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VOLUME 2

VISTAS IN BOTANY

VISTAS IN BOTANY

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Vistas in Botany

A VOLUME IN HONOUR
OF THE BICENTENARY OF THE
ROYAL BOTANIC GARDENS, KEW

Editor

W. B TURRILL

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CONTENTS

	PAGE
Editor's Preface	vii
The Royal Botanic Gardens, Kew *by G. Taylor, D.Sc., Ph.D., F.R.S.E., F.L.S.*	1
Taxonomy General Principles and Angiosperms *by Professor H. J. Lam, Ph.D. (Utr.), D.Sc. (Perth, W.A.)*	3
A Vista in Plant Anatomy *by C. R. Metcalfe, Ph.D., F.L.S.*	76
Plant Biochemistry *by E. C. Bate-Smith, Ph.D.*	100
Causal Plant Ecology *by Sir E. J. Salisbury, C.B.E., D.Sc., F.R.S.*	124
Grundfragen und Aufgaben der Pflanzensoziologie *by Dr. J. Braun-Blanquet*	145
Plant Geography *by W. B. Turrill, O.B.E., D.Sc., F.R.S.*	171
Palaeobotany in Great Britain *by Professor J. Walton, D.Sc., Sc.D., LL.D.*	230
Cytology *by Professor D. G. Catcheside, M.A., D.Sc., F.R.S.*	245
Genes, Chromosomes, and Evolution *by Professor G. L. Stebbins*	258
Viruses *by F. C. Bawden, M.A., F.R.S.*	291
Bacteria *by K. A. Bissett, Ph.D., D.Sc.*	313
Phycology in Retrospect and Anticipation *by Professor W. R. Taylor, Ph.D., F.M.L.S.*	328
Fungi *by Professor C. T. Ingold, D.Sc.*	348
Bryophyta *by Professor P. Richards, M.A., Sc.D.*	387

PAGE

Pteridophyta 421
by Professor Dr. R. E. G. Pichi-Sermolli

Gymnospermae 494
by W. B. Turrill, O.B.E., D.Sc., F.R.S.

Plant Physiology 519
by Professor F. W. Went

Index 533

EDITOR'S PREFACE

THE Royal Botanic Gardens, Kew, since their foundation two centuries ago, have been closely linked with advances in many fields of botany. It is true that a major part of the researches carried out by members of the staff has been in plant taxonomy and in phytogeography, but these in themselves are exceedingly wide subjects overlapping all other branches of botany and, in their modern synthetic aspects especially, they utilize data of many other subjects both within and outside the realm of botany *sensu stricto*. Economic botany, although only incidentally considered in some of the articles in this volume, has also been to the fore at Kew. In addition, the varied investigations that have been carried out at the Jodrell Laboratory range over plant anatomy, plant cytology, plant physiology, and palaeobotany, while plant breeding has been a subject of research in the Herbarium Experimental Ground and at the Potterne Biological Station, Wilts. An important aspect of the service of Kew to botanical science that is often overlooked, or is unknown, is the supplying, through the Director, of materials to institutions and to research workers for observational and experimental purposes. Plants and plant parts of many kinds, vegetative propagules, and seeds are sent annually to many parts of the world in reply to requests, which often state that the material required cannot be obtained elsewhere. It is thus clearly appropriate that a volume published in commemoration of the bicentenary of Kew as a botanical institution should cover a wide range of subjects. The editor has had the somewhat difficult task of determining actual boundaries for such subjects and of suggesting vistas for specialist contributors.

In the large *Oxford Dictionary* the word "vista" is given several definitions. The simple concrete one of "a view or prospect, especially long narrow one through trees, etc.," applies to parts of Kew Gardens. More appropriate to this volume is the meaning of "a view or vision, in prospect or retrospect, of an extensive period of time or series of events, experiences, etc." We are here dealing with vistas in botany, "the science which treats of plants." A synonym of "botany" is "phytology," both words originating from Greek. The earliest references to the use of "phytology" given in the *Oxford Dictionary* are prior to the use of "botany" in English or, at least, in English works: "phytologia" 1647, "phytology" 1658; "botanie" 1697, "botanny" 1706. It might be an interesting study in psychology to investigate why "phytology" has almost entirely succumbed to "botany," although the former is more in accord with, for example, the names applied to such other sciences as "zoology" and "geology" as well as with "biology" and many of its subdivisions such as morphology, physiology, and palaeontology.

Something needs to be said about the use of the designation "biology." By origin, this means the study or science of living organisms, acknowledging that much of the research on them has to be done after the subjects have ceased to live—whatever this means. If, therefore, one divides organisms into animals and plants, biology is simply zoology plus botany. This use of the word seems logical and practical, apart from the difficulties of drawing a line between "living" and "not-living," as exemplified in arguments regarding the status of viruses. Unfortunately, the word "biology" and its derivatives biologist and biological have, not infrequently, been used in a different, and usually restricted, sense, especially as more or less synonymous with ecology (ecological, etc.) or even physiological ecology. It is suggested that this practice be discontinued, for it is surely misleading to talk about "the biology of spiders" or "the biology of flowering plants."

One other criticism of the application of the term, or perhaps one should say the concept, of biology may be made. Even when it is correctly applied as a generic term for botany and zoology all too often the latter is allowed greatly to predominate in the treatment accorded to the two branches. This is frequently noticeable in text-books and in school and college syllabuses and examinations in "biology" and, above all, in popular accounts published in a variety of newspapers and magazines. In passing, one may also note the overwhelming of botanical by zoological subject-matter in the various "nature talks" programmes of the B.B.C. (gardening excepted). All this is a pity because not only is plant life basic to animal life, in the sense that all animals are intimately dependent on plants for their food, but the study of plants, above all by controlled experiments, involves less cruelty than many more or less corresponding researches on animals. No plants have, so far as we know or can discover, either nervous systems equivalent to those of many animals or any kind of consciousness. This is of some importance in introducing biology, especially to children, by the best method of experimenting with and closely examining living material. Even if this viewpoint be challenged it is surely the duty of botanists, professional or amateur, to make certain that the interest, importance, diversity, and beauty of their subject in its many branches is presented to as wide a public as possible. Above all, the study of life histories of plants, their development from spore or seed through vegetative phases up to the diverse phenomena of reproduction needs constant presentation. To do this adequately the botanist has not only to be personally familiar with the advances and problems of his own speciality, but he has to keep abreast, as much as he can, with researches in other fields of botany and allied subjects, and unusual alliances can yield unexpected results often of great importance. Botanists should not "hide their light under a bushel," but should proclaim the educative, practical, and aesthetic value of their subject in season and out of season. This is not

the place to suggest in detail how this should be done but one may just note that there are opportunities in the establishment and extension of activities of the Nature Conservancy, the popularity of gardening, and the controlled development of collecting instincts. Botanists may be envious of the enormous recent popularity of "bird-watching"; it is up to them to show that botany is dynamic and that still more can be done of the widest possible interest under the headings of "plant-watching" and "plant-experiments." Though this volume is not intended to be "popular" in the sense of a series of journalistic articles, it is hoped that it will, among other things, provide a stimulus to the further development of the subject of botany as a whole and that it may provide material for presenting to a wide range of readers and listeners much subject-matter that is new and much that can be looked at along newly opened-up vistas.

Botany is "the science which treats of plants." This definition, however, is none too precise in that it leaves open the question of what should be included in the plant kingdom. There are undoubted organisms, some unicellular such as *Chlamydomonas* or *Euglena* and some more or less colonial as *Volvox* and other members of the Volvocaceae, that are claimed as animals by (at any rate some) zoologists and as plants by (most) botanists. This does no great harm and simply emphasizes the fact that in the apparently simpler groups of organisms there is sometimes no clear-cut division between animals and plants. Rather different problems are set by bacteria and fungi. In various characters, morphological and physiological, these differ from other groups of organisms that are always accepted as belonging to the plant kingdom. They differ, however, still more from animals, and while a few may show some animal characters (as in the Myxomycetes or Mycetozoa) they are most often rightly not included in zoological text-books, but it can be reasonably argued that they should be made into realms co-ordinate with animals and plants. Bacteriology and mycology have in several ways developed along lines independent of botany *sensu stricto* and they have important distinct applied aspects, particularly in pathology, which add to their practical independence. If one accepts for purposes of classification that there are only two realms of living organisms, plants and animals, then the weight of evidence is in favour of including bacteriology and mycology as specialized branches of botany, specialized in the double sense of dealing with peculiar taxonomic groups and in dealing with them by methods different to a considerable extent from those employed in other branches of botany. In various characters the blue-green algae (Myxophyceae or Cyanophyceae) resemble bacteria and if the bacteria be excluded from the realm of botany it may be that the blue-green algae should either be united with the bacteria and the combined group elevated in rank and co-ordinated taxonomically with "plants" and "animals" or yet another "realm" should

be formed. It can be hoped that extended researches with the electron microscope and experimental methods applied to problems of reproduction will give more data for use in working out a new taxonomic delimitation and arrangement of the major groups of organisms.

The viruses raise innumerable and fascinating problems. In some respects they appear to be "organisms"; in other respects they behave so differently from any entities usually accepted as such that for the present their status relative to these remains partly uncertain. That they are of very great importance in the study of plants cannot, however, be gainsaid and a botanist who ignores virology leaves a gap in his education. So far as "groups" are considered the editor has, for this composite work, deliberately included not only algae and fungi but also bacteria and viruses. This is not because he wishes to extend the boundaries of botany to their utmost limits but simply because to include vistas of these groups must, in his opinion, enable botanists better to understand subjects and problems that none would dispute were botanical.

Apart from what groups to accept as "plants," the problem had to be faced of what vistas should and could be included as far as possible to give a general picture of botany in its modern aspects. A scheme was sketched which, after criticisms had been considered and some of them accepted, was considered a practical ideal. This ideal has been largely but not completely attained, mainly owing to one or two expected contributors failing to notify the editor that they would not be able to prepare their articles, until the time factor made it impossible to procure other authors. The most unfortunate omission, from this cause, is that of any special article on plant morphology, though this subject is introduced and in special ways dealt with in several of the contributions. The possibility of including a chapter on plant biometrics was discussed at some length with two eminent biometricians. Finally, their verdict had to be accepted with regret that the subject of biometrics as applied to botany did not lend itself to treatment in line with that proposed for most of the subjects dealt with in this volume. It is true that a number of other subjects might well have been given separate treatment by specialists, as for example, plant embryology. However, this work does not pretend to be a text-book of the whole field of botany but is a series of vistas which can be viewed both independently and as parts of the science of plant life.

Authors of articles were given wide limits in regard to the actual treatment of their subject and as to the length of their contributions. It will be obvious that they have taken full advantage of the editorial leniency and of the courtesy of the publishers. It is no bad thing for personal viewpoints, and even idiosyncrasies, to appear in a composite work on a composite subject. While there has to be specialization which results in ever-increasing analysis by old

and new methods it is interesting to note that many research workers recognize the need for reasonable synthesis, whether by working on a border-line subject or by widening the field of research and extending the methods employed in investigating a subject hitherto accepted as one "in its own right." Claims are made, and substantiated, that modern synthetic taxonomy, phytogeography, ecology, and evolutionary studies, in particular, require the worker to have very broad outlooks so that he is willing and able to utilize data from a great range of what, from other standpoints, can be regarded as special subjects. Even in the study of taxa, the tendency is to utilize taxonomy in the orthodox sense, anatomy, phytogeography, ecology, cytogenetics, palaeobotany, etc., as applied to the group under consideration whenever an attempt is made to describe the given taxon as a whole. It is an excellent sign of the health of modern botany that, except as a matter of convenience to editors, examiners, and, sometimes, readers, boundaries between "subjects" become blurred by the acceptance and use of interconnections.

It may be suggested that *Vistas in Botany* should prove of considerable value to botanical specialists who wish to obtain up-to-date knowledge in subjects other than their own, to teachers of botany and indeed of biology and of science in general, and to many members of the educated public who wish to be informed of the researches that are to the fore in botany in the broad sense. Of special interest and use to many readers should be the historical introductions to most of the articles, the emphasis on modern outlooks and methods, the frank acknowledgement of the limits of our present knowledge, and the clear indications of where future research is needed. For specialists, the bibliographies, sometimes extensive, should be extremely useful.

In accepting the invitation of the Pergamon Press to act as editor of this work the idea was also accepted with pleasure that it was to be published in commemoration of the Bicentenary of the Royal Botanic Gardens, Kew, with the approval of the Director. The writer has been on the staff of this great institution for nearly half a century and knows something of its importance to the science of botany. While this is not the place to give a full history of Kew it seems desirable very briefly to outline a few salient facts regarding the origin and development of this centre of botany whose status as the premier institution of its kind is generally acknowledged throughout the world.

There were gardens at Kew in early Georgian times and even before the House of Hanover succeeded the Stuarts, but it was in (about) 1759 that the Dowager Princess of Wales, the Princess Augusta Saxe-Gotha, started to develop here a royal botanic garden. The early lay-out, stocking, and growth of the garden was controlled, for the Princess, largely by John

Stuart, third Earl of Bute, with whom were associated Sir John Hill and the architect Sir William Chambers. George III, after the death of his mother the Princess Augusta, developed additional properties at Kew. It was from the amalgamation of Kew Garden (especially of the pleasure grounds which extended far beyond the botanic garden proper) with Richmond Garden that the institution obtained and retains the designation "Gardens," in the plural. However, under the superintendence of William Aiton and, later, of his son William Townsend Aiton the importance of the botanic garden greatly increased. In particular the active advice and practical help of Sir Joseph Banks, who succeeded the Earl of Bute as unofficial director, led to the introduction of many new plants. Numbers of special collectors were sent overseas to India, South Africa, West Indies, North America, South America, Australia, and elsewhere. Many of the plants thus obtained are now familiar garden plants in this country and a great many were new to science. In the late Hanoverian period Kew declined and in 1838 the Treasury appointed a committee "to inquire into the management, etc., of the Royal Gardens." The result of the inquiry was that the Gardens were transferred from the Crown to the State and that Sir William Jackson Hooker, then Regius Professor of Botany in the University of Glasgow, was appointed Director in March, 1841.

Sir William immediately commenced a reorganization of the Gardens which were increased in size as a botanical establishment from under 20 to over 250 acres. New greenhouses were built, including the large and important Palm House and Temperate House, economic museums were established, the Lake was constructed, and, in 1853, the Herbarium and Library were commenced. The introduction of new plants of all kinds was continued and many of those that came in were new not only to Kew but to European gardens and, indeed, to botany and botanists. In addition to his very great administrative abilities, W. J. Hooker was a first-class botanist and both before and after his appointment to Kew he published or edited books, periodicals, and papers on a wide range of botanical subjects.

Joseph Dalton Hooker (knighted in 1877) succeeded his father in 1865 as Director of Kew, having served under him as Assistant Director for a decade. He had already earned a high reputation as a botanist from the results of his successful travels in the Southern Hemisphere, from the publication of his large works *Flora Antarctica*, *Flora Novae-Zelandiae*, and *Flora Tasmaniae*, and from his exploration of Sikkim and eastern Nepal. He continued his father's policies at Kew, improving the Gardens, adding to the Herbarium and the Library, encouraging research in many directions, and himself continuing with investigations of floras and of taxonomic groups of plants. During his directorate the Jodrell Laboratory and the North Gallery were built at Kew. The association of J. D. Hooker with George Bentham, who

carried out most of his botanical researches at or in connection with Kew and who presented his extremely rich and valuable herbarium and library to the institution in 1854, culminated in the preparation and publication of the *Genera Plantarum* (1862–1883), which is generally recognized as the finest account of the families and genera of seed-bearing plants that had appeared in any country and it has still not been equalled, much less excelled.

In 1885, Sir Joseph Hooker was succeeded as Director of Kew by his son-in-law, William Turner Thiselton Dyer (knighted in 1899), who held the post till 1905. He was particularly keen on making Kew the centre for botanical information for the British Empire, especially in regard to plant systematics and economic botany. Work was extended on the floras of South and Tropical Africa, following the completion of floras dealing with Australia (by Bentham), India (by J. D. Hooker), and other countries. The *Kew Bulletin* was commenced in 1887. On 1st April, 1887, the Royal Botanic Gardens, Kew, were transferred from the Office of Works to the Board of Agriculture and Fisheries.

David Prain (knighted in 1913) who had served, both as a medical officer and as a botanist for many years in India, was appointed Director in 1905. Kew made steady progress under Prain, in spite of setbacks due to the First World War. In particular, work was increased on the floras of parts of Africa and the European and Oriental collections were added to very considerably. Cambridge Cottage was opened to the public as a museum for British grown timbers. The *Kew Bulletin* was rejuvenated and became established as an official botanical publication worthy of the institution.

On the retirement of Sir David Prain, Arthur William Hill, Assistant Director since 1907, became Director in 1922. He had previously, at Cambridge, carried out valuable research on plant anatomy and later became interested in the taxonomy of various genera and problems of seed germination. He travelled extensively in Europe, Asia, Africa, America, and Australia and was successful in sending various members of his staff on botanical expeditions overseas. He was knighted in 1931. A fine new wing was built to the Herbarium (in 1931) and improvements were made in various parts of the Gardens. Hill was killed by a fall from a horse in November, 1941.

After an interval, during which Sir Geoffrey Evans was Acting Director, Professor Edward James Salisbury (knighted in 1946) succeeded to the Directorship. He had immediately previously occupied the chair of Quain Professor of Botany at University College, London. Though interested in most branches of botany, and with personal experience in many of them, Sir Edward is best known as a plant ecologist and it is very pleasing to have him as a contributor to this volume, both as a plant ecologist and as a former Director of Kew. He had the difficult task of carrying out the reorganization

of Kew after the Second World War. Many of the greenhouses had to be reconstructed and others renovated, notably the Palm House. There were added a new Australian House, a chalk garden, and a clematis wall before his retirement at the end of September, 1956. Scientific research was pushed forward in various directions in the Herbarium and the Jodrell Laboratory.

Dr. George Taylor, formerly Keeper of the Department of Botany of the British Museum (Natural History), is the present Director of Kew. He has not only graciously written a Foreword to this volume but has given it his general approval.

A few words must be said about the publication of botanical research carried out at Kew. Much of this, especially such as is done by botanists who are not on the official staff, is published in scientific journals in many parts of the world. It has long been, and is, recognized that members of the Kew staff should publish their researches under their own names and not anonymously, in whatever way may be approved by the Director, whether in official or outside publications, and permission is very rarely refused. Of official periodicals, the *Kew Bulletin* has, with a break from 1942 to 1945, been published in parts to make an annual volume for many years. The *Index Kewensis*, of supreme importance to taxonomic botanists, is published in (usually quinquennial) supplements and is entirely compiled at Kew. Hooker's *Icones Plantarum* is prepared in the Herbarium and consists of black-and-white drawings and full-length descriptions and accounts of plants preserved in the Kew collections. It is published at irregular intervals (usually one or two parts a year) by the Bentham-Moxon Trustees. The *Botanical Magazine* is the oldest botanical periodical, and one of the oldest scientific periodicals, still continuing. It was commenced in 1787 and its format has not greatly changed from that date in that it consists of coloured plates prepared by trained botanical artists from living plants, with accompanying text, though the latter has been considerably improved as compared with that in earlier volumes. The Hookers took over the editorship of the *Botanical Magazine* and since 1841 this task has been almost continuously undertaken by Directors or by Keepers of the Herbarium, as such or after retirement. Mention must also be made here of the great series of floras of many parts of the British Commonwealth that have been prepared at Kew from the time of the Hookers to the present day. These have been published in various ways. Those now in course of preparation, such as the *Flora of Tropical East Africa*, the *Flora of West Tropical Africa* (ed. 2), and the *Flora Zambesiaca*, are officially prepared and published for the Colonial Office. In addition to papers in numerous scientific journals and to official publications, complete books are frequently being written by present and past members of the Kew staff and published as entities on a wide range of

botanical subjects: monographs, floras, and works on plant geography, plant anatomy, plant breeding, economic botany, and so on.

The present area of the Royal Botanic Gardens, Kew, is approximately 300 acres and they are now officially under the Ministry of Agriculture, Fisheries, and Food, but the Director has a wide degree of autonomy. The main departments are the Herbarium and Library, the Economic Museums, the Jodrell Laboratory, and the Gardens. The first three are under charge of Keepers and the last under a Curator.

W. B. TURRILL.

Kew, November 1958.

THE ROYAL BOTANIC GARDENS, KEW

G. TAYLOR, D.Sc., F.R.S.E., F.L.S.

Director

JUBILEES, centenaries, and the like are suitable occasions for stocktaking and the 200th anniversary of the inauguration of the Royal Botanic Gardens at Kew has given a convenient opportunity to review the progress of the study of botany over two centuries. The march of botanical events in the various branches of the science is recorded in this volume by eminent specialists and in the wide survey the contribution of the successive Kew botanists to plant taxonomy can rightly be regarded as pre-eminent.

