland, and typical steppe animals that had persisted here and there as relicts spread over the new artificial steppe and found favorable conditions for life. Grass-feeding insects are an important element in the communities of the natural steppe. Under agricultural conditions these feed on the cereal grains and thus become serious pests for agriculture. Among insects, the cutworms *Agrotis* and *Hadena* live in grain fields in all parts of the world. The North American aphid *Taxoptera gramineum* has increased from time to time (1890, 1901, and 1907) to such a degree as to become a serious pest for growing grains. The chinch bug (*Blissus*) has already been mentioned. The Hessian fly attacks wheat in the United States, and the migratory grasshoppers devastate grain and pasture fields in semi-arid steppes in all parts of the world.[39]

A large number of birds have become adjusted to cultivated land. Many species are directly dependent on field grains; others find shelter and nesting places in thick stands of grain and hay but feed on insects or small seeds. The English sparrow *Passer domesticus* and the European tree sparrow *P. montanus* are attracted by grain farming and are to be found everywhere in the cities, where they formerly fed mainly on the grain to be found in horse dung. They reach even remote settlements sooner or later, according to distance and degree of isolation by forests and mountains. Neither of these sparrows occurred in Siberia previous to the penetration of that country by the Russians.[11] In Java, where English sparrows were introduced, they are to be found only near the dwellings of Europeans,[9] and the rapid spread of the English sparrow in North America and New Zealand after its introduction was also strictly conditioned by the presence of man. Other sparrows and finches are less dependent on grain farming and are to be found in permanent meadows, but they are certainly benefited by grain culture. In eastern North America the vesper sparrow frequents roadsides; the indigo bunting requires trees and shrubbery.

The early presence of the skylark *Alauda arvensis* in Germany has been proved by the finding of subfossil bones, but their extraordinary present abundance must be dependent on agricultural conditions. The skylark, introduced into New Zealand, is counted as the worst bird pest after *Passer domesticus*. *Mirafra javanica* in the cultivated fields of Java parallels the lark in Europe.[23] The crested lark *Galerida cristata*, a true steppe species, is an inhabitant of such situations as

country roads, railway rights of way, parade grounds, and dump heaps. This species has entered Germany from the east in recent times. It was at first a rare, than an abundant, winter resident; finally a permanent and breeding resident. It nested for the first time in Nürnberg in 1814, in Ansbach in 1850; in 1854 it appeared as a rarity in Augsburg and did not breed there until 1873; it has bred near Stuttgart since 1883.[25] Where horses are common, its principal food supply is the waste grains of horse dung. Suitable nesting places in grain and pea fields have attracted the European reed warbler *Acrocephalus palustris* from its normal reed banks. A notable increase in this species may accordingly be expected.

In the United States, meadow larks and quail find abundant shelter and nesting sites in the thick growth of cultivated fields and meadows, or better, along unmown fence rows.

Under modern game management, in favorable places as in southwestern Georgia, human activities are being directed toward producing advantageous environments for favored species. The result is that, within a few years and without artificial propagation, the population of bobwhite quail is approximately as large in the Thomasville region as it has ever been. This increase has been obtained in the face of relatively uncontrolled predation and of a heavy, even though limited, hunting pressure.[34] Wild turkeys have increased greatly in the same region as a result of the application of similar methods. There is, in fact, a definite movement in various parts of the United States to work out applicable methods of game management that will not be expensive but will provide adequate cover and food for the whole year for selected species. These methods are based on European practice but require decided modifications to meet American conditions.[26]

Abundant seed-bearing weeds furnish food for winter-visitant finches in cultivated fields in California. The number of wintering birds of the species concerned was much smaller in the habitats with native vegetation than in these recently cultivated fields. It is possible that for such birds success in finding winter forage has more to do with actual population density than success in other seasons of the year.[15]

Grain-growing regions, like the original steppe, are the haunt of small and moderate-sized rodents. In Europe and North America such fields support a numerous population of Microtinae, sometimes, by reason of rapid multiplication, in enormous numbers. The field mouse *Microtus arvalis* and its larger relative *M. terrestris* are the European representatives; no less than 57 species and subspecies of *Microtus*

have been described in North America. In Europe, *Microtus* is supplemented by the hamster *Cricetus cricetus,* a true steppe form which is still constantly extending its range to the west, and by the gopher *Citellus,* which is beginning to enter Germany from the east. In North America, the pocket gophers *Geomys* play a considerable rôle in the fauna of the cultivated land, and the ground squirrels *Citellus* afford excellent examples of this adaptability; *C. tridecemlineatus* is completely naturalized in the fields of Illinois and Wisconsin. The gray ground squirrel *C. franklini* has recently extended its range eastward as far as Indiana, but in the Chicago area it is still confined to the vicinity of railways, living on the grain lost from cars. The grain-hauling railroads have thus been effective highways for its eastward spread. In eastern North America the cottontail rabbit and the woodchuck are much more abundant in cultivated regions than under natural conditions. These are forest margin forms, and in general such animals, especially burrowing types, thrive under the conditions produced by man in areas that were formerly forested.

On the other hand, Wood [43] says of an Illinois field in crop: "Apparently nothing but a veritable desert could be more unfavorable for mammalian life than these well tilled fields. . . . In large corn fields of eighty to one hundred and sixty acres, when the corn was about one foot in height and was being repeatedly cultivated and left almost absolutely free from weeds, I repeatedly set traps near the center of the field, at every tenth hill along the rows. . . . The average result of one night's setting was a white-footed mouse in one trap in ten. Very rarely a specimen of short-tailed shrew was taken. If these traps were set near the edge of the field the proportion of traps containing animals was increased." Even so, two subspecies of white-footed mice, a shrew, two spermophiles, and the house mouse live in such situations on the outskirts of Chicago. When Indian corn is shocked up in midwestern fields in autumn, about 90% of traps set about the shocks by mammal collectors contain mammals within 24 hours.