This is not the place to dilate upon the history of Kew—the editor of this work has prepared a separate historical account of the institution in connection with the bicentenary—but I feel obliged to make some observations on the origin and development of the establishment. At the beginning, the Royal Gardens were considered as an assemblage of living plants, many of ornamental value but a large proportion of economic importance. In building up the collection Sir Joseph Banks, who for some 35 years at the end of the 18th century was director in all but title, gave substantial and devoted support to his sovereign George III by encouraging his own collectors, whom he sent far and wide to the various British settlements, to obtain material for Kew. In the early 1800's with advancing years Banks's influence waned and the Gardens languished through neglect. Indeed, there was real danger of their dissolution. However, as a result of timely and enlightened agitation of some scientists, particularly John Lindley, the Gardens were transferred to the State in 1840 and the first official director, William Jackson Hooker, was appointed in the following year. He arrested the decline, gave great impetus to the development of the Gardens and was largely responsible for the lay-out as it exists today. He certainly laid the secure foundations of Kew as a scientific research establishment, with his own library, museum, and herbarium as a nucleus.

Joseph Dalton Hooker, who succeeded his father as director, consolidated and expanded the scientific effort in which he enjoyed the vigorous co-operation of George Bentham. The linked names of Bentham and Hooker arouse feelings of pride, admiration, and gratitude amongst British taxonomists and their work has been a powerful inspiration to later Kew botanists. During the younger Hooker's tenure of office most of the great botanical publications associated with Kew were initiated and in some cases completed. Of particular scientific value were the series of floras of the territories which

were under British influence. But fundamental works such as the *Genera Plantarum* and *Index Kewensis* were also published in this fruitful period. The flow of monographs, floras, and important taxonomic works has continued through the succeeding régimes to the present and it can fairly be claimed that in volume and importance the scientific output of Kew botanists is unsurpassed by any other institution.

The massive contributions to taxonomy have tended to overshadow the more limited output from the Jodrell Laboratory, which was the pioneer institution in this country for research on plant anatomy and physiology. Latterly the emphasis has been on plant anatomy in relation to taxonomy, but plans are laid for using the unique living collections at Kew for physiological and cyto-genetical investigations. It is confidently expected that there will be early significant expansion in the activities of the Jodrell Laboratory.

Nor must Kew's influence in the field of economic botany be overlooked. Advice and material assistance given by Kew botanists have been responsible for the establishment of new crop plants in suitable countries, though it is hardly likely that anything so spectacular and rewarding as the introduction of rubber into Malaya will occur.

Kew is proud of its long traditions of service to botanical science and horticulture and is confident in its power not only to maintain its high position but is poised to add further lustre to its reputation in the field of botanical research in its widest sense.

TAXONOMY
GENERAL PRINCIPLES AND ANGIOSPERMS

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Professor of Systematic Botany and Director Rijksherbarium, Leiden

CONTENTS

PAGE

I. GENERAL PRINCIPLES

1. Terminology and definitions 4
2. Classifiable material, methods, and means 5
3. Characters and groups 5
4. Application to organisms 8

II. TAXONOMY OF ORGANISMS

(*a*) *Static Taxonomy*

5. Terminology and definitions 8
6. Units of classification 11
7. Historical notes 12
8. Limitations and possibilities 14
9. Definition of organic characters 19
10. Homology and analogy 20
11. Sequence of characters 23
12. Primitive and advanced characters 25
13. The typological method 27
14. Taxa 30
15. Systems, keys, and symbols 35
16. Taxogenesis 37

(*b*) *Dynamic Taxonomy*

17. Terminology and definitions 39
18. Pseudophylogeny 45
19. Phylogenetical symbols 46
20. Lines and levels 47

III. ANGIOSPERMS PAGE

21. The static viewpoint 52

22. The dynamic viewpoint 59

IV. FUTURE RESEARCH

Bibliography 68

I. GENERAL PRINCIPLES

The golden rule is:
there is no golden rule.

B. RENSCH, 1934
(in Just [87])

1. *Terminology and Definitions.* TAXONOMY is born out of classification, and classification is born out of necessity: the necessity of surveying multitudes of things or phenomena or whatever else presents itself to our senses and our minds.

Now let us be first of all clear about our terminology. *Classification* has been formed after the Latin *classis*, which is a group or multitude (from a Greek verb, meaning to summon, to call together). Classification, therefore, is group-making.

*Taxonomy** is a term taken from the Greek word for order or arrangement, and taxonomy means the rendering of order. The scope of this "law of order" (cf. Turrill[174]) is the theory or theories dealing with the structure of the system of living things, or, as Danser[39] put it: "The science of the structure of the multiformity of living nature."

Systematics (a synonym to Taxonomy) has been derived from a Greek verb meaning: to put together; accordingly, System (Gr.: systema) is what has been put together.

Unlike many other terms of long standing such as atom and individuum, the ones above have largely retained their original meaning and each of them exerts its own function in the branch of science we are going to discuss. Of them, classification is an art rather than a science, taxonomy is the science behind the art, and a system is the result of both. Let us look somewhat closer at this matter.

Classification, we said, was born out of necessity. Everybody is practising classification in his daily life although most of us are unaware of the fact. The human mind has this weakness: its inability to survey a multitude as such. It is an acknowledged fact that none of us is able to grasp and recognize

* The term was first created in this spelling by A. P. de Candolle (1813); in modern French the orthography is mostly—and more correctly—taxinomie.

more than three objects of the same kind at a glance; four is intuitively valuated as two and two, five as two and three, etc.

In order to master the overwhelming diversity of his surroundings man has to simplify because it is the only thing he can do; and, scientifically speaking, the danger is that he oversimplifies. In order to help him mastering the multitudes he classifies and classification entails subdividing multitudes into smaller ones until they become so small that they are manageable under the distinguishing faculties and abilities incorporated in the human mind. Subdivision requires some idea upon which it is based as well as definitions, interpretations, and eventually names for the smaller groups which result from the process.

2. *Classifiable Material, Methods, and Means.* The possibility to classify is independent of the material to be classified; there is no essential difference between the classifications of concrete or abstract items, living or inanimate ones. Thus, there are classifications of celestial bodies and languages, of rocks and religions, of atoms and organisms, of vehicles and human emotions. The catalogues of our public libraries contain numerous examples of this.

What differs in classification is the value of the results based upon the methods applied; in other words: whether a classification is artificial or natural. No classification of whatever material (except in the theoretical case to be mentioned underneath) can be fully natural, nor is it likely that it is possible to make a fully artificial classification, as we shall explain presently.

3. *Characters and Groups.* In order to be able to subdivide in a more critical way than by mere subjective intuition it is necessary to describe the material to be subdivided. Description of whatever item requires distinction and naming of "characters" of the item or its constituent parts, if any, for classification rests on differences between the objects compared.

Practically all objects show a number of characters, the number being the greater as the complexity of the material increases. An object with only one single character is hardly imaginable for we are by no means sure that even the simplest of the elementary particles which are supposed to "exist," can actually be ascribed only one differential characteristic.

On the basis of this consideration and with the restrictions it involves, only those objects might be called identic which are constituted of the same number of the same atoms in the same arrangement and under the same physical conditions. Even though the number of describable characters might be considerable, there is not a single differential one; consequently such a material, however frequent its parts, does not allow any subdivision or classification.

However, this reasoning has no practical value and only some slight scientific one as it might serve as the academic starting point of a theory of

taxonomy, something like a hydrogen molecule at zero Kelvin, or perhaps rather like elementary particles in the sun's centre.

For the rest, and certainly for all practical and scientific purposes we have to attribute to all objects one or more differential characters. In the theoretical case of only one differential character, there is only one type of classification, viz. into two subgroups, which implies that some of the items possess the character and the others do not; and this is the only case imaginable of a fully natural system. In the case of two differential characters the possible number of groups is 4, of three characters 8, of n characters 2^n.

Since even objects which everybody would call simple, such as marbles, would undoubtedly present a great many differential characters and more complex objects such as vehicles may have hundreds of them and organisms probably several thousands, the number of possibilities for classification becomes fantastically high, whether we want to base such classifications on a single character, or on two or more, consecutively or in combination. This means that a choice has to be made in selecting the character(s) on which the subdivision has to be based and the difficulty or even impossibility of making a fully relevant choice, even if simple objects are concerned, is one of the reasons why a fully natural classification is beyond our power.

This difficulty roots in the fact that it may be hard to define the notion character. When the object is simple and the differential characters are few, there seems, at first sight, not much of a problem here. Of marbles we can, more or less accurately, describe the shape, measure the size, weigh the weight, compare the colour(s) with a standard scale, investigate the chemical composition, the physical properties, etc. Any of these "characters" may serve as a basis for a classification and there is no reason to prefer one of the resulting systems to any other unless some special feature turns up. Such a special feature may be that two or more of the differential characters lead to the same subdivision, i.e. that they are correlated. Even though this need not give rise to particular conclusions, e.g. regarding some historical factor, it is likely that a classification based on two or more characters is intuitively considered more trustworthy, or even more "natural" than if it ensues from one single character only.

Another, and a much more serious difficulty arises on finding that characters are not of the black-or-white type, but that the extreme conditions, e.g. the maximum and minimum weights or sizes of marbles, are connected by a more or less gradual series of intermediates. If such a series is as gradual as, for instance that of the natural numerals (and their decimals), the character in question loses all its usefulness towards our attempts to classify. It may, however, regain its usefulness in a wider context, viz. if it is statistically valid in comparison with another group of marbles.

However, in order to continue our trend of thoughts, we have to leave

this very simple example and make use of a more complicated one, e.g. that of vehicles. Obviously the number of characters is considerably higher here, and it is intuitively felt that, for instance, a classification based upon colour, or weight, hardly serves any purpose, practical or theoretical, except, of course, those of the painting firm or the tax inspector, respectively. Therefore, classifications based on one of these characters will be generally considered artificial ones, though not entirely so, since even colour and weight may in some cases be correlated with other characters, or have some more "intrinsic significance."

If we want to select characters for a classification of vehicles, we feel that their aim or purpose ranks foremost, because, since they reflect the "essence" of the subject, quite a number of other characters must depend on it or be correlated with it. Apparently there are "important" and "unimportant" characters.

Purpose was not mentioned as a character before, yet we feel that it must be an important one, even though it is not easy to define. Now in the case of vehicles we are accurately informed about their purpose, because they are shaped and constructed by human thought and human skill; they are, as it were, matter imbued with the human mind, inanimate extensions of our limbs as, if we well remember, Samuel Butler put it in his persiflage *Erewhon*. In addition, and accordingly, we know of their origin, their construction (ontology) as well as their evolution (phylogeny); we are proud of their achievements because these are our own; and we are aware of their shortcomings, which we try to correct, not only for the sake of their efficiency but for that of our mental satisfaction.

However, on trying to make a classification of vehicles, with all our insight of their purpose, construction, functions, and origin, we may hesitate to decide which of the many characters is or are to be selected as the chief one(s). Is it connected with the environment they have to work in or the substratum they have to move on? Is it the type of power which pushes or pulls them, the method of reducing as much as possible both the external and the internal friction?

Whatever our choice, we will find that all characters are more or less intimately interwoven and that any classification is necessarily a compromise. The choice will greatly depend upon the aim of the classificator, even if he tries to make his classification as natural as he can, upon his personal character, insight, ability, knowledge, and mental power which, of course, have all their individual limits. In addition, even inanimate matter has and hides its ultimate mysteries.

In any case, however, the classificator has to describe the characters of his material to the best of his ability and it will, for instance, be found that such a seemingly simple part as a wheel requires quite some pondering and many

extensions from his first-sight concept, until it covers all shapes, sizes, and functions materialized and imaginable. One attempt might be: "a wheel is a disk-like object able to rotate around a pivot and intended both (or either) to reduce friction and to transmit energy." Besides being wide the definition at the same time becomes very vague which is, of course, detrimental to the usefulness of the character as a differential one, because all particulars, e.g. regarding the material to be used, the position of the pivot, the shape of the disk, etc., are intentionally (and necessarily) omitted.

The same can be said of other "characters" and the conclusion must be that even if all characters could be taken into account, none of the systems arrived at is fully natural but at best a good approximation. And if the system is based on one or a few arbitrarily—i.e. not purposely—chosen characters, it is likely to be artificial though not fully so since no character is entirely unconnected with the origin, purpose, or aim of the item in which it is incorporated. In attempting, however, to construct a system which is as natural as ever we can hope for, the inevitable failure ultimately roots in the human restrictedness which is the restrictedness to understand Life.

4. *Application to Organisms.* If we now turn to the organic world, we find that the above considerations perfectly hold for organisms but that all factors involved are much more complicated.

There are classifications that are admittedly artificial, such as Linnaeus's sexual system, and others which pretend to deserve the name of natural systems. Neither statement is fully correct: the most artificial classifications cannot help containing some natural elements, and the most natural system is necessarily in some—often high—degree artificial.

In organic taxonomy characters are much more numerous and much more difficult to define because they are often of the gradual and variable type (whether or not under the influence of the environment); and groups are much more difficult to delimit because of the fitful participation of characters to individuals. In addition, it must be recalled that we know very little of the origin and nothing of the "purpose" of organisms. On this weak basis we are going to tackle the subject of organic taxonomy and a lengthy story it will be, for the very reason of our poor insight in an extremely complicated matter.

II. TAXONOMY OF ORGANISMS

a. Static Taxonomy

The road which leads to systematic truth is neither short nor easy.

(Camp[84])

5. *Terminology and Definitions.* The science dealing with our attempts to arrive at a classification of organisms which is as natural as possible on the

basis of our knowledge of the moment, is called Plant Taxonomy or Animal Taxonomy, or combining the two: Biotaxonomy.

Recently, W. H. Camp and C. L. Gilly[25] have introduced the term Biosystematy, which Camp later on[24] claims to have won an "ever-widening use by both botanists and zoologists concerned with classification." The aims of Biosystematy are (1) to delimit the natural biotic units and (2) to apply to these units a system of nomenclature adequate to the task of conveying precise information regarding their defined limits, relationships, variability, and dynamic structure.

Although the present writer had used the term in its Dutch version (cf. Lam[99]) it now seems to be more or less superfluous, since it seems identic with what here has been called (Bio)Taxonomy, in its widest and most modern sense. As early as 1940 Huxley has entitled his book *The New Systematics*[80]. In fact, numerous names have been proposed for what, as a sequel to Thomas's New Morphology[166], might be called New Taxonomy (or Neomorphology, cf. Neotaxonomy, in analogy of Neodarwinism, etc.).

In 1951 Eames, in ridiculing rather sardonically the "worship of the 'New' "[48], has, as it seems reluctantly, admitted that the "New Systematics has earned its title," probably because it is more and more using—we are afraid overadored—experimental methods. Non-taxonomists have sometimes reproached their taxonomical brothers with being too subjective, but Danser[39] says of the latter's methods: "a better argument than the intuition does not exist" (in typology, that is) and we think this is the same thing as scientific conscience which is indispensable in all sciences whatever methods they apply. In one of his witty papers Camp called the non-taxonomists "a vociferous group,who think of their branches ofscience as being progressive," a world-wide arrogance of people whose attitude confirms that "special botany" is much wider-minded than the so-called "general botany." A rather amusing illustration of this is a naïve remark in the paper of the experimentator Mrs. Frahm-Leliveld[60] who discovered that "Taxonomy is not merely a catalogue."*

* Only after the present paper was completed in typescript, Rogers's paper[139a] came to hand. We fully agree with his comparative judgment of experimental and non-experimental sciences and it may be a consolation to students of the latter to consider that the experimentalists' ideas about non-experimental science are obviously less sound and less well-founded than in the opposite case, as should be expected since "descriptive sciences" (which actually are interpretative and comparative rather than descriptive, the latter term being equally applicable to experiments) generally cover a wider field which naturally engenders a better balanced judgment.

Justly Rogers says: "We ought to have a philosophy of taxonomy." We realize that the present contribution is not the type of taxonomical philosophy meant by Rogers. As it is it could be called a theory rather than a philosophy. Yet it may be found to comprise fragments of an outline of a taxonomic philosophy as do some other papers quoted in the Bibliography, notably Danser's[39].

Meanwhile Eames, apparently insufficiently aware of the enormous progress of morphology both as a result of palaeobotanical—and experimental—methods, sneers that "this so-called New Morphology still must meet the test" (incidentally, this was published in *The New Phytologist*, of all journals).

Returning to the term Biosystematy, we state that Lawrence[110, p. 169 88], seems to have felt a similar slight uneasiness regarding Camp's concept as was expressed above. He uses the term Biosystematics (cf. also Valentine and Löve[175A]), which we agree is more euphonious than Biosystematy (a term not mentioned by Lawrence although he quotes Camp in his bibliography). But his interpretation of it is different from that of Camp's, for he seems to identify Biosystematics with experimental taxonomy, which "is another term for essentially . . . the same discipline" (footnote). Summarizing, we think we had better maintain Taxonomy (or Neotaxonomy, as long as the term retains some validity, viz. until something still "newer" turns up) as a term to include all methods and ways of approach to the structure of organic systems, and we fully agree with its definition as given by Lawrence in his text.

This opinion implies that we cannot agree with Mason[119] who defines Taxonomy as "the synthesis of interrelationship." In a circular diagram he pictures four sectors representing the system, the research (methods), the material (documentation), and nomenclature, respectively. We do not deny the usefulness of such a diagram, nor that of the explanatory text, but we are of the opinion that Taxonomy is a science, in which such auxiliary tools as documentation and nomenclature are unequivalent partners in comparison with methods (among which ranks Biosystematics) and results.

In how far it will prove to be possible to project a suitable nomenclature covering taxa of all imaginable ranks, is hard to say if the condition should be that it should fit in the present Code. Voices are being heard saying that a fundamental revision seems inevitable so as to arrive at "something wholly different from Linnaean nomenclature, something so designed as to give certain and definite names to certain and definite groups" (de Candolle, 1867, in Camp[24, p. 126]), including "the subspecific categories as well (Camp and Gilly[25, p. 382]), but we are rather of the opinion that the wisdom and the practicability of such a procedure seems questionable. It would seem unreal to burden the Code with a nomenclatural system below the species level (cf. § 14).

There are several outstanding reviews of modern taxonomic work or of special facets thereof. Of these we would call special attention to Turrill's extensive paper on taxonomy and phylogeny[175], Danser's posthumous and accordingly unfinished and somewhat fragmentary but very personal theory of systematics[39], focusing on typology, Constance's encyclopaedic

paper on a century's work on Angiosperm taxonomy[31], and Van Steenis's recent study on the delimitation of smaller groups, with particular reference to the Malaysian tropics[156].

6. *Units of Classification.* Before entering upon some historical facts issuing into present-day taxonomy, we will first have to decide upon the nature of our objects. In marbles the unit was just one marble, in vehicles one vehicle. In organisms the situation is less obvious. Could we, for instance, say that the unit is an "individual," one single plant, one animal? Again, at first sight, there seems to be no difficulty at all; an oak tree and a horse, though of complicated shape and build, are limited in space and time, and they can be described, or so it seems. "The main criterion," says Du Rietz[46, p. 337], "of an individual should be its physiological autonomy."

However, consider the case of those plants which are propagating vegetatively by means of bulbils, stolons, rooting rhizomes which may fall apart; lichens which in a dry period crumble and fall to pieces, each part giving rise to a new "individual"; plants (Bacteria, Flagellata, Lower Algae) and animals (Coelenterata) which continuously split up or sever parts or make "buds." Where does the old individual end and the new begin? Would it be sufficient to accept Du Rietz's definition of an individual?

As has been pointed out by Father Jeuken[85], "Individuality is the tendency of the single organism towards undivided subsisting totality. A being is an individual in the measure in which this tendency towards undivided subsisting totality is realized." In short, individuality is not the same thing in different groups. It may be called perfect in unicellulars, but in colonies the cells shift part of their individuality to the colony and a greater part in multicellular plants or animals, until cellular individuality becomes almost negligible, the cell having turned into a part of an individual of a "higher" totality.* In social animals, and *a fortiori* in man, the individuality, however distinct and sharp in the shape, grows vague in another sense: here the individual is a member of a still higher totality, and in a way the same is true for a plant or an animal in a cenological association.

Regenerating power is playing its part here, decreasing as division of functions among cells, tissues, and organs increases. The "higher" individuals, as we have seen, have sometimes vague individual limits. Are one-egg twins—suppose they have arisen from one spermatozoid and one egg-cell—one or two individuals? What if they remain partly connected (Siamese twins)? "For a man," says Jeuken, "the presence of two heads (the brain being the instrument of the spirit) would seem to suggest a double personality." Where lie the limits of the individuality in symbioses, e.g. Lichens,

* In vehicles the same phenomenon can be observed when two or more "individuals," whether identical or different, are combined into an "higher unit" such as is the case in trailers and trains.

and *Hydra*, in which the components may occupy any percentage of the totality?

But there is more. Not only in space, but in time the limits of the individual may be more or less vague. This is most evident in the vegetative propagation just mentioned but it is no less true for the generative reproduction, each "individual" being a periodical phenomenon in the life of the "Keimplasma," which is like a narrow river running through a series of lakes.

However, there is still another reason, and a very cogent one, for not considering the individual the true unit of subdivision: the dimorphy or even polymorphy during ontogeny and the sexual dimorphy of both plants and animals. Whereas it is self-evident that juvenile and adult forms, both in plants and in animals, however different (regarding plants cf. Cockayne) and able to be forced into permanency (cf. *Hedera helix*), belong together because we can follow the transitional phases of their development, it is evident that the male and female belong together because these together —and only these two—are able to reproduce their kind, a process which, with sufficient time and attention, can also be followed without the discovery of any gaps.

From the above considerations, which have partly been taken from Danser's papers, it must be concluded that the true unit of subdivision in organisms is the Life-cycle, or perhaps rather its hereditary factors determining all processes, shapes, reactions, and vicissitudes to be observed by whatever means and from all possible viewpoints in following the development of what emerges from a fertilized egg-cell (zygote) or a spore, the growth, the rise through youth to the adult state, the production of a progeny and, as a sideline, the decline to death and decomposition. "The primary aim of taxonomy," says Danser, "is to obtain as complete a knowledge as possible of the life-cycle of the living being." Baehni's remark (cf. Lam[96]) that the first aim of taxonomy is to determine the name of a plant, can hardly be taken seriously, unless for taxonomy we read classification, and even so the point seems questionable. The same holds for Bremekamp's remark[20] that the aim of classification is to be serviceable.

7. *Historical Notes.* This, of course, is our modern vision and the science of taxonomy has only arrived at it after the many vicissitudes of a long history. A number of most competent botanists (Constance[31], Copeland[33], Gundersen[69], Lawrence[110], Matthews[122A, p. 73], Rendle[137], Schaffner[144, p. 129–31], Soó[150, p. 270–1], Sprague[154, pp. 439, 441, 449], Thorne[173], Turrill[174, p. 344 ss, 175], Valckenier Suringar[163], Valentine and Löve[175A], Wettstein[181]) have reviewed the salient points of this history, and it is comprehensible that most of these are dealing with higher plants. This relieves us of the task to deal with the subject here in more than a cursory way.

Although some of the scholars of the ancient civilizations gave some thought to the philosophy of taxonomy, one can hardly speak of systems, as far as plants are concerned, before the western Renaissance period. In early times knowledge of plants was entirely restricted to local plant lore; nobody was interested in the numerous plants which were of no use to mankind. The relatively few that were, including the cultivated plants, of which Vavilov[177] has revealed in so splendid a way the history as an experimentally based continuation to A. de Candolle's survey of 1886[27], were provided with local names and their products probably had obtained a more or less widespread trade name in the small world of the ancient civilizations. Not only because of the small number of plants consciously recognized but also because of the practical attitude towards plants and the very limited means of mutual communication, no need for a system of any description was felt at the time.

When the first scientific interest awoke, its products were still very much influenced by the practical value of the plants, and classifications were all artificial. Gradually, however, scientific curiosity increased, and the first purely intuitive and very fragmentary natural groups were recognized. This implied that distinction was made between admittedly artificial groups and natural ones, e.g. poisonous trees and Leguminosae, respectively, though a clear insight as to their theoretical differences and their mutual connections was not yet recognized.

As in so many other sciences, the 19th century brought along important improvements. The microscope opened up the way to treat the lower groups in the same manner as the higher ones had enjoyed for so many centuries and the lag of the former is still felt in our days now that we begin to realize that some of the lower groups, notably the Fungi, are vying with the flowering plants in diversity and numbers of taxa. In addition, the ideas of evolution made the time-honoured constance of all creation waver and very gradually these dynamic views impregnated ideas on classification and taxonomy. These views were supported by several new discoveries: a better knowledge of life-cycles (Hofmeister), Mendelism and the great rise of Genetics after its rediscovery by De Vries, Correns, and Tschermak, and the no less spectacular progress of palaeobotany. Genetics and palaeobotany, starting at opposite ends, both imbued, though in very different degrees, by the pre-eminent factors of motion and time, are still endeavouring to meet and the possibility seems to dawn that they will somehow succeed in due course, e.g. in the field of genetics of morphogenesis of ramification (cf. Lam[108]).

This development from practical knowledge on a very limited scale to pure science of world-wide scope (and, if we restrict our notion of "world" to our planet, perhaps soon even wider) has engendered the recognition

that, as far as taxonomy (not classification!) is concerned we are still stammering infants. We have learned to realize that if we wish to understand what the structure of the world of organisms is, no viewpoint should be ignored, no evidence, however remote it may seem, neglected. In addition to the above-mentioned sciences, many fields have already been explored besides the traditional morphology: anatomy, histology, embryology, cytology, ecology, palynology, phytochemistry, specialized parts of morphology (floral morphology, vascular supply), morphogenesis, experimental taxonomy, physiology, geography, parasitism, grafting possibilities, statistics, comparative linguistics (and, in animals and man, also ethology, behaviourism, and psychology). Indeed, that the classical taxonomy is chiefly based upon morphology is due to the fact that, as Danser remarks, man is a "visually gifted animal." Should dogs be intelligent (and interested) enough to make classifications they would certainly primarily make one based on scent.

So far, however, most of this work has been incidental and unco-ordinated except perhaps as regards anatomy (Solereder, Bailey (cf. Constance[31]), Metcalfe and Chalk[122], Puri[136], Greguss[68]), embryology (Maheshwari[117], and chromosome numbers (Tischler, Darlington and Wylie[40])), and they refer exclusively or mainly to higher plants.

Thus, according to Valentine and Löve[175A], the science of taxonomy went through three phases, viz. (a) exploratory, (b) systematic, and (c) biosystematic, and the conclusion is that plant taxonomy in its last-named phase, as Constance[32] puts it, "is just getting under way on an attractively infinite task."

Thus, plant-taxonomy is on its way from the traditional herbarium-systematics or alpha-taxonomy to the ideal of omega-taxonomy which, as Turrill[174] says, "should be a completed classification of all biological (i.e. botanical) knowledge"; or, as he expressed it in his extensive paper of 1942[175, p. 690] such a classification . . . "is an ideal . . . which in the process of attempted attainment must make taxonomy what it should be, the focal point of biology."

We may have left the purely alpha-taxonomy some way behind us, but we have hardly passed any of the next stations. However, we agree with Constance[31] when he states that "systematic botany is healthy but in a state of profound transition."

8. *Limitations and Possibilities.* A most natural system of the organisms would be one in which *all* characters in the above sense had been taken into account. The reader can by now imagine how far we are from this aim, not only because of the limitations pointed out above, but in view of the past that of by far the greatest number of species the life-cycle in its entirety is unknown.

Each separate group requires its own method of approach, because an irrelevant question put to Nature necessarily results in an inane reply. The

chief subdivision of Bacteria, for instance, may be based on shape, but all subsequent ones have to deal with their metabolic processes (cf. Kluyver and Van Niel[90]).

Lichens require the application of chemical compounds reacting to specific substances. Like many lower plants, Algae and in particular Fungi, following their ontogenetical development, growing them, and testing their reactions to various environmental factors, form a substantial part in the investigation of their natural relationships.

Classifications of higher plants, i.e. Cormophyta, according to Lam[104] comprising Astelocormophyta or Mosses and Stelocormophyta or vascular plants,* rests almost exclusively on herbarium specimens which means that plants larger than an average herbarium-sheet (say 30 × 50 cm) are only known in a mutilated or fragmentary state, which can hardly be compensated by even the most complete annotations of the collector. In general, of course, their life-cycle is well known, but not specifically. It may be argued that it is hardly or not worth while to investigate all particulars of a life-cycle for each separate species, even if enough man-hours were available to do this job. But it must be emphasized that similarity or even identity of many details in larger groups is all too often taken for granted and that for that very reason parts of the life-cycle are simply ignored.

Whereas the general impression is that additional information from other than the traditional sources confirms previous conclusions, the cases are not rare in which taxa of, morphologically speaking, doubtful position can be marshalled into a more satisfactory track on applying evidence from auxiliary fields. As regards wood anatomy, for instance, examples of this thesis may be found in the work of Janssonius[84].

Most of the authors who have indulged in historical surveys have dealt in a more or less lengthy way with the modern aspects of taxonomy and particularly in its auxiliary evidence from other sciences. While some of them, such as neomorphology, statistics, etc., will be dealt with in the paragraph on Angiosperms, we deem it appropriate to mention some recent results obtained by others.

A most interesting and promising auxiliary field is phytochemistry. If it could be supposed that "the essential of organisms lies in the chemical structure of fertilized egg-cells and meristem cells" we have to make at least this restriction that we do not know where "life" comes in. In addition, even if the statement were, or could be proven to be, true, we are probably very far from a chemical explanation of all life phenomena (cf. Grant[66]).

* In introducing an interesting system of the higher taxa in the Pteridophyta (in the traditional delimitation), Pichi-Sermolli[180a] proposes the term Cormobionta for Cormophyta, subdividing them into Bryophytonta and Stelophytonta, the latter into Pteridophyta (with 6 classes ending in -opsida) and Spermatophyta.

As to the services rendered by chemistry to plant-taxonomy, we have to remind the reader of the serological method introduced by Mez c.s. In spite of its extensive work and spectacular results (or so it would seem), which made taxonomists prick up their ears some decennia ago, uncertainties regarding the procedure have given the method a reputation of insufficient trustworthiness and by now it is almost forgotten (cf. Danser[39], p. 175).

McNair[121] who was so bold as to design a system of Angiosperms on the basis of some supposedly specific substances, found that several points of Engler's system could be confirmed but others not. His idea is that the higher the organization of a plant is, the higher are the molecular weights of related substances under the same climatic conditions. He was rather severely criticized by Darnley Gibbs[63] and by Weevers[180]. The latter showed that McNair's work rested on a false premise and was carried out with insufficient accuracy. It is certainly true that there is a positive correlation between the morphological system and the sharing and participation of compounds, or rather a particular combination of substances. The more complex a substance is, and, accordingly, the greater the number of directed and accumulated mutations supposed to have co-operated towards its composition, the greater is the certainty that an occurrence in two or more taxa of that substance points at a true, i.e. genealogical, relationship.

Very good reviews of recent work in this line have been published by Darnley Gibbs[62, 63] whose aim it was to contribute towards "that elusive goal of the botanist—a real phylogeny of flowering plants" (cf. § 17–20, § 22). Stating that "once a system has been widely adopted it has the effect of 'freezing' systematics," he gives some examples of where phytochemistry may assist plant-taxonomy, sometimes confirming morphologically based conclusions (e.g. in *Eucalyptus* and in pointing out that *Davidsonia*, sometimes placed in the Saxifragaceae, sometimes in the Cunoniaceae, had better be inserted in the first-named family; in fact it was, in 1952, raised to family rank), sometimes stating that no correlation with a proposed system could be found (e.g. rhaphides regarding the monocot system of Kimura). Gibbs also showed that evidence from several sciences could, at least partly, be interpreted chemically as well: physiology, grafting possibilities, parasitism, and possibly all anatomical and morphological processes which may be supposed to be determined or at least accompanied by chemical processes.

Another recent work on the relationship between taxonomy and phytochemistry is that of Blagowestschenski[17B] and his school. It also reviews much Russian work and provides a useful survey of our knowledge of this field of research. Though imbued with the Lysenko doctrine, it explains an interesting approach to the problem, in which Grossheim's system serves as a basis. On the analogy of Sewertzow's aromorphosis, Blagowestschenski introduces the concept of arochimosis, based both on the capability of the

plant to form more or less complicated substances, and on a comparative method in which specific catalases are tested regarding their reaction on one grammolecule of H_2O_2 as to the activating environmental energy (the thermic coefficient), expressed in g-calories, needed to accomplish their specific reaction. The amount of energy, accumulated in the specific catalase, determines its energetic value. The higher this value, the greater its capacity to lower the amount of environmental energy needed. Products of a specialized metabolism tend to lower the energetic value of the plant. The groups in which these products are abundant are considered the more advanced ones, and these tend to become stable and little susceptible to environmental influences. In primitive (old) groups, however—by Blagowestschenski often preconceivedly, it seems, so indicated on morphological grounds—the thermic coefficient is high, the energetic value low, and the metabolism little specialized. It is, however, admitted, that there are some irregularities and that the rule is only applicable to "plastic" groups, in which the metabolism can be influenced in one way or another, particularly in young stages of the ontogeny. According to Lysenko we should not *auf die Gnade der Natur warten,* but *ihre Gunst nehmen.* Enzymes (active proteins) are the only initiators of life processes; therefore *besteht (es) kein Bedürfnis nach Genen und ihren Kombinationen.*

As regards parasitism, Buhr[21] has pointed out that animal parasites are sometimes very fastidious on which plants they live, and the same is known of gall insects which are often very good taxonomists, even regarding species or varieties. A similar remark was made by Baumann[17A]. This has undoubtedly a chemical basis.

Little and fragmentary though the contribution of phytochemistry to plant-taxonomy is as yet, it is certainly a science of the future and it is highly promising not only towards taxonomy but towards morphogenesis as well (cf. Melville in Lam[108]). In view of what is already known in this field, in view also of the very widespread facts that certain motile cells attract each other, or are attracted by chemical substances, or even in general that all motion in plants is supposed to have a chemical basis, one wonders whether the term affinity in taxonomy may have a deeper significance, and might actually be in principle or in origin, a chemical, i.e. an electrical or energetical affinity. But then, we cannot forbear from asking again: where does life come in?

Another modern approach of taxonomy is that of cytology, notably of chromosome portraits, including numbers. Some geneticists seem inclined to overrate the importance of this evidence, probably because the chromosomes are the carriers of hereditary factors, but outsiders are mostly of the opinion that chromosome characters do not necessarily weigh heavier than any others since they, too, are subject to Mendelian laws. In fact, the correlation

with morphological taxonomy is of the same order here, and recently Frahm-Leliveld[60] published a comprehensive paper which both reviews earlier work and is intended to lay the foundation for future investigations. Basing herself on Darlington's atlas (Darlington and Wylie[40]), she compared trustworthy results of 51 Angiosperm families of all major groups, comprising some 20 per cent of all known genera and some 8 per cent of all known species, with one of the modern systems (Pulle[135]) which she finds "a useful apparatus." Unfortunately, one preliminary conclusion must be that "considerations on the relative age of the families . . . are impossible." For the rest, her methods are statistical with all risks inherent to these (cf. § 21). It was found that the Dicotyledons have a curve with one peak for polyploidy at a basic number of 10, whereas the Monocotyledons have no less than four peaks at 11, 14, 17, and 24, each of these peaks being a "turning point" for increase to decrease of polyploidy percentage. The author infers from this that the monocots are less well balanced and younger than the dicots. The following results seem significant: polyploidy decreases as the basic number increases; polybasy (i.e. more than one basic number) in a genus may either mean that the morphological genus concept is of doubtful value, or that the genus in question shows a subdivision into two or more clearly related groups; in some cases polybasy had perhaps better be explained as a polyploid series; basic numbers range from 3–41 (34 cases) in dicots, from 3–60 (32 cases) in monocots. For each family percentage of basic numbers (as compared to dicots or monocots, respectively) were plotted against percentages of polyploids, and the resulting curve, mostly a gently sloping one with the final value as its highest point, was compared with the corresponding curve for the dicots or monocots, respectively. These curves showed which families were above, and which below the average for each group. In general, however, the taxonomic implications are not very clear, and perhaps this is partly due to the fact that the author is not a taxonomist proper. Some more attention should have been given to similarities or differences among families regarding polyploidy as well as to influence of discontinuous distribution. Something in this line has been done by Anderson and Sax[5] in considering the systematic position of the Hamamelidaceae (connections with both Rosaceae and Saxifragaceae). However, we agree with Rollins[140] who admonishes us not to overestimate—as Darlington himself is supposed to do—the importance of, for instance, chromosome numbers since these have been found unstable even in what is considered one single species, but he admits that outstanding results have been obtained in some spectacular cases (Babcock with *Crepis*; Goodspeed with *Nicotiana*).

To conclude this paragraph we want to say a few words on experimental taxonomy (cf. Andreas[6]). This new field of research is not only the aim of

those taxonomists who wish to free themselves of the odium of subjectivity, but just another conscious method to get rid of the traditional species concept. Its field is wide and overlaps that of physiology in so far as three ways are open to observe the reactions of the plant under various environmental conditions: one of these is to bring the plant under laboratory conditions (the phytotron: F. W. Went at Pasadena, R. Bouillenne at Liège), a second one is transplanting plants into different habitats (Kerner, Bonnier, Clements, Marsden-Jones and Turrill), and a third one investigating populations along ecological gradients (Turesson; Clausen, Keck, and Hiesey).

An interesting geographically determined concept is Huxley's cline of which Zimmermann[189] has given an illustration regarding *Pulsatilla* and Lam[93] regarding meiomery in the gynaeceum of *Canarium*. It was shown by the splendid work of Clausen, Keck, and Hiesey in California that such clines, ranging from the coast to the high Sierras, actually consist of a number of constant "races" whose variabilities overlap each other, from which natural selections pick out what is fitting the environment of a particular area. If these constant races have to be considered the outcome of a diverging evolutionary process so that a genealogical relationship is to be assumed, the term constant should, of course, not be taken too strictly.

Genetics which, of course, helps in distinguishing the phenotype and the genotype and contributes to the relationship between hereditary factors and characters, has also given rise to the recognition of various infraspecific taxa and so have ecology and genecology (i.e. the demeanour of genes under the influence of environmental factors). A number of them have been enumerated by Camp and Gilly[25] and Danser[39]. They range from very vague descriptions, such as that of Gilmour and Gregor's deme[64] to circumscript varieties or subspecies and more than one experimental taxonomist has expressed his misgivings as to the nomenclatorial implications of this development.

Another method in which the experiment meets herbarium-taxonomy halfway is the mass-collection which was introduced by Anderson and Turrill some twenty years ago. The idea was to collect a great number of specimens of critical parts and deal with this material by biometrical and statistical methods. We have not heard much of it lately, perhaps because its results were sometimes confusing rather than elucidating, particularly in those populations which are introgressively hybridizing (Anderson[3]).

9. *Definition of Organic Characters.* In § 3 we came to the conclusion that even in classifications of non-living objects there may be a considerable difficulty in defining characters. While there is no essential difference regarding organisms, because the main source of the difficulty is the restrictedness of the human mind, it will be readily realized that the difficulties in describing characters of organisms (§ 4) are disproportionately greater—if we are

permitted to use this word in a case in which the proportion is unknown; first because the material is so much more complicated and, secondly, because it is not only matter but (perhaps or possibly or probably) more than matter alone, viz. matter endowed with life, a condition whose bearing on our reasonings is utterly unknown, which implies that purpose, which can be successfully introduced in vehicle classification, is ruled out regarding organisms.

It must be stated here that obviously geographic distribution is definitely *not* to be considered a character as some taxonomists have sometimes been inclined to do. For the rest, however, a character may be borrowed from any field and any observation, morphological as well as physiological, etc., and in any case these characters, or rather the range of their variability, is determined by genetical factors, though in most cases we know very little of the exact relationships. In fact, as Turrill[175] remarks, it is often impossible to say what an organic character is or what it is not, since in some cases a number of characters are determined by one single genetical factor, whereas in others what is considered one single character depends on a number of genes. Just[87], accordingly, says "genetic analysis of taxonomic differences is still in its infancy."

In organisms an additional difficulty is that definitions of characters imply interpretations of organs, and interpretations are likely to be subjective, which, of course, greatly influences the natural and differential value of characters.

All this purports to show the extremely vague and unstable basis of the classification of organisms. Measurable characters have lost much importance regarding the life-cycle, except in so far as they may indicate the average or the extremes, in short the variational curve which may or may not be influenced by environmental factors. In the first-named case we speak of phenotypical variation—Sprague has aptly referred to such characters as plastic—in the second one variability, if any, is called genotypical because its various manifestations are ascribed to hereditary differences. The fact that long-range environmental influences, whether by inducement in the Lamarckian sense or by selection in the Darwinian one, apparently lead to forms which are very similar to those which have come into existence by internal factors only, forces us to distinguish between homologies and analogies.

10. *Homology and Analogy.* There is a fairly extensive literature about these subjects (cf. Boyden[19] and Mason[120]) and, accordingly, some considerable confusion and even more uncertainty. This is why we have to face the facts and try to get some insight into this important matter.

Homology as referred to organs is usually defined as the state of similarity in origin, versus similarity of form and function which is called analogy. What exactly does this mean? Does this definition cover all facts?

Homology (see also Deyl[42], p. 73–4), or morphological equivalence, ontogenetically rests upon unequal cell-division, i.e. differentiation. Two daughter cells of a cell-division which differ in form or function or both, are of the same origin and therefore homologous, however much they may ultimately differ. The same is true for the tissues of organs to which they give rise. Therefore identic twins are, so far as we can judge, fully homologous, and the same can be said of two organs of which one rose from one daughter cell of a division and the other from its twin, even though the organs may differ in form and (or) function.

This type of homology can be checked but all other types are doubtful with the full range from very likely to most unlikely. The most unlikely cases, only brought into discussion, of course, if some similarity strikes the observer and calls for an explanation, are comprised under the concept of analogy. Consequently there is a gliding scale between the two extremes; one could also put it thus: analogy is a very remote and unexplained type of homology since indication of direct relationships by a chain of cell-divisions fails to turn up.