Controlled forests

Regulated forests are the civilized analogues of natural forest. As yet these are but little developed in the United States; in many parts of Europe they are particularly extensive. Forestry as a division of agriculture endeavors to produce the greatest possible income. Roads and lanes are cut to facilitate the care of the forest, the

marketing of its products, and the control of forest fires. Reproduction is regulated, and in so doing the species of trees are selected according to the requirements of man. A natural forest can thus be transformed into an artificial one. For economic reasons cultivated forests are frequently restricted to a single species of tree, and uniform stands replace the original mixed forest. Numerous factors have been in operation for some centuries to favor the propagation of conifers over that of hardwoods in areas subject to such control. Fir and pine are frequently planted alone because they bring the highest return, although stands of these conifers are exposed to special dangers in the temperate zone. The planting of pine, in particular, has made notable advances since the middle of the past century. The cutting of timber is simplified by cutting off specific areas completely and planting them anew. The result of such plot culture is a stand uniform not only as to species, but as to age as well, and areas differing widely in the age of their timber may thus be juxtaposed.

The fauna of such artificial woodland differs in important respects from that of the natural forest, in consequence of the altered habitat conditions. Old and injured trees that might contain hollows are removed. Hornets and wild bees, which place their nests in such hollows are thus kept out; numerous birds use hollows for shelter or nesting sites, and so the stock dove *Columba oenas,* the wood owlet *Strix aluco,* the woodland eared owl *Asio otus,* the common roller *Coracias garrulus,* and many others are discouraged. The marten and the dormouse (*Glis glis*), are robbed of their living quarters. Woodland lanes and roads create numerous interruptions and openings in which grow wild berry bushes such as brambles, elderberry, and dogwood. These openings attract numerous animals, just as do the natural openings, the stream courses, and the forest borders.

The selection of the species of trees is a primary factor in the determination of the animal population. In Europe, virgin stands of trees of a single species are practically restricted to high mountains and the subpolar regions. This is not true of North America, where nearly pure stands of conifers are found locally or on an extensive scale in many parts of the continent and even in Central America. In cultivated temperate hardwood forests extensive damage, such as is caused in coniferous forests by the bark beetle *Bostrychus stenographus,* the gypsy moth *Lymantria monacha,* the pine lappet moth *Dendrolimus pini,* or the bordered white moth *Bupalus piniarius,* is quite unknown. Such pests are not of especial significance in cold regions and in mountains above 700 m., since unfavorable temperature

conditions keep insect reproduction within bounds. In the German climate, pure stands of conifers afford the most favorable conditions for the increase of these pests on account of facilitation of dispersal.

Pure stands of conifers also favor the increase of adapted birds such as the crossbills *Loxia,* the coal tit and crested tit *Parus ater* and *P. cristatus,* the golden-crowned kinglet, and the siskin. In Europe these often constitute, with the common chaffinch *Fringilla coelebs,* the entire breeding population. Capercaillie, black woodpecker, ring dove, and woodland eared owl are also found in coniferous forest. As soon as even a few hardwoods are scattered among the conifers the variety of the bird population is increased. The red deer *Cervus elaphus* does not find sufficient food in coniferous forest, and it damages the trees by stripping bark from them if artificially maintained there.

The difficulties produced by pure stands of timber are further increased when plot culture is carried on. This form of forest management in Germany has brought an enormous increase in the large brown snout beetle *Hylobius abietis.* These beetles congregate in cut-over areas to lay their eggs in the stumps; the larvae develop in the bark of the larger roots and pupate the following year. On emergence, the beetles then attack the young trees that have been set out in the meantime. The arrangement of breeding place and food supply is thus favorable to this species in the highest degree. Many insects abound in plantations of young trees, such as the broad-bodied sawfly *Lyda,* a number of snout beetles (e.g., *Pissodes*), goat chafers, and many Microlepidoptera. Tall stands of fir saplings, before thinning, afford shelter to many animals. Such sapling thickets are especially favored by birds for their nesting sites.

Destructive forest fires, originally mainly set by lightning, have been increasingly the result of carelessness by tourists and campers. Such fires bring in their wake one of the most familiar of developmental plant successions, and, when not extensive, produce forest openings favorable to animal life. When extensive and severe, the stage is set for erosion and loss of soil, with permanent damage to the biota.

In the eastern United States the rather generally neglected farm woodlots are also rich in animal life. Thanks to their small area, their borders have a relatively great extent, and the conditions of food supply are favorably influenced by the neighboring cultivated fields. These woodlots accordingly resemble the forest islands of a savanna. Such woodlots, together with hedgerows, form a focus of interest to the relatively new American movement for "game management," the

object of which has been to promote the supply of wild game in the countryside and for the general public in the same way that "gamekeepers" and hunting preserves have been maintained in Europe, though with quite different social aspects. American studies on the game supply have been based soundly on fundamental ecological studies under the able leadership of such men as Aldo Leopold,[26] Walter P. Taylor,[36] and Paul Errington,[4] whose names are quite as familiar in ecological journals as in *The Journal of Wildlife Management.*

The active development of ecological science in Russia since World War I has been focussed on the relations of animal life to human economy; but, as in the American development of "wildlife management," pure science has been involved to a large extent. At the Oxford center of studies on animal populations, it was found desirable to employ translators to make the Russian publications available. Some of this literature is summarized in Kashkarov's *Fundamentals of Animal Ecology* (2nd ed., 1944).[22]

Orchards, gardens, and parks

Whereas artificial steppe and artificial forest are conspicuous for a fauna impoverished in species though rich in individuals, gardens and parks, even though in and around towns and villages, favor the presence of a great diversity of species. This is in correlation with the variety of plants and the diversity of aspect of this environment, where lawns, shrubbery, and groups of trees form a strong contrast to the uniformity of the agricultural landscape. Orchards, vegetable and flower gardens, planted walks, cemeteries, and parks recall the borders of forests and natural parklands or savannas and, like them, are thickly inhabited.