A fairly widespread type of homology has been described by Vavilov[176]. His homologous series in variation are very striking in legume seeds, grass ears, etc., but they may be observed in many families. The point is that "on the basis" of generic characters the same specific patterns repeatedly turn up in related genera. The term homologous, of course, is fairly speculative here though not too much so since the similarity of the genera seems to guarantee a certain relationship.

In other cases, however, conditions are much more doubtful and sometimes of far-reaching implications. Of this we have already met with examples in discussing the occurrence of identic chemical substances in supposedly related or supposedly unrelated taxa. In one of the following paragraphs we will come across some other examples, notably the double fertilization in Angiosperms, a development considered so extreme that on it the monorheithry (monophyly) of the class is supposed to rest.

Another example from unexpected quarters is that of identical ideas, springing up as it seems "independently" in the minds of "unrelated" men. We all know that in a given period, identic theories present themselves in different men and we are mostly content in explaining them by saying that the times are mature for such ideas. A very striking example is the following one: it is reported that both Darwin and Wallace, at a mentally crucial period of their lives, happened to read Malthus's essay on population, and that both, quite independently, were struck by the idea of natural selection as applicable to evolution. We hesitate to declare this a case of homology but we would certainly not think of it as a pure case of analogy, although a certain amount of chance cannot be denied. And even the very arrangement

of items in the present contribution to this book shows many signs of "homologous" variations in that the same subjects return in various paragraphs.

An extremely likely homology is that between two leaves of the same plant. Though there need not be a direct connection through cell-divisions, their similarity in way of origin, position (phyllotaxis), shape, anatomy, and the possession of a virtual or potential axillary bud are generally accepted as sufficient proof of their equivalence. There is little doubt in accepting the same for leaves of different related plants, the less so as the relationship is considered closer.

Thus, although the likelihood of homology or rather the homology itself decreases because of the decrease in supposed relationship, it is generally believed that all ordinary leaves of Dicotyledons, Angiosperms, Phanerogams (the probability of homology decreasing in this order) are homologous organs, both on account of similarity in some points which are considered essential (phyllotaxis, axillary bud) and of a more or less continuous series of intermediate forms.

However, serious doubt begins to take possession of our reason when we jump to the lower Cormophyta and even more so on proceeding to the higher Algae. Is a fern leaf with no clear phyllotaxis, no axillary bud, an entirely different anatomy, often bearing sporangia on its underside, homologous with the leaf of a dicotyledonous plant, with which it is not connected by intermediate forms? How about the leaf of a *Lycopodium*, *Equisetum*, *Psilotum*, *Delesseria*? In the last-named case all hesitation is gone and there is no doubt about the verdict analogy. No full analogy, however, for all living things are at any rate connected by at least one common character: Life. And the other cases occupy intermediate positions in which subjective ideas, theories, and hypotheses may play a part as to which position in the series the organ in question is supposed to deserve. Where no clear intermediates are available it is obvious that a solution of this problem is not to be expected from the method of comparing recent plants.

Our considerations on homology do not end here. Let us consider other parts of the same plant than the ordinary green leaf. It is generally acknowledged that cotyledons, bud scales, bracts, bracteoles, sepals, and petals all have leaf nature, are all "phyllomes": they are more or less clearly connected by intermediates and show similar properties regarding position and axillary bud, though sometimes with slight and pardonable—or at any rate pardoned —deviations (alternation of petals) or the production of an axillary bud under most unusual circumstances only. Accordingly, all these organs are generally considered homologous with the ordinary leaf, and so are, for similar reasons several other aberrant forms (metamorphoses) such as thorns, tendrils, pitchers, etc. Matters are getting still more complicated when organs of

different origin—as shown by series of intermediates—develop into forms of exactly or almost the same type. A well-known example of such convergent forms is thorns which are intrinsically leaves and thorns which are clearly axes (stems). In the paragraph on the Angiosperms we will be in a position to give a partial explanation of this phenomenon; for the time being, however, it may suffice to state that we must suppose that no such similar results of different lines of development can come into existence unless the genome (the complex of hereditary factors) allows it.

In cases in which more or less uninterrupted series of intermediates are available the explanation is usually evident. Unfortunately, however, they are often absent or dilapidated, and this is particularly the case, for instance, in the most crucial parts of the Angiosperms, the flowers.

Regarding the stamens and the carpels—and according to some theories other floral parts as well—for instance, there is no consensus. On the contrary, this is the field of an almost passionate controversy. For though some stamens and carpels leave not too much doubt about their morphological equivalence, regarding others serious objections against such an interpretation have been expressed. Again, there is no way of resolving this problem along objective lines by simply comparing living structures. We shall see in another paragraph (§ 17) that next to the ontogenetical one-time homology another type of homology is to be recognized, the phylogenetical one. Before entering upon that subject we will first have to round off our considerations on taxonomy and classification of organisms in the stricter sense.

11. *Sequence of Characters.* As may be inferred from the above, in any classification a choice has to be made as to which characters are most important and which are to be used in some subsequent place; also the order of selection has to be determined. It is obvious that here lies and lurks another source of confusion and subjectivity, and we have to face the question on what grounds that selection is made. The answer is not encouraging, and it is hardly suitable to form part of a scientific method, for it reads: intuition. Of course we can try to gild this bitter pill and disguise the truth either by giving characters a firmer footing by bringing them as much as possible in the exact sphere, e.g. by making them measurable, or by attempting to give intuition a scientific dressing. However, intuition it remains and intuition is belief, the acceptance of the connection of things otherwise than by causal reasoning. And the man of science is usually suspicious of intuition in others.

Meanwhile the matter is not quite as black as all that. A "good" character usually means a character with little variation among a large number of specimens, and therefore mostly called a constant character.

As we have seen, characters of inanimate objects are "perfectly" constant and stable as long as they are not judged through the spectacles of Life, i.e.

man. In organisms, however, even the "objective" characters are variable both in space and time and we have to put up with averages, frequency curves, tolerances, or ranges.

Yet one character may show less variability than another one and for this reason alone be given preference. In addition, however, character constance is usually considered in connection with supposed high age. If opposite leaves are correlated with interpetiolar stipules and an inferior bicarpellary ovary, each of these characters in the group concerned (Rubiaceae) is constant *and* supposed to be of a relative high age, because variability is generally believed to be the initial condition and the acquisition of "advanced" conditions in large groups is supposed to take a relatively long time. Accordingly the three characters mentioned above are "good" differential ones, particularly in combination, and others come next in the establishment of a sequence.

Also it may be added here that constant characters are generally typical for larger taxa and that there is some correlation between constancy of characters and the size of the taxa they determine. Constant characters are often called constitutive characters or organization characters (cf. also § 20). It is upon them that homologies are based, and some of them lack any clear relation to function or environment (phyllotaxis, number of flower parts, zygomorphy*). They may have originated by some spontaneous mutation, if such a thing exists.

The most constant, most widespread, and oldest character of organisms is life, that of the green plants the presence of chlorophyll, that of the vascular plants the tracheid. This way of reasoning leads on to the typological method we will have to discuss later on; for if tracheids are said to be a differential and constant character of all vascular plants, we actually mean to say that they belong to their ground plan, which does not prevent the fact that in one or two representatives of that taxon they may well have vanished secondarily.

Less constant characters, often determining smaller taxa, are considered of generally lower age. They may well concern the same phenomenon, e.g. opposite leaves, which may in one case characterize a large taxon such as a family, in others are only occasionally found. This supports the idea that conditions like these have a life of themselves, that they develop from some more primitive state (cf. § 12 and § 17) and tend to grow with the taxon or even "conquer" and "invade" other taxa. They may serve as a basis for less important or minor homologies.

Variable characters, in various degrees, often show some connection with a

* Nelson[135] says that zygomorphy can be induced by gravity. Leppik's experiments[113, 114, 114a, b, c] seem to prove that certain pollinating insects are able to recognize the number of flower parts.

function or with the environment and consequently are sometimes called functional, adaptive, or epharmonic characters. We agree with Sprague[154] that "plastic" is a more appropriate term for these characters. They often occur in small groups only or are found scattered in related or unrelated taxa. For this reason they give rise to the interpretation of analogy (torpedo shape of various swift water animals; hairiness in plants, leaf-size, flower colour, chemical products, etc.). In some cases it might be assumed that they originated as "acquired" characters by means of "induced" mutations.

The above distinction into fixed constitutive and non-constitutive or plastic characters is a very vague one and is only valid in a general way, but it supports the impression of a very gradual scala in the series between homologies and analogies. This phenomenon seems to be a very general principle in nature, both inanimate and living. It has often been ignored because man is inclined to simplify matters on account of his limited faculties. And the conclusion must be that wherever sharp limits are observed, the cause is either that man sees them as he wishes to see them for his own purposes, or that they have been brought about by some secondary processes. The latter point is concerned in the genesis of taxa which will be discussed later on (§ 16). It is connected with the conclusion of some authors who intensively studied natural groups, that there is no essential borderline between characters of taxa of various ranks (cf. Lam[92]). On the other hand, however, Deyl[43], presupposing that there are fundamental differences between higher taxa and lower ones, is of the opinion that these differences rest on the distinction between constitutive and non-constitutive characters and that they depend on the activities of certain chemical substances, called organizers (for constitutive characters) and determinators (for non-constitutive ones), respectively (cf. § 16), which can co-operate or counter-act one another.

12. *Primitive and Advanced Characters.* Taxonomic literature teems with such expressions as reduction, primitive, and advanced, yet these concepts are often very loosely applied, very insufficiently defined and not at all standardized.

It must be stated first of all that primitive and advanced, strange as it may seem, are historically static concepts. Many taxonomists (Turrill[175, p. 483, 88, 527]; Just[87], Bessey, Engler[56], Hallier[74], Swingle, a.o.) have published lists of characters which they consider primitive or advanced and while there are a number of these about which there is a more or less general agreement, several others have raised serious misgivings in other investigators. It is also clear that the interpretation of organs is not only a matter of personal insight but also of the state of knowledge of the moment.

There is some common opinion on the following points, all based on "insight," "experience with life phenomena," and "intuition":

primitive (within one single groundplan)	*advanced*
functional freedom	decrease of such
independence of environment	increase of dependence on environment
limits none or not sharp	sharp limits
variation (i.e. gradual transitions between two types of organs)	constance (i.e. gaps between two types of organs)
no specialization (i.e. more than one function to one form)	specialization (i.e. a special form available for every function)
no special adaptations	adaptation to extreme conditions or functions (parasitism, aquatic Angiosperms)
many organs and functions present	loss of organs or functions (chlorophyll in Angiosperms)
free organs	coalescent organs
and a great number of detailed ones.	

In every single one of these series there is a hidden phylogenetic thought. For an investigator who points out that free petals represent a more primitive condition than connate ones accepts this order in his mind because he assumes—in most cases probably correctly—that connate leaves have developed from free ones and are therefore representing a younger phase in the series. He may be right in one case and wrong in another, and he will never be sure.

Take, for instance, the condition of alternate leaves (leaves arranged along a spiral, or rather helicoid line) which are supposed to be more primitive than opposite or whorled ones, merely on account of the supposition that it seems a more simple and original process that leaf primordia at a growth point originate at regular intervals one at a time, than as it were periodically and gushwise. This may be so in many cases but in any particular case there is no certainty, chiefly because we do not know what the ancestors looked like. To this one might object that somewhere in the line of ancestors the whorled condition must have sprung from an alternate one, since the argument given above stands as a general principle. On pursuing this trend of thoughts we ultimately arrive at the beginning of life and in the present case it appears to be a pursuance *ad absurdum* because at that time (as we know now) leaves did not yet exist. But it may strike some gap in the system so that, for instance, the question is justified whether one family of vascular plants originated from a certain group of higher algae with some sort of alternate arrangement of leaf-like appendages and another from another group with opposite appendages. If this could be demonstrated and it were found that the two conditions in algae are interchangeable or occurring in equal numbers, or even that the whorled condition was clearly the original one, for instance because it occurred in all juvenile stages, the whole assumption might lose its footing.

The same reasoning can be applied to all characters. It may be true that in some cases, such as those of free and connate organs, the connection between primitive and advanced seems to be beyond reasonable doubt, but there is never a complete certainty. And there are many other cases in which either of the two possible assumptions can be defended.

The latter possibility is based upon the fact that besides progressive series regressive ones are supposed to exist, the last-named ones being the result of a process called reduction, another notion of doubtful standing (cf. § 17, § 21). As reduction is usually understood as a loss of diversity and accordingly simple forms are issuing, there may be much confusion in comparing them with originally, not secondarily, simple organs. It is obvious that such cases may give rise to more than one interpretation and to sharp controversies. An example which will be discussed later on are the simple flowers of many Monochlamydeae.

13. *The Typological Method.* This use of the terms primitive and advanced is, in our opinion, one of the weak points of the typological method, or for short Typology. The doctrine of typology is a taxonomical one which emphatically denies any phylogenetical implication. It roots in Goethe's idealistic morphology and the doctrine of metamorphoses. One of the focal points of typology is the ground plan or basic plan of a natural group, a ground plan being an imaginary plant in which every describable character is represented in the most primitive form found in the taxon under consideration. It is very unlikely that such a plant really exists but, as Danser[38, 39], one of the exponents of modern typology, says, *Magnolia* comes very close to it. In this context a natural group is a taxon with one single ground plan (typus). As a matter of course larger taxa encompassing smaller ones have groundplans including those of those smaller ones, or, in other words, the groundplan of a taxon is composed of all characters which are common to all smaller taxa comprised in it.

The construction of a groundplan is evidently a fairly subjective enterprise, since it is based upon the subjective concepts primitive and advanced. The main difficulties are the correctness of the interpretations and also the question where to stop in the imaginable series of character phases. Obviously this depends on the amount of our knowledge at the time of the construction. The more intimately we know a plant the more perfect our groundplan can be. Now the question is, what is intimate knowledge?

In many groups of lower Cormophyta, for instance, it clearly makes all the difference if we believe that information taken from fossils should be added to that gained by the investigation of their living relatives. But even if we, for the moment, discard that measure, it may be very difficult to find a firm basis for deciding on the most primitive state of a character. In some Angiosperms, for which typology was clearly conceived, the

difficulties do not seem impassable. Restricting ourselves to the flower for the whole life-cycle, we might say, for instance, that the floral groundplan of the Magnoliales could be described as a flower with a long axis, an helicoid arrangement of numerous free phyllomes, in which the transition from bottom to apex is very gradual (though admittedly with some gaps between stamens and carpels, because this is the most "primitive" condition found in the order), the growth tip with a capacity of continuing its growth, the stele with tracheids, anthers with four sporangia, carpels with two-sided marginal placentation, each with several apotropous ovules with two integuments, fruit a follicle, dehiscing ventrally, seed with a viscous endosperm, and a relatively large embryo.

It is significant that in typological considerations *Magnolia* is always the favourite example. We never came across a construction of a groundplan of, say, the Salicaceae, or Piperaceae, or Pandanaceae, and we think for good reasons, viz. that we do not understand these families as we think we do the Magnoliaceae.

The same holds true regarding, for instance, the lower Cormophyta. Could we imagine what the groundplan of the leptosporangiate ferns would look like? As to the gametophyte we may feel fairly sure: a smallish thin green flat thallus, pointed at one end, bilobed at the other, attached to the soil by colourless rhizoids, sessile archegonia with fairly long necks and perhaps more than one egg-cell, and protruding antheridia.

But suppose we were entirely ignorant of palaeobotanical data, could we imagine the appearance of a primitive fern leaf? Would we think of iso-dichotomous nervation as a primitive character? Would we have an idea of what a primitive indusium would look like, or what the anatomy of the stele would be?

No, we believe that typology, however useful a tool in some taxa of which we are tolerably sure of the comparative interpretation of their organs, is quite insufficient to serve as a basis for classification in many other groups, notably those in which the interpretation of the crucial organs, by whatever cause, is open to doubt. It also becomes inapplicable as the taxa considered decrease in rank, because it is impossible to recognize their groundplan. For them, Danser says, the syngameontic method is valid.

Danser[38, 39] who was in principle an adversary to all phylogenetical implications in typology, which method, in his opinion, was the only reasonable and sensible one in taxonomy, states that "systems usually styled phylogenetic owe this for the greater part to the admission of scientifically unjustifiable theoretical admixtures."

This or a similar attitude is comprehensible and, indeed, adapted by many one-time taxonomists* such as Van Steenis[156], who is undoubtedly one of

* However, cf. § 18, on the inquiry by Fosberg.

the most experienced practical taxonomists of our days. While fully agreeing with him that practical taxonomy is not served by speculation, it must be stated that man's natural curiosity often tempts him to look further and deeper even though the picture becomes still less clear. A great many taxonomists just cannot help "looking beyond," surely to the detriment of practical taxonomy; but what we are here mainly concerned about is a theoretical survey of problems connected with classification.

Meanwhile, we are afraid that typology can be addressed a similar reproach as its adherents do to phylogenists: the subjectivity with which the terms primitive and advanced (or derivative) are applied is unscientific and it is not only justified but the obvious thing to do to consult whatever evidence can be obtained from palaeobotany in order to complete the picture of the groundplan (cf. § 17, § 21).

The objections raised to the typological method, however, do not mean that it should be altogether abandoned. On the contrary, in a restricted sense, it may render valuable services to the taxonomy of selected groups in that it forces us to give attention to all particulars which might have escaped us otherwise, and to see a species as a "momentary realization of a line of evolution" (Faegri[57]). If cautiously and critically applied it may also help in disentangling related series in which gaps may lead to unjustified connections, as is demonstrated by the following example, taken from Danser[39]:

Let I and II represent two related parallel series of (characters incorporated in) taxa:

I A B C D E F G H I K L M
II N O P Q R S T U V X Y Z

However, if the two series show gaps, one might be tempted to consider these gaps natural discontinuities (instead of the horizontal line between the two series) and accept, for instance, groups, here separated by vertical lines:

A B C .	. . G H . . .	K L M
N O P Q	. . S T U . .	. . Z

Obviously there is much subjective judgment here too because it is all important which character or characters are first of all chosen to separate the series. It is here that Danser says: "a better argument than the intuition does not exist."

So long as these series are uninterrupted, the consecutive character phases have a good chance to be read and interpreted as belonging together.

Be this as it may, a fact is that, as we shall see in the paragraphs on the Angiosperms, new opinions have arisen which have for a source partly

palaeobotany, partly a closer scrutiny of plant form. It may well be with this in mind that Arber[7] pointed out that a distinction must be made between idealistic morphology (on which the typological system is built) and materialistic (evolutionary) morphology; and Thomas[169] quoting this with the remark that both are valid modes of approaching the study of plant form, concludes that "a completely new approach to the problems of plant form must be adopted." Entirely the same idea is expressed by Lam[108]. In how far Typology will be affected by this new development will be discussed in later paragraphs (§ 17, § 21).

14. *Taxa.* The word taxon (pl.: taxa) is a neologism which was first proposed to and supported by the Symposium on Nomenclature at Utrecht in 1948 and adopted by the International Botanical Congress at Stockholm in 1950 to replace the cumbersome expression "taxonomic group" (Art. 8 of the International Code of Botanical Nomenclature). There has been some discussion about the use and misuse of the term in literature (Morton[123], Lam[106]). It was advocated by the last-named author that the term be "unloosenably connected with the Code and should not be used in any other context." However, there was some ambiguity in the rest of the text of the paper in question in so far as "taxon" could also be interpreted to designate any "natural group." We are afraid that the misuse of the term signalized by Morton, of which the above one is a mild example, can hardly be withheld and the best way out—if it is not yet too late for such a measure—would seem to distinguish two types of taxa, the nomenclatural (abstract) one which is "unloosenably connected with the Code" (and which might be called a *nomtaxon*) and the "free" (concrete) one which would be allowed to be applied to any natural groups of objects (individuals, life-cycles) which are characterized by one or more common features (and could accordingly be called a *nattaxon*). These ideas are in good agreement with Shinners's "plea for divers taxons"[147]. If, for the sake of convenience, it be permitted to use the term nattaxon here (without any expectation that it will share the fate of its mother term*), we enter the field of Camp's Biosystematy with its various "kinds of species" and infraspecific categories. However, the term nattaxon reaches farther of course, for it is applicable to groups of all sizes, held together by all sorts of characters. In this sense,

* This is a very good example of differentiation, homology, or even of taxogenesis, in the sense that one of the daughter terms is identic to the mother term and the other one has acquired a new function, both being mutually homologous. Comparative linguistics (an analogon of static taxonomy) or rather linguigenesis (the analogon of taxogenesis) is full of the most interesting examples of phenomena like these. In fact, there is a far-reaching similarity in methods between the evolution of (living) matter and of products of the mind and biological terminology is to a great extent applicable to comparative linguistics. It is my experience that comparative linguists and taxonomists understand each other much better than say physiologists and taxonomists. Accordingly, good amateur-linguists are not rare among taxonomists.

the learned writers of this book, so adequately planned in honour of the Mother of us all, Kew Gardens and its herbarium, would form a nattaxon, ephemerous though it may be.

At this point it may be stated that "taxon" is an abstraction, but a particular taxon is concrete in so far as a group of objects can be called concrete. Taxa are intuitively appreciated and for learned taxonomists it is reassuring that the unbiased minds of primitive tribes living in and of the forest used to apply delimitations of nattaxa in the surrounding flora, which come very close to ours. Their intuition is a natural gift, unhampered by reason; ours is or should be, as Van Steenis[156] rightly remarks, sublimated experience. Earlier in the present contribution we have, in this respect, spoken of scientific conscience.

One way of tackling the problem may be to make out what we may mean in speaking of the size of a taxon. I think the current interpretation of the common expressions a big species, a large genus, an enormous family is a much diversified taxon rather than a wide-spread one or a taxon comprising a great number of (uniform) individuals.

On considering the sizes of taxa generally our impression is that in principle there is no gap in this respect (cf. Lam[92]) from the one-specimen mutation to the Vegetable Kingdom, and that the numerous categories we recognize—many if not most of them overlapping others—are the result of various processes which started to operate as soon as the nattaxon came into being. These processes, some ephemeral, others of very long duration (with all intermediate periods in between) may be external or internal, and on investigating a particular case we try to find out which of these processes have influenced and modelled the taxon in question.

It is quite superfluous to enumerate and describe all sorts of nattaxa or even the processes influencing them (§ 8). They have been amply dealt with in literature (Huxley[80], Camp and Gilly[25], Danser[39], Turrill[174, 175], Valentine and Löve[175A], Du Rietz[46], to quote only a few of the more recent ones in which most of the older literature is mentioned). Mutations (all kinds), interfertility or intersterility, hybridization, environmental factors (climatic, edaphic, biotic, historic), isolation of any kind, and probably some more, are all playing their parts here (cf. § 8 and § 16).

One point which deserves special mention is the significant fact that the number of differential characters involved seems to increase but only in a very general way with the rank of the category. The smallest categories, e.g. point mutations in apomicts, may differ in one single character only, isolated populations like convivia (Danser) in a few, higher categories in more, etc. This does not imply, of course, that all of these characters are of the same importance. In practice two taxa may well be distinguished on account of chiefly one character, such as trimerous flowers in monocots, or

indusia in lepto-ferns, or vessels in Angiosperms, but these striking characters are rarely entirely ubiquitous in the taxon concerned which can only be accurately distinguished by the combination of a great number of characters.

One might ask what the expressions lower and higher taxa actually mean. Obviously they mean something quite different in the expressions lower Algae and higher Algae, in which the terms lower and higher clearly refer to the degrees of organization attained, which can, for instance, be indicated or at least reflected, by the number of different cells (Zimmermann[187]). In lower taxa, however, the significance is categories of lower rank. In the first case nattaxa were referred to, in the latter nomtaxa. Lower nomtaxa are groups which cannot be distinguished but by one or a few little important characters, as far as their mutual relation is concerned, whereas higher taxa are separated by what Du Rietz had aptly called (large) discontinuities, i.e. gaps which are not bridged by intermediates. Obviously there are many gradations here, too. There are always isolated houses between two villages (in which the houses are close together but more distant as one removes oneself from the centre), which do not clearly naturally belong to one of them, in which case the administration has, for purely practical reasons, to decide where to draw the line.

There is a strange paradox existing amongst biologists. If one would ask if a family or a genus consists of specimens (individuals), the intuitive though obviously incorrect answer is likely to be in the negative: a family consists of genera, and a genus of species. Nobody would, however, reply in the negative sense to the question whether a species consists of individuals by saying that a species consists of varieties. Obviously this is so, first because a great many species are—or were—homogeneous enough not to induce the idea of a subdivision, but also because somehow the species is considered the basic taxon.

This opinion undoubtedly rests on the knowledge that there is an intimate relationship between the species and hybridization. Even if we speak of generic crosses we actually mean to say that two specimens belonging to species of what are considered different genera are able to produce an offspring, for nobody would be pleased by the idea that genera or even species as such can hybridize.

As a matter of fact, this way of thinking is rather modern. Linnaeus's first, purely intuitive basic taxa were often what we would now call genera; only later on did he narrow the concept to what we now know as Linnaean species, the category which is still the most appropriate in the study of tropical floras (Van Steenis[157]). However, it seems questionable whether the linnaeon, as Van Steenis puts it, is "the most essential unit of living matter" because "it is probably the source of all smaller taxa" and should be "responsible for the discontinuity of living matter."

Even more refined methods have continued this process down to the life-cycle, and the picture forces itself upon us of a structure whose basis consists of interchangeable units, which become gradually more isolated as one moves outward, the discontinuities growing even wider until separate isolated strands strive upward, their core with a structure like that of the common basis, coated with spongy material whose protuberances or protrusions never reach neighbouring strands.

However, somewhere around the level of the Linnaean species there is some fundamental demarcation. Above this line is the domain of the alpha-taxonomy, the traditional herbarium technique, in which the "lumper" feels at home, below it is the nowadays enormous field of the smaller and smallest infraspecific taxa which require fundamentally different ways of approach to understand them. "Splitters," if out of the alpha-taxonomy school, are most unhappy creatures to themselves because they inevitably get entrapped in the tangle of criss-cross relationships of which their methods show no way out, due to the fact that morphological characters lose their differential importance as taxa of lower rank are studied, owing to the increasing variability by internal or external causes; and they are a nuisance to other taxonomists, who deplore both the dissipation of honest efforts and the useless results which may block better work on the same group for a long time to come.

As it is, the herbarium method assures the greatest certainty regarding the higher taxa, and its reliability rapidly decreases as the species level is getting near. There is of course a narrow "layer" in which herbarium technique and experimental methods (genetics, ecology, experimental taxonomy in general) can assist each other but very soon the signal tells the herbarium taxonomist: hands off. The species also indicates the borderline between micro- and macro-evolutionary research methods, inductive-experimental and deductive-morphological, respectively.

It is quite comprehensible that a feeling of utter despair may creep over the taxonomist who has lost control of his material and sees no way out in classifying it. This, of course, need not go so far as was the case of Krause (1902) who, as Buhr[21] recalls, decided to combine all cruciferous genera into a single one: Crucifera. Neither may it go so far as to demand (Rothmaler[141]) that a taxon should only consist of units of identical descent. Other expressions of despair are found in the nomenclatural sphere: after Camp and Gilly[25] had enumerated and described to the best of their ability a number of small infraspecific taxa, Camp[24] apparently saw no way out in matters of nomenclature and half-seriously suggested the term binom for a "kind of species" because he did not know what a species was; which nobody knows, for that matter (cf. Grant[66] who adopts binom for agameon). In addition to the subspecies, variety, and forma of the Code,

such names of old standard as linnaeon, elementary species or jordanon, syngameon, and modification, ecological terms as ecotype and ecospecies (Turesson) and many others (Clements) as well as cenological groupings, Rensch's rassenkreise, and Danser's comparium, commiscuum, and convivium, Camp describes the following nattaxa: homogeneon, phenon, parageneon, disploidion, euploidion, alloploidion, micton, rheogameon, cleistogameon, heterogameon, apogameon, agameon, phenogen, and stropha. To these doubtless some more can be added, but this is already an impressive list reflecting the activity of many infraspecific neotaxonomists. We are of the opinion that no attempts should be made (as was one time suggested by Camp) to seek a connection with the nomenclature of the Code, though there is, of course, no objection to design a "parallel" system of name-giving for infraspecific taxa. On the contrary, it seems desirable to come to an understanding in this mazy field, if this is possible at all (cf. § 5).

All this is, of course, the consequence of the fervent desire to see taxa as natural entities. This, however, is one of the most annoying stumbling blocks of taxonomy, because whatever method we apply we will never be sure, except in a very few cases, whether a taxon is really natural. Typologists have tried to define this concept by applying their groundplan but as we have seen this is rather subjective and the only other clue that is left to us (if hybridization fails us) is Du Rietz's discontinuity, meaning that a taxon consists of individuals (or lower taxa) which show more resemblance to each other than to any other comparable unit. And here the inevitable and, indeed, valuable intuition enters again as a "deus ex machina."

This procedure is, moreover, hampered by the impression that in principle there are no natural limits, that taxa of consecutive rank may merge one into the next and that no single character can generally be ascribed a particular relation to any particular category. This is why the opinion has been expressed (Hochreutiner[79]) that, in fact, there are no taxa, only individuals . . . "le règne végetal qu'il faudra réunir sous le nom de planta variabilis." With this he meant to say that all delimitations are subjective, human imaginations; life is one single community; even the individual is not fully real; real is only the inanimate world. Another soul in despair.

Others who foster similar misgivings are inclined to attribute some reality to certain kinds of species, but not to other taxa, or if so, to genera rather than to species.

There has been a perceptible inclination lately to sanitate Angiosperm families. Gundersen[69] states that after 1900 no less than 40 genera—most of them monotypical—have been raised to family rank. And while we are under the impression that this figure is rather on the low side, we may add that several families have been split up; processes that still continue and express in yet another way that there is no fundamental difference between

the categories, which, however, need not imply that any particular taxon should not be considered concrete or even natural, be it only in the sense that it is not a product of human imagination, but of natural processes, however various.

15. *Systems, Keys, and Symbols.* A few remarks may be inserted here on the methods which enable us to find the place in the system in which a given specimen is to be inserted. First of all, of course, there is the description of the specimen. In by far the greatest number of cases it will appear that the "species" can be described from that specimen in a very poor and insufficient way only; not only because one specimen only represents a part of the potential polymorphy of the species, but because the life-cycle in its entirety remains unknown to us.

The second move is to do the same with other specimens which seem reasonably similar and as soon as a number of specimens have been compared, a mental picture of the species, its variability and delimitations, shapes itself in our mind. Incidentally, one of the specimens—or the first one which is recognized as unknown to science—may be destined as a nomenclatural type specimen, the type of a nomtaxon. It is obvious that this nomenclatural type has nothing in common with the type of typology; neither is it likely to be typical—in the sense of characteristic or representative—for the species concerned.

This mental picture, whether based upon one specimen or on a number of them, is now put to the test of a Key, if there is any. A key of determination, or analytical key as it is sometimes called, is a list or statement which presents the user with alternative choices regarding consecutive characters. It is here that the sequence of characters, discussed in § 11, is needed. As every choice is one out of two—rarely more—possibilities, the key is sometimes referred to as dichotomous, and there are several varieties possible. Some of these have been described by Voss[179] but it would be worth while to give this interesting subject a fuller and more detailed consideration. If there is no key available, it must be made and the process is repeated on a higher level, i.e. just as specimens have been accumulated until the discontinuity is reached which marks the specific limits, in the same way species are taken together until the generic discontinuity is attained, and so on. This is what Sprague[154] has called the synthetical method, which in herbarium practice is largely intuitive and necessarily so since all methods to make it "exact" have failed both due to classificatory restrictions and to the nature of the material.

As a matter of fact keys are not identical with systems, though they may reflect them in some way or another. Since a system is built up upon the evidence of a great number of characters its representation on a sheet of paper greatly curtails its intrinsic structure, even if an artificial system is

intended. An artificial system, such as the sexual system of Linnaeus, is purposely founded on characters which for the greater part are unconnected historically. Its construction is infinitely easier than that of a so-called natural system, because one need not bother about the intrinsic value of characters, the only aim being to conduct a specimen to the taxon it belongs to. Keys, if therefore alone, are always artificial, although the choice of the sequence of characters may contain some natural features. The expression "artificial key" sometimes encountered in publications, is a naïve pleonasm, suggesting that one time the "natural key" may turn up.

It is entirely illusory that we will ever be able to represent a system on a sheet of paper, for the simple reason that every character involved requires a dimension to represent it.

Lam[94] has devoted some attention to this subject, at the same time discussing the possibilities of picturing systems in order to meet man's wish for visual elucidation. Again, it is evident that in a plane not more than two characters can be used to indicate the place of a specimen (or a taxon) in a system of two co-ordinates, and three if the picture is made in perspective. In applying this method two units are shown in a certain relative position but as soon as actually more characters are involved it is inevitable that subjective intuition plays a predominant part. This is why, for instance, a picture like that which was published by Anderson and Abbe[4] which was meant to show the mutual relations between the genera of Betulaceae by means of globes and sticks, must be considered subjective, even if we are assured that (only) six characters "of known importance" have been statistically valuated in order to "calculate" mutual distances between the genera in the picture.

The same holds true for symbolic arrangements of taxa in a plane, e.g. as circles connected by lines of various dimensions, as have been published by many authors (e.g. Lam[94, 95, 101]; Wettstein[181], Pulle[135], Kimura[89], Deyl[42], etc.).

The impossibility of ever attaining a natural system with the limited possibilities at our disposal is clearly shown by Sprague[154] who proposes to insert in a system obtained by what he calls the synthetic method only those taxa which are clearly natural, leaving out everything which does not distinctly fit in. For the latter cases an artificial system would be needed. It is obvious, however, that this is quite unsatisfactory since it is nothing but a "testimonium paupertatis"; all specimens and taxa that exist belong somewhere, even though we may not know their exact position.

In view of the acknowledged fact that "natural" systems are to a high degree subjective and even more because they cannot be represented by arrangements in two or three dimensions, we fully agree with Crow[37] who advocates that arrangements of museum objects should first of all be based

on their being conveniently surveyable in the most easy and impersonal way, e.g. entirely or partly alphabetical.

16. *Taxogenesis.* In the preceding paragraphs we have already alluded to several ways in which taxa can be considered or imagined to have come into existence. This is another matter of which we know very little for certain, for the simple reason that all taxa but those of the very lowest rank apparently need so much time to shape themselves that the process falls entirely out of the period of our observation. Moreover, the very lowest ones are often so weakly distinguished and perhaps also so ephemeral that we hesitate to recognize them as taxa, incipient or otherwise.

What we may conceive about taxogenesis must, therefore, largely be inferred from circumstantial evidence. The first stage of the process is, of course, increase of the number of life-cycles (individuals) and, accordingly, the area occupied by them. This implies the chance that various modifications of the environment are encountered and invaded and these may give rise in some way or another to breaking up the homogeneity, which, in the meantime, may already have been replaced by some sort of heterogeneity by the occurrence of spontaneous mutations (cf. Faegri[57]).

In case, for instance, the group in question shows characters which suggest an influence of external factors, such as relative small surface, thick cuticle, sunken stomata, etc., in desert plants (in comparison to relatives in a less dry climate) the main taxogenetic factor may be looked for in the great saturation deficit of the air, in average or in the extremes. Such influences might lead to what Turesson has called ecotypes and it may be imagined that ecotypes, if the forming influence gets stronger or lasts longer, may develop into the next higher taxon, the ecospecies, either by an intensified reaction to the environment or by the elimination of certain "marginal" or border elements which deepens and sharpens the discontinuity, or both.

Deyl[43] whom we quoted in a previous paragraph (§ 14) is of a different opinion. He thinks that taxogenesis of higher taxa works through (lamarckian) orthogenesis (and perhaps through alterations in the chemism of the nuclei), and that that of lower taxa is chiefly determined by (Darwinian) selection. Of all ways in which taxa can come into existence (cf. § 8, § 14), hybridization ranks foremost and the sterility of the hybrids is certainly one of the important contributors to bringing about the discontinuities which enable us to distinguish taxa (cf. Grant[66], who gave a good account of "speciigenesis"). It should be expected that as (morphological) differences increase, interfertility would proportionally decrease. However, this is not so, for in several cases the experience is that interfertility suddenly decreases; the cause of this unexpected phenomenon is not known (Danser[39]). The last-named investigator says that it is (theoretically) imaginable that morphologically identical plants are intersterile. He is also of the opinion that lower

taxa do not originate by accumulation of differences and that taxa in general do not come into existence through gradual divergence.

From this it is to be understood that taxogenetic factors may be either of a positive, stimulating kind or of a negative, repressive one. Elimination of "marginal" individuals by selection is probably a wide-spread phenomenon as can be understood by considering that favourable factors in the struggle for existence are or may be distributed rather unequally in a population. Isolation, by whatever means, fertility barrier, ecological factors, geographical distance, etc., helps to widen and deepen discontinuities.

Another, perhaps the only other, positive factor may of course be a favourable mutation but it seems questionable whether it will ever give rise to a more or less permanent taxon—except in the case of apomixis, in which every favourable mutation is successful—unless a fairly great number of similar or identical mutations take place at approximately the same time and in one area which permits the plant to hybridize so that the mutant is allowed to attain the homozygous stage.

Most factors, however, so far as we can judge, are of the repressive nibbling variety and this has undoubtedly given rise to the classical theory, going back so far as we are aware to Darwin, according to which taxa of increasing rank are formed by a process of widening and deepening the discontinuities by an unceasing elimination of the weaker marginals (cf. Anderson in Bartlett[15]). This conclusion again points to some sort of original continuity.

This view, which has the advantage of being simple and one-based, has in more recent times been opposed by the suggestion (Dobzhansky[45], Goldschmidt[65], J. C. Willis[182]) that rare large mutations (system-mutations) should induce a taxonomic jump of considerable extent, e.g. to generic or family rank, and that the more numerous and more frequent minute mutations would subsequently look after the formation of lower taxa on the new level. Deyl[43] is of a similar opinion. Although it must be admitted that some peculiarities in the system might be explained by the assumption that these large mutations occasionally occur, no such mutation which was surmised as such has ever been indubitably proven but this is, of course, not decisive for refuting the idea. Willis thinks that his "hollow curves," the result of a graphic representation of the fact that there are, in a natural group, few genera with many species, and many genera with one or a few species, support the idea of large mutations. Apart from the significance of these hollow curves in general, it must be said that, regarding taxa, the above conclusion chiefly rests on the unproven assumption that all (or most) monotypic genera are young ones and that most endemics are neo-endemics. The current opinion, however, is that vague limits generally signify youth and sharp ones—in increasing gradation—high age (relicts).

So far as we are aware, no one has ever ventured to suggest large mutations

which would create taxa of a still higher rank than a family, and to remain on the safe side it seems best to assume that whatever the "size" of mutational jumps, the discontinuities grow by elimination. This conclusion is supported by the demeanour of intermediates. It is also supported by Heberer[76A] who, though perhaps somewhat too optimistic as to the present state of our knowledge regarding the mechanics of evolution, pointed out that the gaps, so well-known in fossil series, are in favour of the idea of accumulation of minute mutations rather than of that of large mutations (saltations), because in the latter case the new type might be expected to follow its ancestor immediately. The gaps which are actually observed may be explained in various ways (rare, small, unspecialized forms of restricted distribution, subject to rapid evolution), but so far positive evidence is wanting. The "kontinuierlich ablaufende Typogenese" imagined by Heberer—in contradistinction to Goldschmidt's "hopeful monsters"—is termed by him "additive typogenesis." In this, infraspecific taxogenetical processes—the only ones which can be more or less approached experimentally (Heberer speaks of experimental phylogeny)—are supposed to continue acting "transspecifically," thus ultimately influencing the origin of even the highest taxa without disturbing the harmony in successive individuals and types. It can hardly be expected that "hopeful monsters" are harmonious in any sense; moreover, in most groups two of them at least would be required to ensure survival, a male and a female one. In line with this view the gaps suggest jumps which actually have not occurred.

b. Dynamic Taxonomy

Fundamentally the problem of systematics . . .
is that of detecting evolution at work.

J. S. HUXLEY

17. *Terminology and Definitions.* The preceding paragraph dealt with Taxogenesis and since this process involves the time factor, it may serve as an intermediate one between the chapters on Static and Dynamic Taxonomy; another classificatory problem because the line between the two is as vague and arbitrary as that which the authorities drew along one or the other side of an isolated house between two villages.

In our first chapter we tried to explain the limitations of static taxonomy. Advantages were the abundant material available and the great many methods of investigation that could be applied to it. But whereas the delimitation of taxa can be approached from many sides and can therefore be ever more perfected, the interpretation of some of the characters, amongst which are very important ones, left us unsatisfied because the comparison of structures of living contemporaries failed to provide the clue to their true nature. Obviously this clue had to be looked for in the past.

The dynamic taxonomy, on the other hand, while comparatively very poor in specimens and providing material to which only a few methods were applicable, has the enormous advantage that of at least some characters the origin can be traced beyond reasonable doubt.

The typological groundplan in static typology, subjective and inspiring a very limited confidence because of its hypothetic nature, is telescopized in dynamic taxonomy and, however fragmentary, curiously enough gains in reality. The concepts of primitive and advanced are brought to life and become realities too, since at least in some cases they can be demonstrated *ad oculos*, showing "evolution at work" (though in a different sense from that of Huxley's motto in the heading of the present section), showing as they do how forms may be considered to change. Thus typology with the time factor becomes identical with dynamic taxonomy.* And if we contrive to look at this process through the dead material—whether in an "herbarium vivum" or an "herbarium of the rocks" (Seward)—as a function of Life, the observation, however limited, gives us more confidence in considering what may have happened to other organs.

Differentiation, that mysterious process of unequal cell division, with which the young stages of ontogeny abound, is now seen in its long-period results, which provides another support for our impression that Nature is a continuum, whose processes may perhaps pulsate but never entirely stop.