Parks are, in fact, the type of situation richest in bird life in the temperate latitudes. In the years 1898–1903 the Walters record having seen 114 species of birds in Lincoln Park, which lies along the shore of Lake Michigan near the crowded region of Chicago. Central Park in New York is recognized by close students of birds as an ideal station for the study of bird migration and as being the best place for insectivorous transients in the New York City region. Warblers are particularly abundant in this "oasis in a vast desert of city roofs." The great majority of the 186 species recorded from the park have been seen in "The Ramble," an area of about two acres remote from drives. With increasing use of this part of the park by people, the number of nesting native birds was cut from 18 species in 1908 to

8 in 1923, and the number of overwintering species was reduced in the same period from 22 to zero. Almost every individual of the native species now seen in the park is a migrant. In the whole of the New York City region 56 species have decreased or disappeared within the past century.[16,17]

Less than 150 years ago the region now occupied by the city of Chicago and its suburbs, one of the largest cities in the world, was little affected by man; even 100 years ago this held true. Within the past century every habitat in this area has become definitely man-dominated. Of the mammals formerly present, the following are now lacking: Virginia deer, American elk, American bison, beaver, eastern cougar, Canada lynx, bobcat, gray fox, timber wolf, otter, American badger, marten, fisher, and black bear. However, 39 of the 53 species of mammals known to have been in this area recently still remain within 50 miles of the center of this vast assembly of people. The species present include the opossum, mole, shrews, bats, raccoon, weasels, mink, skunk, badger, fox, woodchuck, spermophiles, squirrels, flying squirrel, pocket gopher, mice, the house rat, muskrat, and cottontail rabbit. Some 15 of these are known to survive in parks and cemeteries within the city, while 7 are recorded from the buildings within the area. In city parks the white-footed mouse of the country is largely replaced by the house mouse. Both shrews (*Blarina* and *Sorex*) are still present. The 13-lined spermophile is very common, and chipmunks are to be found in the northern suburbs. The mole is a pest. Gray and fox squirrels are increasing under protection. The flying squirrel appears to be rare. Stragglers from the country, such as the opossum and muskrat, also occur within the city limits. While wild mammals are by no means lacking, the completely man-dominated communities within Chicago differ from the neighboring grassland or woodland by a general reduction in the number of species and of individuals.[33]

In irrigated regions the character of the vegetation and of associated bird and animal life usually resembles that of parks, gardens, and orchards rather than that of the cultivated fields of mid-United States. The San Joaquin valley since 1900 has been changed from an arid grassland, with xeric grasses and herbs and scattered tracts of lupine or atriplex bushes, to a region of orchards, alfalfa fields, green pastures, and artificial streams of running water lined with willows. In 1900 the winter birds observed included a few horned larks, fewer meadow larks, and occasional burrowing owls, with more frequent savanna sparrows and, in damp places, pipits. Grinnell estimated the bird

population at that time to have been one per acre or less. Now in the same region one finds more species and vastly more individual birds. The horned larks and burrowing owls are gone, but the meadow larks have increased in numbers and in addition there are great numbers of Brewer blackbirds, of mockingbirds, goldfinches, swallows, phoebes, and killdeers.[14] The present population is estimated at ten birds per acre, an increase of more than tenfold as the result of the activity of man. The increase in the Imperial Valley has been still greater, and in California as a whole Grinnell thinks that while a few birds, such as the trumpeter swan and the whooping crane, have become nearly or quite extinct, the introduction of the English sparrow and of the ring-necked pheasant and others has left the bird fauna of California at as high a number of species and subspecies as it had in 1848 before the gold rush. Similar relations hold in Illinois.[6]

Buildings

Houses and other structures afford a substitute for rocky cliffs and may be regarded as artificial cliffs. Barn swallows (*Hirundo rustica* in Europe and Asia and *H. erythrogaster* in North America) are now mainly dependent on man for nesting sites, resorting to the eaves of barns for their mud nests equally in Europe and in the United States. In North America the chimney swift has moved into chimneys from the hollow trees formerly occupied and may occur in flocks numbering thousands. The cliff swallow has moved from its cliff nesting sites to the more abundant artificial cliffs furnished by man, and other American swallows exhibit various stages of transition from the use of natural nesting sites to the adoption of artificial ones. Night hawks now nest by thousands on the flat roofs of city apartment houses instead of on dry ground as in the past. Phoebes nest in barns and under bridges, and bats fly into the artificial caves furnished by belfries or attics. The artificial canyons provided by the stone and brick buildings of large cities, with their cornices and window ledges, provide an evident equivalent of the rocky ledges on which the rock-dove nests in Europe. They are appropriately inhabited by the rock-dove descendants, the feral domestic pigeons. Occasionally the cliff-dwelling duck hawk (*Falco peregrinus*) pursues such prey into this habitat.

Finally, there is a whole group of commensals and parasites directly associated with man and his dwellings. Among these are the silverfish (*Lepisma*), cockroach (*Periplaneta*), house cricket (*Acheta domestica*), bedbug (*Cimex lectularius*), clothes moth (*Tineola bisel-*

liella), house fly (*Musca domestica*), house mouse (*Mus musculus*), and house rat (*Rattus norvegicus*). These forms are dependent upon human culture, and are not to be found, for example, in ruins. Their association with man has a long history. They have followed him around the earth. Where man does not live, neither do they. They are accompanied by a host of less closely associated forms varying with climate, vegetation, and surrounding animal life.