As several authors have pointed out (cf. Lam[94, 101]), static taxonomy is concerned with the system of organisms of one time. If the word time, in this context, is taken in not too narrow a sense, it leaves room for such micro-evolutionary processes as changes occurring in a few consecutive generations, the effects of hybridization, and the like. These changes are, evolutionarily speaking, insignificant and their direction can no more be indicated than fluctuations in our climate, observed during some centuries, are significant as to whether or not we are approaching a new ice age. The methods of static taxonomy are therefore mainly those of comparison, as we have circumstantially discussed in the first section of this paper, and although some taxonomists at least may feel tempted to explain some of the notions involved (such as primitive and advanced) with the implication of a longer period of time than is actually allotted to the basic principle of static taxonomy, it must be admitted that the latter to some extent can be considered a separate discipline with operating methods of its own.

If this principle is recognized, the next stop is to admit that, each time showing its own system, consecutive time levels show the changes between the older and the younger systems. Theoretically, of course, this is clear but in practice the scarcity of fossil data allows only the recognition of some

* Baumann[17A, p 21] identifies the "New Morphology" with what he calls "typologisch-phylogenetische Morphologie."

few connections between two levels, or rather, in some periods the number of such connecting lines may be quite considerable (such as in the Carboniferous), in others they may be extremely scanty.

From this alone it follows that the choice of time levels is largely dependent on the material available. Accordingly, it is impossible to estimate the average stretch of time to be considered between two consecutive levels, also because evolution seems not to proceed at a regular rate. Moreover, even if a couple of million years (or even less) may be traceable in the very youngest periods of geological time or in any others where certain methods, such as those of palynology, or in the study of varves (cf. Zeuner[186]), allow us almost to follow annual changes, in most other periods it is impossible to state with any degree of accuracy how long a time has elapsed between two clearly recognizable taxonomic, or, for that matter, floristic levels.

Be this as it is, one thing can be stated with a fair amount of certainty, viz. that in dynamic taxonomy the vertical connections are the most outstanding feature. This implies that fossil evidence is an indispensable element in dynamic taxonomy. In fact, dynamic taxonomy is the science of the system of organisms of all times and is therefore probably the branch of biology which studies the living world in the broadest possible way. Its ideal is the true phylogenetical system.

There is much confusion about what exactly the phylogenetic method in taxonomy is or should be and what is meant by the expression phylogenetic system. Let us, therefore, again be first of all clear about our terminology.

Phylogeny literally means the development of a phylum, a phylum in this context being synonymous to a taxon. Had the word taxon been invented at an earlier date phylogeny would perhaps have been termed taxogeny. Whereas the basic abstract concept of taxonomy is the taxon, one might conceive that its phylogenetical counterpart would be phylon. However logical and desirable this should be, it is not very well feasible because a very similar, in fact, identical term, phylum, is in general use for the largest taxon within the vegetable kingdom. As a three- (or four-) dimensional equivalent to taxon became more and more needed, two terms were created, hologeny (Zimmermann[188, 189, etc.]) and genorheithrum (Lam[95]); hologeny being a combination of consecutive ontogenies (generations) and their phylogeny, originally applied only to single characters, later on also to taxa; genorheithrum meaning a stream of potentialities comprised in what in static taxonomy is a taxon. We will speak of these concepts more circumstantially in the next paragraph. Although the terms are very closely related, I think there is some reason to keep them apart and not to consider them synonyms, for a hologeny rather involves a process, or processes, and a genorheithrum is what one might call a taxon in four dimensions, or what sometimes has been called a phylogenetical group, or a phylad (Grant[66]).

Whereas genealogy is the tracing of the ancestry of individuals, phylogeny is the tracing of the origin and development of groups (Turrill[175]).

Obviously, in practice it is very difficult, and in many cases impossible to define a given genorheithrum, which is composed of chronologically consecutive taxa that are supposed to be genealogically ("vertically") connected and "horizontally" limited. The difficulty, of course, roots in the very imperfect knowledge of the discontinuities of the successive taxa, less so in the discontinuities in time, i.e. when the genorheithrum in question was reported for the first and the last time.

This is why phylogeny can never or very rarely—e.g. in cases in which fossils are extremely copious during a long period, such as in Foraminifers—serve as a basis for a system. The basis of a system must necessarily remain the living plant world for only this allows us to determine taxial discontinuities and the only thing we can do regarding fossils is to try and insert them as far as possible in groups which have been recognized in living plants and only if this appears to be impossible, to create new ones.

On the other hand it must be emphasized that phylogeny without fossils is an inane notion. It must also be stated that the development of characters or semophylesis as it has been called (Zimmermann[187]), is much easier and more trustworthy than that of taxa; in fact group phylogeny exists only on the strength of semophylesis.

What may be the force behind these developments need not be discussed here. Suffice it to state that the writer of these lines gets more and more convinced that mutation pressure and natural selection alone cannot be responsible for all phenomena we observe. We are rather inclined to join Schaffner[145] who speaks of an "internal creative principle, dependent on the nature of the protoplasma involved," in which statement we would prefer to substitute "directive" for "creative."

Of late, some investigators have tried to stipulate some ideas as to which processes might be visualized to be responsible for phylogenetic or semophyletic alterations. Baumann[17] enumerates some of these which look very much like static derivative series but are emphatically described as phylogenetic ones *im Gegensatz zu rein typologisch-descriptive Aufzählungen.* They are mainly growth processes referring to Angiosperms. Thorne[173] gives a list of fifteen points, together forming what he calls "a working philosophy" and expressing what, in his opinion, is primitive and how evolution may be expected to operate. Although correctly stating that every plant and every character of any living plant has a long history behind it, his deductions are chiefly based on observations of living plants and should therefore be considered with some scepticism.

Similar methods have been worked out by Lam[92] and Van Heurn and Lam[78] regarding the Burseraceae but their "phases" are rather expressions

of typological considerations, and the same must be said of Schaffner's work[144] based on that of his teacher Bessey. His ingenious series from Bacteria to the Dandelion (in 101 phases) and the like are little more than wishful dreams, and so are his ten "fundamental progressive stages in the evolution of plants."

A most ingenious method has been worked out by Leppik[113] who points out the close correlation between rust fungi and their host plants. The former are considered a very old group and, though Leppik does not mention any fossils, he states that the simplest types (with one host) are found on ferns, more advanced ones on Conifers (two hosts), still more advanced ones on Angiosperms (three, four, or five hosts) of which the more primitive ones are those with three or four hosts. Although unfortunately no exact chronological data are available, all this is most interesting, if of little practical value.

More really phylogenetic though admittedly deductive are the fundamental processes of the evolution of form, expressed more or less independently by Lam[101, 102, 108] and Zimmermann[191], the main points being next to differentiation such growth processes as overtopping, planation and webbing, recurvation, fusing, contraction, shifting, and reduction.

A few words must be said here on the phylogenetical meaning of such terms as reduction, primitive, and advanced (cf. § 9).

Reduction, with its forced explanation in static taxonomy as a decrease of polymorphy which is hardly comprehensible ontogenetically, now becomes mainly the result of selection rather than of anything else, and we are afraid that this is but seldom realized by taxonomists working with living plants who always compare contemporaries and freely use the term reduction without seeing the process as a dynamic one.

In our opinion reduction can mean either of two things. One of these is that an organ in successive generations shows a decrease of size and differentiation. Remnants of such organs, called rudiments, may betray their former significance and the fact that not rarely vascular bundles seem to be most resistant against removal, is the source of much controversial discussion (Puri[136]).

The second explanation of reduction which has often been ignored but none the less seems real enough to be seriously considered, is that there is no actual disappearance but that the simple structure is originally simple and not the result of a process of decrease. It might then be visualized that a simple structure, found in an ancestral population in a subsequent divergence develops in such a way that in a part of the population it retains its original form, while in other parts it may variously advance. If after a long time the populations containing the advanced phases of the structure disappear and the population with the simple structure is the only one which survives, one

may hesitate whether to consider it originally simple or the victim of reduction. This is particularly poignant when fossil evidence is lacking and this is, for instance, the case in Angiosperms among which groups with simple flowers, such as some families of the Monochlamydeae, have given rise to sharply controversial opinions.

Let us, also as an illustration to our remarks in § 12, mention just one example. In 1932 Diels[44] discussed a curious plant of so far mysterious systematic position, *Circaeaster agrestis*. He states that comparison with material of the ranunculaceous *Kingdonia* convinced him that *Circaeaster* is to be included in the Ranunculaceae, in which, however, it is to be considered *das am extremsten reduzierte Mitglied dieser grossen Familie*.

This expression is nothing but a symbol, a reflection of a superficial impression which has never been tested on its real significance. It presupposes a derivation from some more diversified plant (or rather ancestor) and depends on what is accepted as the groundplan of the family. If this groundplan should involve a flower with many, say 10 petals (or sepals) and *Circaeaster* has only two, one might, of course, speak of a reduction but only in one of the following senses: either the ancestral stock of plants which could reasonably be considered ranunculaceous showed a variability in which both 10 and 2 petals were included, and then one of the types with 2 petals may have survived as what we now know as *Circaeaster*; or the ancestral stock had flowers with a larger number of petals and that number through a series of ontogenetical processes of cell divisions which appear in decreasing numbers becomes reduced in later periods. The last-named possibility would be the only one which would really deserve the name of reduction but it is very likely that much that is designated by that name should actually be explained as the result of selection. However, as far as the Angiosperms are concerned we are entirely ignorant since fossil evidence is almost completely missing, and is not likely ever to become so abundant as to enable us to solve problems of this type. In some other groups, however, notably the Pteropsida, there is some hope that we will be able to check which of the two processes have taken place and in what proportion.

Primitive cannot mean anything else but old, in a relative sense, i.e. in a natural group or in a series of character phases which are recognized as homologous. Advanced, in the same sense, means younger. If, within the the same genorheithrum, the older types show large leaves and the younger types small ones, the large leaf is the primitive condition, the small leaf the derivative one.

Homology and analogy retain their significance in dynamic taxonomy. They are primarily static concepts but their application can profitably be extended into the past as has, indeed, been successfully done by the adherents of the telome theory. They play an important part in the choice between

monophyly and biphyly or, as Lam[94] termed it, monorheithry and birheithry (-phyly being restricted to the absolute concept). The question whether a given taxon should be considered to root in a homogeneous or a heterogeneous ancestry can, if at all, be solved on typological considerations, viz. by investigating whether it is possible to recognize more than one groundplan. This is, for instance, quite obvious for the Sympetalae and probably also for the Monochlamydeae. For the Angiosperms as a whole, however, the question is less easy to answer, and this problem will be discussed later on. Speaking quite generally, it is our impression that bi- or polyrheithry is a much more frequent phenomenon than is usually believed, but of course here too, there are all possible gradations.

In conclusion of the present section we have to unburden ourselves of the following remark.

We have the impression that the majority of biologists, notably those working in one time-level, i.e. in the present, simply do not see the importance of the historic factor. They work with their material without realizing that every living being, including themselves, has a history behind it reaching to the beginning of life on earth. Every organism is bound, nay fettered, to its genome which determines the variability of all its forms and functions; and this very genome has developed to what it is today which implies that "everybody is talking after his own fashion" and cannot help being as he is and doing as he does. This alone explains much which cannot be explained by observations on living material.

18. *Pseudophylogeny.* As is the case with such terms as primitive, advanced, and reduction, taxonomic literature teems with so-called phylogenetical schemes. A bitter battle has been and is being fought between taxonomists who at all costs want to keep their minds and methods free from all phylogenetical implications, and those who cannot help pondering how what they observe may have been brought about. The first category, often conscientious men of principle who at no price will give in, irritated as they are by the "unscientific" and "irresponsible" manners of the other party, tend to exaggerate and wrong themselves by neglecting harmless though useful evidence; the second take a more serious risk in so far as they may be tempted to take speculations for facts, thus spoiling a noble profession and giving it a reputation of superficiality and lack of scientific responsibility. It is the same sort of reproach as the one experimentalists tend to express towards non-experimentalists and the reverse, the pot calling the kettle black.

Not very long ago Fosberg[59] made an inquiry among American taxonomists, asking them to state whether or not they allowed themselves, during monographic work, to be influenced by thoughts about phylogeny and evolution; 75 per cent. of them answered in the affirmative. In fact the number of bold "phylogenetical conclusions" is amazingly great. Turrill[175]

expressed himself about these products, and we emphatically agree with him, in the following words: "So much of what is termed phylogeny rests on deductions from assumed premises which have not been subjected to adequate tests of their validity. It is, indeed, pseudophylogeny." We may be allowed to add that it is nothing but an expression of the authors' opinions on the interrelationships in the taxon studied. Lam[94] has mentioned and pictured a number of such schemes.

Therefore such statements as that by Schaffner[144]: "Taxonomy is based on assumed phylogenetic relationships . . . (and) must reflect a correct evolutionary theory" are confusing. To our mind, taxonomy has to make a sensible use of all available evidence both from recent and from fossil plants. The resulting system will necessarily be deficient but it may be the best one that can be made at the time.

19. *Phylogenetical Symbols.* In a previous paragraph (§ 15) we have explained that our schemes do not permit us to represent more than three separate characters (cf. Lam[94], Sporne[153]), and that all charts in which a greater number of characters are involved—as will be the usual case regarding organisms—are to a certain, often a high degree, subjective, even if these characters have been evaluated statistically. As a matter of course this disadvantage is much less serious in semophyleses (cf. Lam[93]) than in group phylogeny because in the former a much smaller number of characters may be involved, or even one, two, or three, which can be adequately valuated.

However, as far as genorheithra are concerned a phylogenetical symbol is a very imperfect tool indeed to illustrate our ideas or surmises on what happened in evolution. In using two-dimensional schemes the ordinate is to represent time, and the abscissa differentiation. Properly speaking, the changes of not more than one single character in one single sense can be indicated. Assuming that a mutation leads to a change which consumes no time, it can be represented in the chart by a short horizontal line. Accumulation of a number of mutations in the same direction can be assembled and represented by a sloping line, the angle of which is proportional to the relative evolutionary rate. Vertical lines mean: no change. In accordance with the principles here explained sloping lines can only be leaning to the right-hand side of the chart, unless one would wish to visualize the process of reduction in the sense of decreasing differentiation, in which case under certain circumstances a line sloping to the left would be justified.

Most modern phylogenetical schemes, e.g. those published by Zimmermann[187, 192] and Lam[94, 97, 100, 101, 102, 104, 105, 106], are constructed along these lines though in some of Zimmermann's charts one or two lines may curve to the left for no obvious reason.

As we saw, it is evident that phylogenetical trees of this type regarding taxa are necessarily still much more speculative than those regarding separate

characters. They are entirely intuitive, rooting as they do in circumstantial evidence alone. At best they represent the subjective opinion of a phylogenist on a sort of residuum of facts that, out of a great many of which perhaps several were for some reason or other just neglected, happened to have come to his knowledge and to which he happened to be receptive.

However, in either case it is a picture which is very different from the old type of "tree" of Haeckel's time. In case monophyletic origin is assumed, it takes the shape of a leaning shrub with one main stem coming out of the supposed ancestral group, and with all lateral branches growing more or less steeply upward on the right-hand side. Horizontal lines through this phylogenetical "shrub" (in German called "Stammstrauch" by Henning (1927) and "Stammgarbe" by Wilckens (1919), i.e. phylogenetical sheaf) give an insight into the taxonomy of one time. In fact, the whole scheme is built by connecting groups of one time to corresponding ones in the next.

Zimmermann's hologeny which was already quoted in § 17 is, as it were, a part of a genorheithrum looked at through a mental microscope: a slowly ascending helicoid line (the vertical symbolizing the time factor), each rotation representing either a single or generally a number of life-cycles in which no changes occur until a mutation or perhaps a number of consecutive mutations lead up to a change which is represented by a "ramification" in the helicoid line. This ramification which, of course, means a differentiation, is usually of the type of a continuing main axis and a lateral branch; if it were a bifurcation this would be a symbol of two different forms (or functions) instead of one evolving out of the original one.

By this type of scheme Zimmmerann has shown his ideas regarding both taxa [189, 192, 196] and separate characters [188, 193, 194, 195, 196].

In all graphs discussed above great alterations and long times were involved. Some attempts have been made to visualize ideas about phylogenetic events in short periods. Some of these (Hayata, Danser, Rensch) have been reproduced by Lam[94] who added a few more of his own design and quoted literature containing similar projects (e.g. Shull). A very recent scheme is that of Grant[66] who designed a hypothetical sketch symbolizing ideas relative to the possible development of a genorheithrum (a "phylad") in micro-evolution, showing that "species" may form a "phylogenetic reticulum."

20. *Lines and Levels.* As was stated above floras of consecutive periods may be connected by lines regarding the development of single characters. On studying the nature of these characters it appears that those which we above have called constitutive and which were supposed to be not or very little influenced by external factors, are also the constant characters of our one-time systems, characters relative to the general structure, the type of ramification, and the reproductive organs; of some of these we have the impression

not only that they show a relatively narrow range of variability in one-time taxonomy but that their evolutionary rate is largely independent, steady, and slow.

On the other hand those characters which we have called functional, adaptive, or plastic, give the impression of evolving more quickly, which is comprehensible because keeping pace with a changing environment is a vital necessity. It is not our present task to discuss whether these changes are being brought about by natural selection, induced mutations, or both; suffice it to state that here just as in static taxonomy there is a gradual series of intermediates between the two extremes: on the one hand the dead-slow evolution (if any) of the oldest constitutive characters, and on the other the short-period one of the youngest plastic characters, the latter merging insensibly into the phenotypical changes which may even occur within one and the same life-cycle.

The distinction into fixed (constitutive) and plastic (adaptive) characters need not imply that there is a fundamental difference between them, as Deyl[43] has suggested. The impression is rather that there is no demarcation line between the two and that plastic characters gradually get less plastic, that functional characters get fixed and insensitive to the environment and that they at long last become constitutive or, as Plate has put it, included in what he calls the "Erbstock," the immovable hereditary skeleton consisting of homozygous factors which can no longer escape from the genome.

However, dynamic taxonomy, while having the advantage of showing the correlation between time and change, has this one drawback compared to its static sister that it cannot provide us with the whole gamut of characters: it shows a strong predilection for the constitutive characters which indeed have the best chance to come to our knowledge in view of the relative scarcity of the material and the relative longevity of the characters. Plastic characters and even many functional ones do not show in fossil material and if they do they are so rare that it becomes hard logically to connect them over the gaps between two periods. In addition their variability cannot be checked experimentally.

This situation implies that it is often a matter of taste where to place a given character in the range between constitutive and adaptive and this condition is likely to give rise to as strongly controversial opinions as the concepts homologous and analogous.

To mention only one or two examples we may recall the notations Spermatophyta and Praephanerogamae.

As the name Spermatophyta indicates, it covers a group of plants which have managed to form seeds. Obviously, however, the delimitation of this taxon depends on the definition of the concept seed. It may meet common

consent if we state that the habit of forming seeds is a direct consequence of the development of heterospory.

Heterospory in its turn can easily be visualized as a differentiation of the condition of iso-(or homo-)spory and it seems likely that this differentiation evolved through a more or less long series of minor stages. There are indications in the fossil record that this is so, e.g. in the palaeophytic fern *Archaeopteris*; a recent example is *Equisetum* which shows an incipient heterospory. Not only on account of what has become known in fossils but in considering the distribution of heterospory in recent groups and also on purely theoretical grounds, the conclusion seems justified that the differentiation of isospory into heterospory has repeatedly developed independently, is polyrheithric. What exactly does this mean?

It means that we have the impression that the differentiation in question takes less time to develop than the extreme constitutive characters, that it is less constitutive than, for instance, the type of ramification or the position of the sporangia, though it is not yet or no more to be considered clearly functional. Heterospory may have originated by the action of some internal urge rather than by that of environmental factors. This conclusion, however purely intuitive or based on circumstantial rather than on direct evidence, would explain why heterospory occurs or occurred more or less occasionally in Lycopsida, Sphenopsida, Pteropsida until it finally became a constitutive character in Phanerogams. In the two former groups it was not included in the groundplan, in the last-named it is. In the lower groups (Lycopsida, Sphenopsida) it is a convergent analogy, in the higher ones (Pteropsida, Phanerogams) it is more likely to be an homology, since in them many significant characters are correlated so as to suggest group-phylogeny.

A similar situation is discernible as to the forming of a seed. Its development has clearly been gradual, too. It may have started with the condition in which the megaspore did not become detached from its sporangium but remained attached to it; an acquisition providing both for a better protection of a vital organ and for a better nutrition in the way of an incipient parasitism of the young sporophyte on the old one with an ever-diminishing mediation of the decreasing gametophyte. As soon as the megaspore permanently remained attached to the mother plant—a development which probably furthered the already diminished part played by the gametophyte—and the archegonia were fertilized in the megaspore, the embryo naturally remained for some time at least attached to the mother plant and the seed was born. However, it had still to go a long way until it developed into the highly developed Angiosperm seed which falls off at an early stage, contains a full-grown embryo, and has acquired the faculty of maintaining its viability (germinating power) for a longer or shorter time.

This process, too, seems to have occurred more than once in groups with

different groundplans, so far as we know at least twice, in the Lycopsida and in the Phanerogams, and we might be tempted to speak of a semophyletic birheithry here. This is the reason why the designation Spermatophyta is irrelevant if the Lycopsida are included and superfluous if they are not.

Regarding the seeds a similar thing has happened. Not very long ago Emberger[52, 53, 55] proposed to subdivide the Phanerogams into two groups according to the stage at which fertilization takes place and whether or not a fallen "seed" contains an embryo of some description or merely an unfertilized gametophyte. Those groups in which the "seed" does not contain a more or less full-grown embryo and in which fertilization does not explicitly take place on the mother plant (Pteridospermales, Cycadales, Cordaitales, and Ginkgoales) are taken together as Praephanerogamae, the others being the true Phanerogams.

This view, although valuable as a statement, has met with some opposition (Martens[118], Lam[102, p. 063]), mainly, it seems, because Emberger to some extent has confused what we might indicate as lines and levels, respectively; the lines being the vertical connections based on constitutive characters, and the levels being as it were, stages or phases in a development which, without being devoid of all homological implications, by their "independent" occurrence seem to be of a more or less different nature (mind that we said this was to some extent a matter of taste). It must be added, though, that Emberger admits to realizing the difference, for he distinguishes between "lignées" and "embranchements," stating[55] that an "embranchement" "est une unité qui groupe les lignées d'un même stade phylogénétique . . ."; elsewhere he refers to the "embranchements" as "paliers phylogénetiques" (phylogenetical storeys or levels). Yet somehow Emberger's subdivision, which clearly tears apart groups with the same groundplan (such as Cordaitales and Coniferales), seems to have been meant as a vertical (taxonomical) rather than an horizontal (stagial) one.

A similar "mistake" though on a still bigger scale seems to have been made by Greguss. Greguss as early as 1918 published a paper[67] in which he suggested that the system of the vegetable kingdom clearly shows three lines, distinguished by the degree of sexual differentiation: isospory (equal spores produce ♀ gametophytes), homospory (equal spores produce ♂ and ♀ gametophytes), heterospory (unequal spores produce ♂ and ♀ gametophytes, respectively). In heterosporous plants the lines continue into the conditions of isospermy (dioecious), homospermy (monoecious), and euspermy (hermaphroditic). This system was supposed to be supported by the assumedly weak connections between the groups of the Bryophytes, Pteridophytes, and Gymnosperms. Quite recently Greguss[68] published another paper, suggesting a new system, equally showing three "lines" of development, this time according to the basic type of ramification,

monopodial, dichotomous, and verticillate, and again apparently intended to cover all plants, although the Thallophytes are involved in a lesser degree than in the first paper.

As Lam[107] has pointed out, this method, in which the earlier considerations on sexual differentiation are shifted to a subordinate position, results in a system in which what we deem natural groups are torn asunder, while others may feel "bien étonnés de se trouver ensemble." Some main lines in Greguss's concept are:

Monop. I. Chlorophyta—Musci—some Lycopsida—some Psilophyta
Coniferales—Gnetum and Dialypetaleae—Monochlamydeae.

Dichot. II. Phaeophyta—Hepaticae—┬—Psilotaceae
├—Filices—some Lycopsida
└—some Psilophyta

—Pteridospermae—┬—Cycadopsida
├—some Coniferales—Welwitschia
├—Taxales
└—Ginkyoales

—Monocotyledones.

Vertic. III. Charophyta—Sphenopsida—some Coniferales—Ephedra—Casuarina.

Yet, on closer inspection and on recognizing bits of what we consider "lines" in Greguss's chart, it must be admitted that we are not in a position absolutely to refute even such ideas as seem quite absurd to us now. Just as the "sublime" and the "ridiculous," and just as virtue and sin and their logical extensions, freedom and prison, may be only a step apart, the decision as to which is a "line" and which a level may depend on a minute difference. For black and white are much more rare than their intergrades, and every phylogenist is inclined to stick to his own concept, products of his character and his education (or genome and environment) and it would be pitiful if he should allow himself to become blind to other possibilities. Would this meet Bailey's[11] "need for a broadened outlook"?

Another example of this trend of thought is the introduction of the concepts stachyospory and phyllospory by Lam[97, 100, 101, 102, 104, 106, 108]. His theory is chiefly phylogenetical and is an extension of Zimmerman's telome theory; it will only be briefly mentioned here in so far as it has any bearing on classification. Lam recognizes in the Cormophyta groups in which the sporangia are primarily borne on axes (stachyospory) and on "leaves" (mixed syntelomes). The character of stachyospory is fully correlated with the lower groups (Psilopsida, Lycopsida, Sphenopsida, and perhaps Bryopsida) but in the higher ones the two conditions (of which phyllospory is considered the derived one) are less distinctly separated,

although even in those groups one may speak of taxa which are preponderantly stachyosporous (Taxales, Coniferales, Chlamydospermales) or preponderantly phyllosporous (Pteridospermales, Cycadales). In some groups there is a difference in this respect regarding the two sexes (Cycadeoidales, Pentoxylales, slightly also in Coniferales) in all of which the male organs (as the more exposed ones?) show a distinct tendency towards phyllospory. These ideas do not radically affect our opinion on the lines of the system, as the principal groups (classes) remain intact, but amongst them these classes may be gathered on the basis of the concepts just described, into two superclasses, a stachyosporous one and a phyllosporous one.

These considerations lead us to our last chapter, containing a few remarks on the Angiosperms, the dominating group of our time. Dominating at any rate psychologically since some groups of Cryptogams, notably the Fungi, more and more appear to approach the Angiosperms in diversity.

The Angiosperms, however, spectacular and extremely useful to man as they are, have a reputation of being the best known group of plants. They should, indeed, be the best known group since they have been studied during a much longer period than any other group of plants. That this is an error will be shown in our next chapter; and that this condition is entirely due to our lack of knowledge of fossil Angiosperms clearly shows that taxonomy can greatly profit by palaeobotany, nay, is condemned to remain crippled if its evidence is willingly or knowingly withheld.

III. ANGIOSPERMS

Une structure florale a son origine lointaine
dans un système de ramifications. . .

NOZERAN[129]

21. *The Static Viewpoint.* In order to get an idea of what the Angiosperms are we might apply the typological method and try to construct a groundplan of the group as such.

As we have seen in § 13 the construction of a groundplan depends first of all on the interpretation of the characters, or rather the organs. On looking into this matter, it will soon be found that, particularly as regards the organs which on account of their stable characters are primarily used for basing classifications upon, viz. the flowers, there is a great deal of confusion. There may have been a time in which it was blasphemy to consider a flower anything else but a modified vegetative shoot; this Goethean idea is by no means generally accepted in our days.

This problem is, of course, closely connected with that of the quest for the primitive Angiosperms. Whereas in the next paragraph we will consider this point in the light of dynamic taxonomy it is our present intention to see how taxonomists have tried to approach it with one-time methods.

Of old, two groups have enjoyed preference for the position of the most primitive Angiosperms, the Polycarpicae (Ranales, Magnoliales, etc.) and the Monochlamydeae or Apetalae. Of these two, the latter is the most controversial one, the point being that the often very simple flowers may be considered either originally simple or secondarily reduced. Regarding the Polycarpicae there is a fairly general consensus that they are "primitive," i.e. that their groundplan allows the assumption of the flower as a modified shoot specialized for reproductory functions.

Now taxonomists have always shown a strong predilection for considering the Angiosperms strictly monorheithric. This opinion is primarily based on the impression that a complicated process like that of the double fertilization and everything connected with it, which is generally considered the main—or perhaps the only—truly differential character of the Angiosperms, can hardly be expected to have occurred more than once "independently," since it is supposed to have required a number of directed mutations which must be thought of as a very rare phenomenon. A secondary point is that the bisexual flowers seem to provide a more logical starting condition than monosexual ones. Particularly the first named idea has dominated the minds of generations of taxonomists to the effect of blinding them to other possibilities, the result being that whichever group was accepted as the more primitive one, all others had to be somehow connected with it. This has never led to results which were acceptable to all.

Taking the Polycarpicae as the starting point, quite a number of connections could be made which, though various opinions remained possible, offered no essential objections, except as far as the Monochlamydeae were concerned.

The same difficulties were encountered when the last-named group was considered the more primitive one, and in either case the Centrospermae and the Hamamelidales used to serve as a very doubtful and fragile hinge, about which nobody felt really happy.

Two methods have to be mentioned which were applied in attempting to solve this problem on the level of static taxonomy, statistics and floral morphology.

"Statistics," says Heslop Harrison[76], "is the mathematics of variation, the primary aims of which are to reduce unco-ordinated masses of data." He is of the opinion that statistics is objective and this may be true in the investigation of populations and of mass-collections (biometrics), but our impression is that the method must of needs fail in dealing with taxa, as has been done by Sporne.

Sporne[151, 152, 153] has taken great pains to evaluate Angiosperm families in the sense of primitive or advanced by applying statistical methods. In his first paper[151] he selected 12 "independent characters" which he found

correlated. His definition of a primitive character, being that it is already extant in the ancestors of the group, is of little or no value regarding the Angiosperms, of which no significant ancestors are known. According to him, a primitive family is one which has retained a relatively large number of primitive characters and therefore deviates little from its ancestors. To this the same objection may be raised. Though admitting that a primitive condition can only be checked by consulting fossils, he tries to allow Angiosperms to speak for themselves through the mediation of statistics. He calculates an "advancement index" and concludes that the primitive dicotyledon is a woody plant with alternate glandular stipulate leaves, unisexual actinomorphous polypetalous flowers, numerous stamens and carpels, arillate seeds, and two vascularized integuments. Among the primitive families thus pointed out are several from the Polycarpicae, but also the Euphorbiaceae, Malvaceae, Flacourtiaceae, Bixaceae, and Myrtaceae.

In a second paper[152] he extended the number of characters to 18, concluding that primitive genera are *Magnolia*, *Schizandra*, and *Drimys*.

This work has met with some criticism (Stebbins[155]) and we, too, are of the opinion that Sporne's work, however interesting as a method, is based on too many uncertainties and subjectivities to be considered reliable. In his last paper[153] he did not pursue the subject but in discussing graphical representations he conceived one illustrating his ideas in the form of concentric circles, the radius of which represents the percentage of advancement. In a scheme like this taxa can be placed in their mutual relations with the usual restriction that only one dimension is available to express the relationship.

In the paper in which Stebbins criticized Sporne, he reports about his own work of a similar nature. Comparison of Angiosperm families which were classified either as primitive or as advanced in respect to 8 characters (in 256 combinations), gave him the conviction that these combinations "evolved through the guidance of natural selection" resulting in improvement of fertilization, seed dispersal, etc. Almost half of the 38 taxa (families or part-families) were represented by one out of only 12 combinations. The conclusions do, however, not refer to the problem of the most primitive Angiosperms.

A very attractive method, though little effective regarding the problem under discussion, has been described by Leppik[113, 114, 114A, B, C]. His approach concerns insect pollination, and he convincingly shows that certain insects may directly "guide" flower evolution because there may be an enormously strong food-relation (tropheclexis) between plants and insects, particularly in a biochemical sense. He distinguishes 6 consecutive adaptive stages of flowers and on the basis of fossil insects he asserts he is able to date the periods of these flower types (which, of course, still survive), ranging

from the Jurassic to the present time. This work is of some use for our problem, since the first type primitivus is thought to have resembled *Magnolia*: not sharply coloured, many flower parts. The next types (simplex, radiatus, protectus, capitatus, and zygomorphus) are gradually more adapted to insect pollination which is said to be infinitely more effective than wind pollination.

It must be added here that, if Leppik may indulge in some exaggeration regarding the direct influence of insects on flower evolution, Good[65A], in his recent book, swings to the other extreme. According to him the multiformity in flower types is mainly, if not entirely, due to genomatic processes of an autogenetic nature, i.e. to internal rather than to external influences. If *Cosmos* and *Anemone* show some resemblance, this is due to homologous (or analogous) variation in which natural selection plays no part. Van der Pijl[130B], however, is inclined to ascribe such similarities to similar pollinating processes, though he admits that convergent analogy is a fairly widespread phenomenon. In fact, the term pollination does not occur in the index of Good's book, which is also severely, but we think not entirely fairly, criticized by DeWolf[41A], who thinks that Good's book is "fifty years out of date" by neglecting much modern work on floral anatomy and genetics. It is our impression that it contains enough interesting information to deserve a considerable amount of appreciation, but it must be admitted that its title is misleading.

This leads us to the theme of floral morphology. We cannot think of reviewing the enormous literature on this subject, to which particularly Indian botanists have contributed in recent decennia in a very able way. Suffice it to state that the main point which interests us now is the question whether or not the floral organs are to be considered the equivalents (homologies) of "leaves." The recent publications of both Plantefol[131] and particularly Nozeran[129] present excellent historic accounts of the problems involved including the consequences of Zimmermann's telome theory. Doubt about the Goethean concept of metamorphoses is very old indeed. Schleiden (1837) and Payer (1847) suggested that certain parts of flowers are not equivalents of leaves but are of an axial nature. Coulter and Chamberlain (1917) pointed out that carpels, though originally of leaf nature, have gradually developed into independent organs which can no longer be homologized with leaves. Neumayer[127] thinks that in some cases stamens and carpels are phyllocladia borne in the axils of bracts (perianths) and accordingly he speaks of "androkladien" and "gynokladien." McLean Thompson[170, 171] goes so far as to interpret all flower parts as emergences and Grégoire (1935) states that there is not the slightest morphological (homologous) connection between a vegetative shoot and a flower, all floral organs being "sui generis."

Hunt[79A], on account of the anatomy of four dicot genera, decided that "the" carpel is to be derived from a dichotomous ramification system, more particularly from a three-lobed palmate and three-nerved "appendage," whose lateral wings were supposed to produce the placentas whereas the mid one gave rise to the style. The morphological status of this organ was not explicitly named but it was supposed that both this primitive carpel and the ordinary leaf had independently risen from a common ancestral structure.

Hagerup[70] arrived at the conclusion that in certain families (notably Lam's stachyosporous ones) the carpels are phyllomes though not sporophylls since they do not carry, only subtend, axis-inserted ovules or ovule trusses and accordingly are called false carpels or pseudocarpels.

Wilson[183, 184] who devoted much attention to the phylogeny of stamens thinks that all stamens are reduced ramification systems and is of the opinion that the term sporophyll is no longer valid. To our mind he makes the widespread mistake of numerous investigators who, on the strength of some scattered observations, generalize, speaking of "the" flower, "the" stamen, "the" carpel of the Angiosperms as if it is beyond any doubt that more than one type of these structures could exist in the group.

Lam[97, etc.] is of the opinion that part of the Angiosperms are stachyosporous, i.e. with the ovules borne directly on the or an axis. This condition should be represented in the Monochlamydeae, Helobiae, Pandanales, and some other groups, in which the placentation is axial and the stamens are epipetalous. Accordingly, he agrees with Hagerup in accepting false carpels (pseudocarpels) which he is inclined to homologize with the "stegophylls" of lower stachyosporous groups (Lycopsida, etc.). This is in agreement with Fagerlind's views[58] who thinks that the placenta may be an axillary product of the carpels.

Kretschetowitsch (in Soó[150]) supposes that petals, stamens, and carpels are of an axial nature and other Russian botanists think that all or most flowers are stachyosporous.

Emberger[52, 53, 54] declares that a flower is a biological rather than a morphological unit and describes it as a "buisson contracté d'axes ou de ramifications foliarisées," i.e. a mixture of leaves and axes.

Plantefol[131] who developed, on rather scanty evidence, next to a new theory on phyllotaxis another one on flower ontology, like McLean Thompson, calls all floral organs except the sepals "emergences."* The carpels are described as "des émergences de nature axiale." The two theories are closely connected because organs which have no place on an helicoid line are not considered leaves. The two authors just mentioned are of the opinion that the term sporophyll has no more than an historical significance and the same can be said of the concept leaf (Lam[108]).

* We cannot admire this application of the term, which has of old another use.

Maekawa[115], in an apparently incompleted theory, takes a diametrically opposite position in declaring all lateral organs, including emergences, ligules, sporangiophores, and integuments as being of leaf nature. Despite his rather confused reasonings he arrives at some conclusions which more or less concur with those of Lam and which result in a system of which the main subdivision (Stelopsida vs. Phyllopsida) is, in fact, based on the principles of stachyospory and phyllospory. His comparison of *Austrobaileya* and *Ginkgo*, however, is fundamentally erroneous since in the former there are true sporophylls (in the traditional sense, which according to Lam, holds in the phyllosporous groups) and in the latter leaves subtending sporangiophores.

Deyl[42] agrees that floral organs are not necessarily of foliar nature. The flower must have been formed directly out of sporangia. Nozeran[129] whose extensive and admirable paper is only the outset of a larger work, is less extreme in his expressions. Stamens (to which his paper particularly refers) are no organs "sui generis" but contracted from earlier forms. Angiosperm flowers have an enormously complicated development behind them and many of them have by no means reached a more or less final state. This is what Emberger has called "état préfloral." Some of them look like contracted inflorescences, the Cruciferae have "almost flowers." "Dans sa simplicité apparente," says Nozeran, "la 'fleur' cache souvent une grande complexité d'organisation."

Thomas[169] says that floral organs are "new structures due to changes in the growth of the reproductive axes and not to modifications of pre-existing leaves" and "distinction between branches and leaves . . . has no fundamental significance."

Lam[108] who has briefly summarized the history of the ovule, as well as of the concept leaf, agrees that both "flower" and "leaf" no longer deserve a place among morphological terms. The integument, which Hagerup in one of his later publications recognizes as the "true megasporophyll" (in Conifers) may, in Lam's opinion, in some cases (Chlamydosperms, some Monochlamydeae), be homologized with pseudocarpels. However, if Emberger, for that very reason, combines Gnetales, Piperales, and Juglandales into one group, he again confuses lines and levels.

The above communications represent an impressive amount of evidence that the morphology of the Angiosperms is on the move. Under these conditions it is impossible to construct a groundplan of the class in its entirety and the cause of this may be that the Angiosperms are not what they have been often so stubbornly considered to be, monorheithric. This problem will be discussed in our next paragraph.

Before entering upon that subject we may be allowed to add a few scattered remarks on recent or less known opinions regarding the system of the Angiosperms.

A little known work is that of Heintze[77] on the "phylogeny" of the Cormophyta. Despite its extent it is not very elucidating, and his (pseudo-phylogenetical) schemes of supposed relationships are little convincing. Stress is laid upon the Angiosperms but nothing is said about the relationship with lower groups. Gnetales appear somewhere between "Dicotyledons" and Polygalales, *Casuarina* is derived from Fagales.

Burtt Davy[22] published a short account of the Dicotyledons comprising a list of 10 character series and Barkley[12, 13, 14] gave a useful list of "Anthophyta" (orders, families, and selected genera) followed by some pseudo-phylogenetical schemes, in which the Magnoliales are considered most primitive.

Lam[97, 98] conceived a new system of the Cormophyta in which the Angiosperms were considered birheithric, on account of supposed stachyo- and phyllospory. In a later paper [100] the idea was worked out and represented in a three-dimensional graph. It is supposed that the distinction into a stachyosporous and a phyllosporous group is older than that into Mono- and Dicotyledons, because the first subdivision is of a very ancient date. This idea which has met both with poignant disapproval (Eames[48], Parkin[130]) and with emphatic agreement (Suessenguth and Merxmüller[161]) will be discussed again in the next paragraph.

Soó[150] whose system will be discussed in the following paragraph, accepts 50 orders and 293 families, of which 41 and 248, respectively, are in the Dicotyledons.

Novák[128] gave (in Czech) a survey of the Angiosperms with a relationship scheme starting from the Ranunculales. Recognized are no less than 68 orders and 379 families, of which 56 and 324, respectively, in the Dicotyledons. Salicales, Casuarinales, Batidales, and Lamiales are of admittedly unknown connection. The connection between Ranunculales and Monochlamydeae is partly through the Hamamelidales, partly through the Papaverales. All Monocotyledons are connected with the Ranunculales through the Alismatales.

Deyl[42] has given a detailed survey of the Monocotyledons.

Kimura[89] published also a system of the Monocotyledons and, though admitting that fossil evidence is indispensable for understanding phylogeny, he gave a pseudophylogenetical scheme on a more or less typological basis, both in two and three dimensions. Monocotyledons have three types of cotyledons, one with two equal cotyledons (Nymphaeaceae), a second with unequal ones (Gramineae), and a third with one cotyledon. The group is considered monorheithric.

Boivin[18] admitting that every organ has its history and recognizing the lack of fossil evidence published an account of the families of Tracheophytes, based on 15 series of characters, introducing a new nomenclature of higher

taxa (above the order), e.g. Monopsida and Dicopsida, subdivided into Folliculidae-Achenidae, and Lignidae-Herbidae, respectively.

Cronquist[36] gave an outline of a new system of Dicotyledons with the Ranales as the most primitive group, and based upon additional evidence from the fields of embryology, anatomy, palynology, and serology. Of the 47 accepted orders, of which he adds a key, 13 are without clear connection with others, and 8 of these (of the Sympetalae) are mutually related. There is a suggested linear arrangement of the 270 families.