Tropical regions

The conditions described previously in this chapter are based primarily on the North Temperate Zone. The broad outlines of the story of the effect of man's activities upon animal distribution are essentially the same for the tropics, with the exception that both climatic and biotic conditions tend to make his alterations of nature more difficult to accomplish and quicker to disappear once his efforts relax. The depths of the primeval tropical forests are relatively less populous than its edges. Man's activities extend the forest margin conditions and create more sorts of niches, accordingly with richer animal life. Man's activities in planting tropical fruits allow an extension of fruit-eating birds and bats, and even the gorilla is said to be on the increase in parts of mid-Africa where fruit growing has been attempted.

The clearing of forests and the introduction of fence or telephone posts and wooden buildings have created new niches for the abundant wood-eating termites of the tropics. Houses have furnished new habitats for various tropical animals, among which, in addition to termites, large cockroaches, various snakes, and wall-climbing geckonid lizards deserve particular mention. The geckoes, especially, have actively invaded the habitations of man. One small shack in the tropical rain-forest of Panama had been built but a few weeks before it had one of these flycatching geckoes resident therein. In the nipa palm houses of the Philippine Islands, the associated animals depend in part on the surroundings. Scorpions, spiders, centipedes, millipeds, and harvestmen are present. Cockroaches head the list of insects, termites follow; *Bengalia* flies feed upon the termites. Ants and book lice are common. Caddisflies from near-by streams rest under the eaves. Ant-lion pits occur in the dry soil under the stilt-mounted houses. The cocoanut nymphalid butterfly (*Amathusia phidippus*) sometimes nests in the houses. There are mosquitoes, flies, wasps of various sorts, bees, and beetles, including three species of Lampyridae and bamboo borers (Bostrychidae). The usual list of vertebrates includes a tree frog *Rhacophorus leucomystax;* several geckonid lizards, and a large mon-

itor lizard (*Varanus*), which is a chicken thief; several bird species including the sparrow *Passer montanus*, which both roosts and nests in these houses; and bats, both insect- and fruit-eating.

The clearing of tropical regions, if carried to an extreme and if long continued, produces an impoverishment of the native fauna. This is especially well shown if one compares Java with Borneo, or Puerto Rico with the neighboring Santo Domingo. In Puerto Rico the native mammalian fauna has practically disappeared, and even the iguanid lizards (whose flesh was palatable) have become extinct.

In India the general story is similar to that for North America but with a tropical set of animals. The increasing agricultural pressure has reduced the carrying power for wild life of the Indian steppes. The larger animals disappeared from cultivated regions in the following order: (1) rhinoceros, wild pig, and wild buffalo, all of which breed in swamps; (2) elephant, lion, and tiger; (3) nilgai (*Portax pictus*), deer, and antelope. Most of these are still present in some numbers in a few favorable regions. This general process has been accelerated in the last 300 years; within 150 years, 77% of the acreage near Oudh came under cultivation. Here and elsewhere in India, marked changes have occurred even since 1880. Near Oudh, the wolf is the only large carnivore now left in densely populated regions.

The upper Ganges plain, now practically treeless, once supported a forest, which was thorny toward the south and west and luxuriant near the Himalayas. Elephant, buffalo, and rhinoceros were formerly common. Lions ranged widely into the steppe region of India; they are now restricted to a small area in the extreme northwest. This is the last phase in the reduction of the range of the lion in western Asia, where successive stages are documented in historic records since the time of Herodotus. Tigers were hunted near Delhi until the middle of the nineteenth century; they are now practically absent from that region. Following the decrease in large carnivores there came the usual increase in deer and rodents such as is now occurring in Canadian forests. With further destruction of woodland and more intensive agriculture, wild ungulates also decreased, and there followed the increase in insects, birds, and small mammals such as squirrels and rats, like that which is now taking place in parts of the United States.

In unusually dry seasons both human and non-human populations are brought to the verge of starvation, or may actually starve. During such years the remaining antelope herds invade farm lands from their normal refuges in more barren hills. All sorts of plants are eaten;

there is severe overgrazing, which brings back earlier stages of the vegetational succession, and a reinvasion of large predators results.

Aquatic life

In order to lessen the danger from floods and to make the rich bottom lands available for cultivation, the courses of rivers are straightened and their banks are protected by levees or even faced with masonry. Quiet bends and stretches of dead water, which are rich in plant life, disappear, and with them go the feeding and spawning grounds of many fishes and the resting sites of aquatic birds. Dams, built for power, bar the way to the migrations of fishes and furnish breeding grounds for mosquitoes. The refuse of factories pollutes the water and makes it unsuited or even poisonous to many animals. On large rivers the steamboat traffic causes a continuous disturbance of the water, and this traffic necessitates the dredging of channels. Dredging destroys the mud and sand habitat of countless mollusks, worms and insect larvae, and thereby lessens the supply of one type of food for fishes.

When forests are removed, forest margin conditions frequently remain along roadsides or fence rows and in farm woodlots, which harbor a number of forest margin animals. When swamps are drained the effect upon the contained animal life is more striking, and the proportion of the original fauna that is eliminated is even greater than in deforestation as usually practiced. In California the birds displaced by draining such swamps include the herons, rails, gallinules, song sparrows, yellow-throated warblers, and tule wrens, and, if there was open water, coots, terns, and several species of ducks.[14] Fish, frogs, salamanders, turtles, snakes, and mammals are all eliminated, to say nothing of such swamp-dwelling invertebrates as snails, crustaceans, and hydrocolous insects.

Pollution of streams

An even more deleterious effect has been produced by man by the dumping of industrial waste and city sewage into rivers or lakes. A dramatic instance of this is given by the opening of the Chicago drainage canal in January, 1900, whereby the city wastes, formerly, in part at least, emptied into Lake Michigan, were carried down to the Des Plaines and finally to the Illinois rivers. Fortunately the ecology of the latter stream had been well studied, particularly in the decade before the opening of the drainage canal, and fortunately also these studies were continued on an intensive scale for the two decades fol-

lowing, so that we have a fairly complete record of the results of this experiment in waste disposal conducted on a geographic scale.

The so-called Sanitary Canal increased the average flow of the Illinois River by 86%; the mean rate was over 8000 cu. ft. per second before the canal opened. The mean water level was raised about 3 ft. The rooted vegetation along the margin of the old river and of the old river lakes was flooded and killed and replaced in part by aquatic plants. The greater depth caused a decrease in temperatures, especially in summer temperatures. Although the Illinois River was not a clean stream before the Sanitary Canal opened, nevertheless the amount of contamination passing Peoria, 170 miles from Chicago, was increased two and one-fourth times by the material brought in by the canal.

One of the first of the biological effects of the Chicago sewage was to convert the lower Des Plaines and the upper Illinois rivers into a vast open sewer with water grayish in color, offensive in odor, and containing in summer only septic organisms such as the sewage fungus *Sphaerotilus* and the Protozoa * characteristic of foul water. Sludge becoming 8 ft. or more deep collected along the bottom in slack waters and in late summer contained millions of tubificid worms. Fishes were absent in summer, although they appeared in winter, as did certain hardy invertebrates such as the pond snails *Planorbis* and *Limnaea,* and Entomostraca.

Before the Sanitary Canal opened in 1900, the first green plants characteristic of clean water appeared in summer between 35 and 46 miles from Lake Michigan; in 1911 they were found only from 80 to 110 miles downstream, and optimum conditions for such plants were to be found 145 miles away; by 1918 this had receded about 25 miles farther. The tendency of the grossly contaminated area to creep downstream has been increased by the construction of retaining dykes to decrease the amount of land overflowed by the heightened level of the river. The lower river is less affected than it would have been otherwise, owing to the construction of aeration dams in the upper stream.

Below the region of heaviest contamination the amount of plankton increased greatly after the opening of the drainage canal. For 1897–1898 plankton organisms averaged 3 cc. per cu. m. of water throughout the year; for 1909–1910 the average was 5.07 cc. The amount present

* *Carchesium, Vorticella, Epistylis, Oikomonas, Bodo,* and *Paramecium putrinum.*

during April, May, and June, when the newly hatched fish are plankton feeders, increased from a mean of 6.6 cc. to 17.9 cc. Coincident with this increase in food organisms for young fishes and with the increased size of breeding grounds made available by the higher water level, the number of fish caught in the lower Illinois River increased in the decade following the opening of the drainage canal. The explanation of this increase is complicated by the fact that European carp had become established in the river shortly before the opening of the canal and found the new conditions in the lower river favorable for development. It must not be forgotten that in achieving this result the upper hundred of the 270 miles of the length of this river had been rendered unproductive so far as commercial fishes were concerned.[7, 7a] Unfortunately this is not atypical in America; in the upper Mississippi River, about 100 miles of flow is needed to allow the stream to recover from the sewage dumped into the river by Minneapolis and St. Paul,[41] and for the first half of this distance the river is grossly polluted.

Intentional and unintentional transport by man

In Chapter 5, in discussing the means of animal dispersal, attention was called to man's effectiveness in transporting his domestic animals, which have frequently become wild in their new environment, as have horses in South America, cattle in the same continent and in Australia, and pigs and goats on many islands. The similar introduction of the dingo into Australia by the aborigines, and later of rabbits there and elsewhere by the Europeans, has excited much comment. Game animals have also been distributed by this means; the fallow deer was introduced into central Europe from the Mediterranean area, and the pheasant from the Pontic districts; the latter has since been released in numbers in North America; the mufflon has been introduced in the Carpathians and the Harz in recent times; even kangaroos have been freed in the game preserves of large landholders in England.

The honeybee has been introduced in all parts of the world by Europeans. The snail *Helix pomatia,* which was brought by the monks into North Germany as a food for fast days, is now restricted to the sites of old monasteries. The south European *Helix aspersa* has been introduced in many places, from Canada to Argentina in the Americas, in Capetown, Madeira, the Canaries, St. Helena, Mauritius, the Seychelles, Australia, Tasmania, New Zealand, Norfolk Island, and in the Loyalty Islands.[35]

European colonists have taken other animals besides useful ones

to their new homes, as reminders of their native land. Birds have been especially favored in this respect. As already stated, the house sparrow lives now in North America as in Java. In South Australia it is accompanied by the starling, bunting, and the finches *Carduelis carduelis* and *Chloris chloris,* and in North America by the starling. In New Zealand the voices of European birds predominate on the woodland border; no less than 20 species foreign to the islands have been introduced. Thomson's account of the introduction of animals into New Zealand makes a thick book, and one of unusual interest.[37] In the Hawaiian Islands near cities one finds Indian mynahs, Singapore doves, European sparrows, and Australian parrots.[19]

Man has introduced the pests of his cultivated plants with them, such as the potato beetle, Hessian fly, the sugar-cane cicada, *Perkinsiella,* and San José scale, and also has transported other forms with the earth about roots, such as earthworms, ants, *Phylloxera,* and snails. Scarcely a native earthworm is to be found in the cultivated regions of Australia, the Antilles, and many places in South America. The tropical species of land planarian *Bipalium kewensis* was first described from Kew Gardens in England. Lizards frequently make the journey from island to island in the canoes of the South Sea Islanders. The flower-pot blind snake *Typhlops braminus* is found from Madagascar to Formosa and even in the Hawaiian Islands, whither it has been carried in flower-pots or in earth about plant roots. About 500 species of animals, mainly insects and spiders, are known to have been brought to Hamburg by shipping. Other forms include 4 species of lizards, 7 of snakes, 2 of amphibians, and 22 kinds of snails. The wide difference between transport and establishment of a species is shown by the fact that only about 5% of these forms have established themselves, and these only under special locations, in the warm tanbark of tanneries, and in hothouses.[24] A large tropical cockroach has become established in the basements of large American museums. In America we were formerly familiar with a transported tropical fauna brought in with bananas, which involved, among others, cockroaches, spiders, salamanders, frogs, lizards, snakes, and even small rodents and opossums. Banana ships are now fumigated, and this means of animal transport is no longer effective. The loss in the spread of popular interest in zoölogy is perhaps to be lamented.

Parasites of man and his house pests have followed him everywhere; the brown rat and the house mouse and all sorts of small vermin such as house flies, bedbugs, fleas, and lice are well known. An interesting example of unintentional transport by man is furnished by spread of

the sand flea *Tunga penetrans* * in Africa. The female of this species bores into the skin of man, especially beneath the toe nails. Native in Brazil, this species was brought to Ambriz in a ship's cargo in 1872; it ranged from there along the coast, and reached the Congo in the same year and Benguella in 1875; by 1885 it had established itself on the entire coast from Sierra Leone to Mossamedes. covering 22° of latitude. It extended inland first along the principal caravan routes, spread by the porters. By 1898 it had reached Zanzibar. Thus this animal spread across Africa in about 25 years.[20]

In North America many of our worst insect pests were brought accidentally from Europe. These include the Hessian fly, wheat midge, gipsy moth, brown-tail moth, European corn borer, elm-leaf beetle, leopard moth, woolly apple aphid, cabbage butterfly, cabbage aphis, clover root borer, asparagus beetle, imported currant worms, and many cutworms.

Accordingly, great care is now exercised in the United States to avoid the introduction either of new pests or of apparently harmless animals which, if released from the control of their normal environment and the biotic control of their natural enemies, might become pests. In addition to quarantines maintained at ports of entry, interstate and interregion quarantines are established. As a result of their experience with introduced insects that became pests, the Bureau of Entomology of the U. S. Department of Agriculture years ago set about the discovery and importation of important natural enemies of introduced species. This means of biotic control was notably successful with the coccinellid beetles *Novius cardinalis*, which were imported from Australia to hold the cottony cushion or fluted scale in check, and the same method has yielded beneficial results in numerous other instances. Thus man attempts to restore the balance of nature that he himself has destroyed; despite obvious difficulties, this has now become a standard procedure in pest control.

How disastrous may be the introduction of exotic animals without their accompanying predators and parasites is exhibited in renewed dramatic form in the establishment by the Japanese of the large African land snail *Achatina fulica* in the Pacific Islands.[26a] Even with new poisons and all his mechanical resources, civilized man has thus far been unable to cope with this creature. Its hordes devour impartially garden and field crops and native vegetation; its crushed bodies make road pavements as dangerously slippery as does sleet;

* = *Sarcopsylla penetrans*.

and the decaying bodies of its dead burden the air with a miasma. Biological methods afford the best promise of control, but from past experience it is necessary to be cautious with the introduction of predators lest they in turn become pests, like the mongoose in the West Indies and Hawaii.

The introduction and spread of exotic plants often presents striking parallels to the animal phenomena. One of the most instructive histories is that of the calamitous introduction of prickly pear (*Opuntia* spp.) into Australia. From its use as a hedge plant in the mid-nineteenth century, it spread until by 1925 it occupied, to the complete exclusion of agricultural use, more than 30,000,000 acres, with an equally large area also very badly overgrown. Governmental action by a "Prickly Pear Board" was then directed to the study of cactus diseases and of insects that feed on cactus. The resulting introduction of the Argentine cactus moth *Cactoblastis cactorum,* whose larva bores in the cactus stems, has led to the complete control of the cactus and to the restoration of most of the infested land to agricultural use.[30]

The South American water hyacinth *Eichhornia crassipes,* introduced into southern United States as an ornamental plant, has become an extraordinarily persistent weed, clogging waterways and greatly modifying the waters it takes over and covers. Its history has been the same in Java, Australia, and other parts of the world. In the climatic zones to which it is adapted, no effective means of stopping its spread have been found.[12, 31]

Direct eradications *

In addition to all the more or less indirect or unplanned influences of civilization upon the natural animal associations, man affects associated animals directly by the systematic destruction of those harmful to his apparent interests and of forms that afford a source of meat. The larger vertebrates are most exposed to extermination, as they are easily found and as their control is of the greatest importance to man. Accordingly, they disappear more and more from cultivated regions. Crocodiles and hippopotami formerly occurred in the Nile as far north as its mouth, but have long since been driven back beyond the Falls of Assouan and now are not regularly found below the junction of the Blue and the White Nile at Khartoum. Predatory animals such as

* The data given here concerning mammals have been checked when possible against accounts in G. M. Allen's *Extinct and Vanishing Mammals of the Western Hemisphere, with the Marine Species of All the Oceans* (1942), and Francis Harper's similar treatment for the Old World (1945).

the bear, wolf, lynx, and wildcat have either disappeared entirely in western Europe and from central United States or have become very rare. Lions have been exterminated in much of South Africa and along the Mediterranean coasts of Africa. Only 85 individuals of the Laemmergeier (*Gypaëtus*) were observed in Switzerland in the years from 1800 to 1887; the Swiss subspecies is now extinct. The number of golden eagles (*Aquila chrysaëtus*) in the same country was estimated as not more than 300 in 1914. Some species of owls are becoming scarce, and the osprey is now rare in many places.

The larger herbivores are warred against to an almost equal degree, to protect the cultivated field and to obtain meat. Of 16 species of hoofed mammals in Switzerland in the Pleistocene, 9 occurred in the time of the lake dwellers, and 5 remain at the present day.[11] Wild horses and aurochs are entirely extinct; the European bison or wisent *Bison bonasus* persists only in small man-kept herds; and the European elk (*Alces*), still found in Russia and Scandinavia, is restricted in Germany to a few reserves in East Prussia. Red deer, roe deer, and wild pigs would have been exterminated long since had they not been preserved for the hunt. In North America the enormous herds of bison of former times are gone. In Cape Colony the elephant persists only in small remnants under government protection in the Knysna area and in the Addo Forest on the lower course of the Sunday River. Many species of antelopes, formerly abundant in Cape Colony, are now entirely absent. In India the best mammalian populations are in the government-reserved forests; even there tigers are few in number, and ungulates are much reduced.

In western North America the Fish and Wildlife Service of the United States has engaged, on a vast scale in an active campaign of rodent and predatory animal control or extermination by means of poison. Such mass destruction of animal life may be a necessary concomitant of the spread of the human species, but it must nevertheless be deplored by biologists as based on insufficient knowledge of the ecological problems involved, and more especially when there is an indiscriminate broadcasting of poisons.

The destruction and extinction of many races of mankind have gone hand in hand with the spread of the civilized peoples. The complete extermination of the original inhabitants of Tasmania, the problem of whose racial affinities was scarcely understood before they had vanished forever, may be recalled as the most flagrant example of this phase of man's destructiveness.

Disease and facilitation of its spread

More recently man has turned his attention to the eradication of disease-producing organisms and of their carriers. None of these attempts has been completely successful, but the campaign against the organisms producing yellow fever and the *Aedes* mosquito carrying them has been sufficiently successful on a geographic scale so that temperate and subtropical areas are now exempted from this plague, and the organisms producing the disease are being hunted in their tropical lairs as relentlessly as ivory collectors ever hunted elephants. Local successes have been won, as for example in the Canal Zone in Panama, in the similar struggle against the malarial parasite by attacking its bearer, the *Anopheles* mosquito, and by keeping these mosquitoes from biting infected persons. In this warfare, tropical, mosquito-eating fishes are annually introduced into northern waters where they are annually winter-killed, but where they do give partial relief from the mosquito plagues of the summer, and some cold-hardy fish populations are evolving.

The most effective control measures have been those that destroy the breeding grounds of the harmful species. Reduction in numbers in the face of a spreading civilization has usually been in proportion to the reduction in suitable breeding niches. Conversely, where man's activities have increased breeding habitats, then the other members of the community have increased in numbers of individuals, and, if the niches are varied, in number of species as well.

The introduction of *Anopheles gambiae*, the bearer of an especially virulent malaria, from Africa into northeastern Brazil in 1930, its rapid spread and the resulting unparalleled epidemic of fatal malaria, and the subsequent eradication of the mosquito from the area in which it had gained foothold, by a joint campaign of the Brazilian government and the Rockefeller Foundation, form a sequence of events only too familiar, in one form or another, in the modern world. An active campaign for the extermination of *Anopheles gambiae* from the more than 20,000 sq. miles of tropical scrub and forest and river bottom to which it had spread by 1939 engaged the efforts of more than 2000 doctors and technicians and their helpers for two years. Contrary to the most optimistic expectations, the mosquito was driven back to an area of about 12,000 sq. miles by 1940 and was wholly eradicated in the second half of that year, evidently by the combination of unknown factors with the directed warfare. The cost of the campaign exceeded

$2,000,000. Not a single *Anopheles gambiae* could be found by the most intensive search in 1941.

This calamitous invasion and the costly countermeasures may have been the result of the introduction of a single airplane-borne fertilized female mosquito. The necessity of the stringent regulations now in force for the fumigation of intercontinental airplanes needs no further explanation than the fact that in 1943, two years after the last *gambiae* mosquito had been seen in Brazil, live *gambiae* were found on planes from West Africa, and five female *gambiae* were found to have reached dwellings near the Natal (Brazil) airport. Thus only constant vigilance can prevent the repetition of such invasions of disease vectors; and many diseases other than malaria, and disease-bearers other than mosquitoes, have become dangerous to the whole world as one of the results of the advance of civilization.[8]

Conservation

So great have been the changes in the vegetation and animal life of the world with the spread of civilized man, that over wide areas the natural phenomena of geographic zoölogy and of ecology in general are completely secondary, approachable from the agricultural or economic standpoint rather than from the biological. The importance of the study of the conditions of life, undisturbed by the gross effects of civilization, has been increasingly appreciated in recent years. The principal hope for the preservation of natural conditions for the future, in temperate latitudes and probably in much of the tropics as well,[1] lies in the establishment of state and national parks, in which primitive conditions are maintained, to serve as refuges and sanctuaries for wild life.[25] It was a memorable experience for the junior author to find the great volcanic peak of Tongkoko at the northeastern tip of the Minahassa peninsula of Celebes, with its rich forest vegetation, dwarf buffalo and babirusa, black apes and tarsiers, mound builders, and flying lizards, set aside as a wildlife refuge by the government of the Netherlands East Indies some time before 1929, and referred to as a "Natuur Monument." The vast Parc National Albert in the Belgian Congo and the Kruger National Park in the Transvaal are examples on a grand scale of such wildlife preserves in the tropics and subtropics.[3] Throughout the world there has been a notable growth of appreciation of the aesthetic and other non-economic values of the untouched wilderness, exemplified in North America by the "Wilderness Society."

An expanding modern human culture like that of white man in North America or New Zealand tends to progressive and unthinking

exploitation of natural resources without consideration of the long-term results; and unfortunately only too often there has been thoughtless waste of resources more valuable or more important than the short-term advantage gained. European agriculture and forestry had largely established a state of balance before the rise of modern mechanized agricultural techniques, and in older countries generally a kind of stabilization has long since been reached, though sometimes only after great losses of natural resources, as in the deforested and eroded areas of China. Even among many otherwise primitive peoples subsistence agriculture has reached a high state of development, in which terracing of slopes may be carried to an extent impossible under an exploitive economy.

The fact that in unrenewable and renewable resources alike, the United States had been conspicuously thoughtless in its over-all economy came to be realized, or at least publicized, only about the beginning of the present century. The conferences called by President Theodore Roosevelt in 1908 and 1909 brought into focus the lines of thought involved in what we have come to think of as the "conservation movement" in North America.

The more far-reaching implications of the conservation movement in the United States [2, 10, 18, 29] concern long-range problems, the halting of waste, the stabilization of the renewable resources of water, soil, and vegetation, and, in general, taking thought as to man's long-range habitation of the earth's surface. In North America and in the parts of the world developed by white man only in the nineteenth century, the problems of substituting "development" for "exploitation" and of halting waste on public lands are acute.[13, 32] The need for wise conservation policies is recognized even in the more optimistic forecasts of our economic and social future.[27, 40a]

Questions as to the future expansion of human populations in the tropics, depending on the control of the specifically tropical diseases of man and of his domestic animals and on the expansion of tropical agriculture, bring up grave doubts as to the productivity of soils in regions of heavy rainfall. Consideration of the problems of soil resources and soil conservation on a world scale tend to be pessimistic [21, 28, 40] and to emphasize the urgency of the problems facing all mankind in the further expansion of its populations and in its further conquest of the earth.

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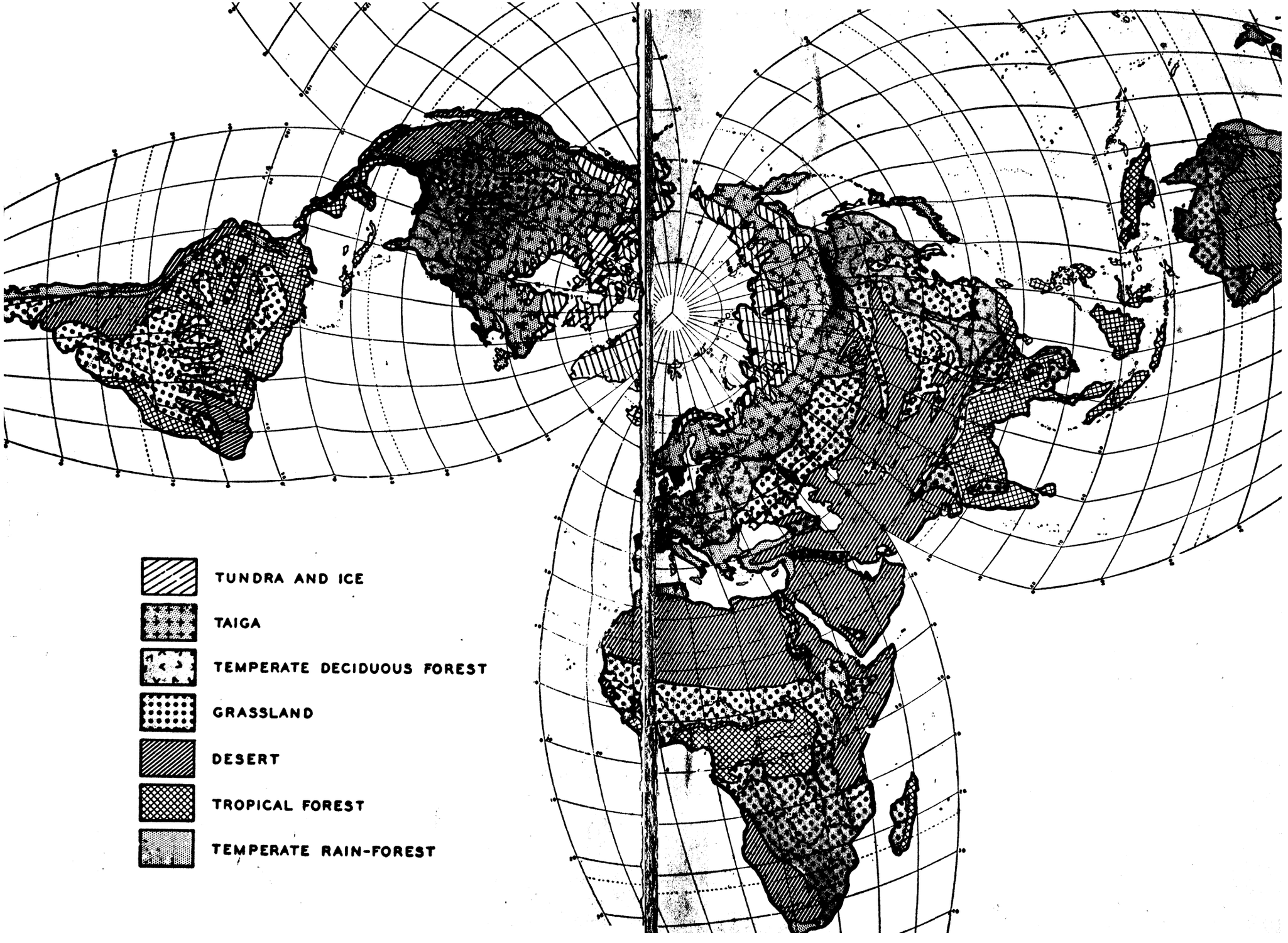
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