To conclude—very appropriately—we have to mention an attempt by Copeland[34] to look into the future. Meanwhile the idea is not to predict what the next dominating group will look like, but what we might think of the future development of our systems. The result seems reasonable enough though the practical usefulness may be doubted. Copeland advocates the acceptance of large orders, which are not necessarily strictly describable, and whose names will have to follow the rule of priority. His idea is only 22 orders, some of which comprise such unexpected combinations as Ranales and Piperales.

The remark may be inserted here that if "Ranales" are mentioned both in the present section and in the following one, this need not implicitly mean that only the herbaceous Polycarpicae are meant; the term may in some case stand for Polycarpicae as a whole. It seems necessary to emphasize this here, since everybody agrees about the primitiveness of the woody Polycarpicae but there is some difference of opinion regarding the herbaceous ones as well as regarding the supposedly related Helobiae.

An abominable mystery.

CH. DARWIN

22. *The Dynamic Viewpoint.* According to Sprague[154, p. 442], phylogenetic connections of Angiosperms are entirely speculative and Turrill[175, p. 514], expresses the same opinion with almost the same words. Constance[32] is even less optimistic in saying that there seems to be a rather general agreement that "sufficient evidence to formulate a . . . satisfactory phylogenetic arrangement of flowering plants is not yet available."

The cause of this is evidently the lack of significant fossils. Fossil material of Angiosperms abounds from the Lower Cretaceous onward, but flowers are extremely rare. However, even in the oldest periods in which Angiosperms started to form any appreciable percentage of the flora, the leaves have a most familiar appearance and inspire sufficient confidence to assume that several families and even genera which are known to us in the recent flora, existed even then. This is supported by remnants of wood and, occasionally, seeds. We must, however, realize the possibility that other types which may have been true Angiosperms (whatever that means), have

not been recognized as such because they could not be placed in any of the families known to us.

The conclusion must be that in order to satisfy our natural curiosity, we have to rely on evidence from recent plants, occasionally supported by what palaeobotany can tell us about floras of the past.

As far as our evidence reaches, no single character in the fields of angiospermy, wood anatomy, type of leaf, flowers, or integuments (Lam[108]) is sufficient by itself to characterize the Angiosperms as a class, the only differential character being the double fertilization and the development of a secondary endosperm connected with it. It is not likely that all families and, still less, genera have been investigated regarding these processes. In view of the rather large diversity of the embryosac we would not be surprised if a similar diversity would be detected as to the development of the endosperm and accordingly the double fertilization.

However this may be, the fact that in some Chlamydosperms a sort of initial stage of double fertilization has been observed in which the second generative nucleus is allotted a (not very effective) fertilizing task, diminishes the discontinuity even of the recent Angiosperms (cf. Lam[108]). In fact, the class can only be distinguished by a combination of characters and as the most important of these, as it seems, are hidden in the ovule our hope of ever detecting their initial stages in fossils is practically nil.

This may be just one of the possibilities to explain the "sudden rise" of the Angiosperms, but there have been many more conjectures to solve what Darwin has called the "abominable mystery" (quotation from Axelrod[10], cf. Heberer[76A]).

McLean Thompson[170] is of the opinion that flowers are comparatively young structures but young cannot mean younger than the Lower Cretaceous unless it is assumed that the leaves ascribed to, for instance, *Populus* from that period belonged to a plant which bore no "flowers."

A diametrically opposite opinion is that of Greguss[68] (and information by letter) who thinks that the Cormophyta did not originate from some Alga but right away from some unicellular plant and that the Angiosperms may have a very old origin from this stock with a very gradual development of what is now called a flower.

The idea that the Angiosperms are actually older than has thus far been anticipated on account of the explosive development in the Lower Cretaceous is, indeed, gaining ground. Thomas at one time[165] suggested that the Jurassic Caytoniales may have been the Angiosperm ancestors. In subsequent publications, however[167, 168], he gradually abandoned this opinion (cf. Harris[75]) and recently[169] he declared, impressed as he was by the spectacular finds of *Glossopteris* and *Gangamopteris* fructifications in South Africa (Plumstead[132, 133, 134]), that it is quite possible that "the real

ancestors of the Angiosperms may yet be found in the Triassic of South Africa."

Plumstead, in her turn, though on botanically rather doubtful grounds, thought she had struck the real ancestral group in *Glossopteris*, but it may be supposed that this suggestion will suffer a still shorter life than Thomas's idea.

It may be added that a growing number of botanists, palaeobotanists, taxonomists, and phytogeographers (Camp[23], Bailey[11], Suessenguth[159], Axelrod[10], Croizat[35], Deyl[42]) suggest that the "cradle of the Angiosperms" was somewhere in the southern hemisphere, the best chances being the South West Pacific area where an agglomeration of "primitive types" (both phyllosporous and stachysporous) is found.

In addition it may be mentioned that Axelrod, in a suggestive paper, ascribes the lack of old Angiosperm fossils to the possibility that they inhabited tropical upland regions where fossilizing possibilities may have been scanty. He dates the origin of the class in the Permian or Triassic eras.

Thomson[172] expresses a similar opinion; he is certain that Angiosperm pollen is known since the Lower Jurassic, and supposes that the class roots in Pteridosperms with a cupule with many seeds.

Lam[100, 101, 102, 104, 105, 107] is of the same opinion at which he arrived by elimination of all groups which are less likely to have been, or harboured, Angiosperm ancestors.

The well-known palaeobotanist Kräusel carefully retraced fossil evidence of Angiosperms concluding that most precretaceous finds are very doubtful indeed. *Montsechia* and *Suevioxylon* (both Upper Jurassic) may have been Angiosperms but they may have been something else as well. To keep on the safe side he does not believe in precretaceous Angiosperm fossils.

Lam[100] gave a list of the oldest Angiosperms reported in palaeobotanical literature. Leaving pollen finds apart, the picture shows the significant fact that the oldest "indubitable" Angiosperms were both Monochlamydeae and Ranales; of these the latter seem to have appeared somewhat earlier than the former. It may be significant that the Hamamelidales, so often indicated as the link between "the two primitive groups" of Angiosperms, are known since the Middle Cretaceous (*Platanus*). Unless *Nymphaea* is considered a Monocotyledon, that group only appears in the Middle Cretaceous (Pandanales) and Upper Cretaceous (Palmae). Axelrod states that about the Middle Cretaceous no less than 36 Angiosperm families were known. The Sympetalae appeared in a much later period.

On surveying the many theories and opinions about the origin of the Angiosperms we arrive at the following picture, which, though admittedly far from complete, is probably sufficiently representative:

1. *Monorheithry* (based upon double fertilization)—a. *Euanthium-theory* (based

upon bisexual flowers). This is the classical view based on Goethe's metamorphoses, according to which all lateral organs are leaves. The flowers are originally bisexual. Janchen[83] enumerates only twelve investigators (1888–1939) in favour of it but the impression is that the majority still prefer this view according to which the Polycarpicae (Ranales) are the most primitive Angiosperms. Some recent adherents are Copeland[33], Bailey[11], Plantefol[131, more or less], Eames[48], Rodriguez[138, 139], Lemesle[111, on anatomical grounds], and Constance[31].

An origin from the Pteridosperms is advocated by Sargant[143], Thomas[165], Lam[97, etc.], and Němejc[126, or more directly from the Psilophyta]; (cf. Deyl[42] who denies both the euanthium and the pseudanthium theories because the difference between flowers and inflorescences is not greater than that between single and branched sporangiophores). Plumstead[132–134] supposed *Glossopteris* to be or to be near the Angiosperm ancestral stock, mainly because the "fructifications" are supposed to be bisexual.

An origin from or from near the Cycad or Cycadeoid stock was accepted by Arber and Parkin[8, 9], Hallier[74], Darrah[41], Chadefaud[28], and Tachtadzjan (1948). Of these Chadefaud conceived an ingenious but little acceptable theory of the development of bisexual Angiosperm flowers by various processes of reduction and alteration of sex.

Frenguelli[61], in an interesting palaeobotanical survey, arrives at a more or less intermediate conclusion in so far as he derives the Angiosperms from the common ancestors of Caytoniales and certain Cycadaeoidales (*Wielandiella* and *Williamsoniella*). His ideas are closely related to those of Suessenguth[158], Darrah[41], and Rothmaler[142], and the writer of these lines is inclined to join these investigators; this, of course, does not exclude the possibility of bi- or polyrheithry, which is largely a matter of definition of the ancestral stock, as will be mentioned under birheithric schemes.

Rothmaler conceived a new system with a new and rather cumbersome nomenclature, distinguishing in the "Spermatophyta" four classes: Gymnospermophytina (Pteridospermopsida, Cycadopsida), Stachyospermophytina (Ginkgopsida, Cordaitopsida, Coniferopsida, Taxopsida, Ephedropsida), Chlamydospermophytina (Bennettitopsida, Gnetopsida, Welwitschiopsida), and Angiospermophytina.

b. *Pseudanthium*-theory* (based upon simplicity of flowers). Raised by Wettstein and stating that the Angiosperms are to be supposed to have had common ancestors with the Chlamydospermales, particularly *Ephedra*. The flowers are unisexual and the most primitive Angiosperms are the Monochlamydeae (Apetalae), particularly *Casuarina*. Janchen[83] enumerates

* Good[65a] refers to flower-like inflorescences as pseudanthia as well and, properly speaking, this use of the term can hardly be objected to. What is obviously happening now can have happened before.

twenty-two authors (1872–1948) in favour of this theory, including himself. Janchen's characterization of the Apetalae strongly resembles that of Lam's Angiospermae stachyosporae[100].

A precursor, as it were, of this view, is the system of Suringar[162] which, like that of Engler[56], accepted three primitive groups (Monochlamydeae, Polycarpicae, Monocotyledons) of which the first-named one was considered the most primitive one.

Campbell[26] hesitates between the pseudanthium and Engler's ideas but his ultimate decision is in favour of the former.

Wilson[183] who conceived the theory of "the" stamen as a contracted ramification system, later on[184] pictured a series of "hypothetical reconstructions" of a primitive Angiosperm on the basis of the telome theory with ultimately a single, terminal, infolded (phyllosporous) carpel with marginal ovules, and a (stachyosporous?) stamen clearly reduced from a mixed dichotomous structure, both inserted at the apex of a flat leafed branchlet. This curious reconstruction is certainly one of the possibilities which only has to be turned into a three-dimensional one with helicoid phyllotaxis and and axillary buds to be acceptable as an Angiosperm.

Iljin[80] says that the euanthium-theory is untenable and though he thinks that more than one "starting group" can be accepted (Monocots, Ranales, Centrospermae, *Casuarina*, etc.) his conclusion is to derive the Angiosperms from the ancestors of the Chlamydosperms.

2. *Bi- and Polyrheithry* (based upon the incompatibility of the controversial monorheithric concepts)—In § 17 it was stated that bi- and polyrheithry in static taxonomy can be traced by constructing the groundplans. If the groundplans of two taxa ultimately completely converge into a new groundplan which encompasses the two original ones, the conclusion is monorheithry. If they remain separate, they are not compatible and the outcome is birheithry.

In dynamic taxonomy, the typological method is not applicable because group phylogeny is almost entirely subjective and, for the rest, based upon intuitive combinations of semophyleses. What we actually do in practice is, indeed, first to get an impression regarding the groundplan of the group; if the result is that there are two or more groundplans, we decide on bi- or polyrheithry, as the case may be, and our second step is to look for an ancestral group among fossils.

Now our decision about mono- or birheithry largely depends on what we know of fossil groups, notably on what impression we have about their discontinuities or delimitations. For example, if we should decide that one part or one group out of the recent Angiosperms could reasonably be derived from one fossil group, say the cycadalean stock, and another group from, say the Pteridosperms, the Angiosperms would automatically have to be

called birheithric. If, however, closer investigation revealed that the cycadalean ancestors and the Pteridosperm ancestors had better be combined into one group, the Angiosperms would be monorheithric and the ancestral group would have to be considered the common ancestor of two divergent lines.

Again, however, if, on still closer scrutiny, the ancestral group should, in spite of its naturalness, appear to comprise two subordinate groups, birheithry turns up again. In fact the concepts mono-birheithry root in that of taxogenesis. In its most absolute sense, monorheithry would mean descent of a taxon from one single life-cycle and as it is not likely that this is a frequent phenomenon one may safely conclude that the concepts are always of a relative nature. The following communications are to be read in the light of the above considerations.

On cytological grounds Anderson[1] supposes that perhaps both the Gnetalean ancestors and the Cycad ancestors, i.e. ancient Gymnosperms with 7 and 12 chromosomes, respectively, may have contributed to the recent Magnoliales, which, as a group, are considered primitive.

Hagerup[70, 71] on account of flower structure and particularly the ovule and its integuments, suggests two lines of development, one from Lepidospermales (on the erroneous assumption that the stegophyll would be homologous with the integument of Conifers) to Coniferales (with a branch to Cordaitales), through Gnetales to some Angiosperms (Monochlamydeae), and one from Filices through Cycadales to Angiosperms (Polycarpicae). Faegri,[57] though emphatically in favour of certain of Hagerup's organ derivations, does not agree with the above-mentioned lines, but Emberger[53] generally agrees with them.

Mägdefrau[116] published a diagram from which can be inferred that both the euanthium and pseudanthium theories can be maintained, the links being Pteridosperms (Caytoniales)–Ranales and Psilophytales–Protolycopsida–Coniferopsida–Monochlamydeae. Gnetales are not mentioned.

Lam, in a long series of papers[97, etc.], defended the thesis that on account of the incompatibility of the pseudanthium and euanthium theories and the fact that the oldest Angiosperms known for certain belonged to either the Monochlamydeae or the Polycarpicae, the Angiosperms are at least birheithric, in this sense that they may have originated from fairly antipodal groups of the Pteridosperms, one with stachyosporous, the other with phyllosporous tendencies. It is his opinion that these two conditions, so clearly separate in lower Cormophyta, meet in the Pteridosperms which are supposed to have covered a very wide range of types. Lam[100] furthermore believes that the two groups can probably also be recognized in the Angiosperms though he admits that a considerable number of families do not clearly belong to one of the two, perhaps due to the very complicated

alterations and the very strong contractions most flowers have been subjected to. Stachyosporous families (e.g. most Monochlamydeae, Ranales?, Spadiciflorae, Pandanales, Helobiae?) would be those with axis-borne ovules, the ovules single or in trusses in the axils of stegophylls (pseudocarpels); the stamens are of axial nature and are equally axillary (epipetalous), sometimes showing traces of dichotomy both in the filaments and in the insertion of the 2 or 4 sporangia. Phyllosporous groups are those with all organs, including stamens and carpels (both true sporophylls), in helicoid arrangement, in principle with intermediate forms (except between stamens and carpels). In the discussion to Plumstead's paper (Lam[105]) corresponding diagrams of the two supposedly primitive flower types were pictured, in principle agreeing with the pseudanthium and euanthium theories respectively. In his most recent paper (Lam[108]) he concludes that the two types have probably to be taken not too strictly since the distinction leaf vs. axis has probably long been taken in too absolute a sense (cf. Bremekamp[20A]). The possibility must be seriously considered that organs of an intermediate nature exist, as has also been intimated by Grégoire, McLean Thompson, Plantefol, and others. These Lam[108] refers to as stachyophylls, a notion which would include such structures as cladodia, phyllodia, and the like.

This theory has been severely opposed (cf. Lam[103]), mainly by ontogenetically working anatomists and morphologists (Bailey[11], Eames[48], Wilson[185], Baum and Leinfellner[16], Eckardt[49, 50, 51], J. Parkin[130], and some others). All stick to "the" carpel in the traditional sense and if this is a preconceived idea, this stubborn attitude is, as far as Lam is concerned, a fighting of windmills, also because all these authors base themselves on ontogenetical grounds, i.e. on static taxonomy; this even shows in the title of one of Eckardt's papers[49] (systematic, where he should have said phylogenetic). Lam is of the opinion that static observations may or may not have a bearing on phylogenetical conclusions, but are in no case alone decisive. More or less in favour of Lam's theory or of a similar opinion are Mägdefrau[116]; Frenguelli[61], Maekawa[115], Suessenguth[160], Suessenguth and Merxmüller[161], and Baumann-Bodenheim[17A].

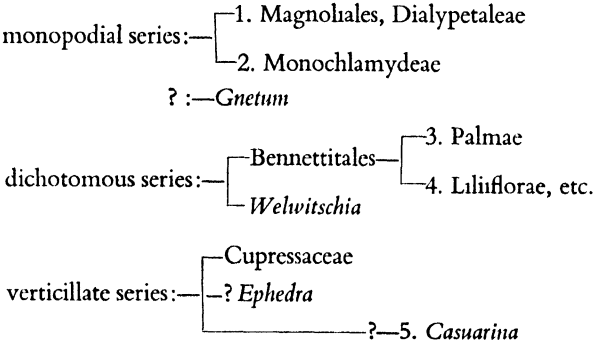
As regards the double fertilization and the secondary endosperm, we may add here that there may be some exaggeration in the assumption that their coming into existence would necessarily require a rare series of accumulative mutations. This is a mere surmise, and nothing is actually known, so that the possibility of the process having been brought about more than once independently can certainly not be ruled out altogether.

Soó[149] published a "phylogenetic" system, and though confessing himself as an adherent to the euanthium theory his diagram is clearly birheithric, as he hesitatingly admits in his text, the two branches being the classical ones of the two opposing theories: Gnetales (or Coniferales)–

Monochlamydeae, and Bennettitales (or Caytoniales)–Polycarpicae (Ranales). In his second paper (Soó[150]) he points out that on palynological grounds there should be some relationship between Bennettitales and Gnetales. He also gives a useful account of Russian literature on the subject, in which both monorheithry and bi- or polyrheithry find their supporters. Soó now belongs clearly to the second category though he sees occasional "horizontal" connections between the two groups.

Deyl[42] is of the opinion that both the Ranales and the Monochlamydeae may be primitive. His idea is that the Angiosperms as such root in the Psilophytales, which would imply that they would be of very ancient descent (Devonian). He also thinks that the herbaceous type is older than the woody one. This is not in agreement with Eames's opinion[47]; contrary to what one observes in ontogeny, it seems that in phylogeny the woody stele has dissected. Sinnott and Bailey[148] are of the same opinion; on old isolated islands the flora is predominantly woody. Cockerell[30], however, supposes that the Angiosperms may have started as small herbaceous plants in upland areas with scarce fossilizing possibilities. After having developed into woody plants, these might have given rise to the modern weeds which then should be secondarily herbaceous. He advocates making a thorough search in older beds, Triassic, or even Permian.

Finally, we have to mention some polyrheithric schemes. Amongst these Greguss's system[68], which was already discussed in § 20, ranks foremost because of its unusual structure. Actually, it is pentarheithric:



Fagerlind[58] thinks that the Angiosperms have polyrheithrically originated from an unknown ancestral group, having common ancestors with the Gnetales, more or less independent groups being Casuarina, Polygonales, and Centrospermae (and derivatives), Tricoccae (and derivatives), a number of Monochlamydeous orders, and the Polycarpicae–Monocotyledons. It may be added here that Moseley[124] considers *Casuarina* not primitive, but derived from Hamamelidales-like ancestors.

Just[88] states that the opinion that the Angiosperms are polyrheithric

gains ground; also that they are older than has so far been anticipated. His ideas are related to those of Fagerlind[58] and Lam[97].

Let us, in conclusion, make a remark concerning the future. Axelrod[10, fig. 12], estimates that the period between the first appearance of a major group and the beginning of its dominance is of the order of 30 million years. Considering that the Angiosperms *are* the dominating group of our days, it might be presumed that the next one is already in existence.

Assuming that the Angiosperms are the only group of living plants which can be considered likely to deliver the next dominating taxon, this may be another factor why they seem so confusing. Meanwhile, the picture given in the foregoing pages is not very reassuring as it inspires little confidence that we will ever solve Darwin's "abominable mystery" unless palaeobotany sends us a beam of light. For it seems unfeasible to say which group or groups of Angiosperms, if any, would really belong to a future dominating group rather than to the one we stubbornly keep considering an homogeneous class on its acme. Or might the Monochlamydeae c.a. be the older group in retreat, and the Polycarpicae c.a. the group of the future, or is the system of the Angiosperms so confusing because the future group is already represented among them? In treating a theme like the present one, it seems appropriate to end with a question, so why not the above one?

IV. FUTURE RESEARCH

In conclusion of this rather sketchy survey of what Taxonomy is in our days, we may be allowed to make a few remarks on its future. In accordance with the "system" of the contents of the present contribution, these remarks naturally fall into two categories, a static one and a dynamic one.

As to the static facet of Taxonomy we will, of course, have to continue our exploration of unknown parts of the flora of our globe. In view, however, of the rapid destruction of natural vegetations by man, Constance[31] wrote: "it is a moot question whether one group of men will succeed in recording the remaining unclassified organisms before other men succeed in inadvertently destroying them." In addition to this task it is, as Rollins[140] pointed out, at least as important to complete our knowledge on taxa which are as yet insufficiently known, as to describe new ones.

In addition to the above as well as to our remarks of § 7, we may add that future research should focus on the following points:

1. Continued research about the details of life-cycles of representatives of all groups, including families, part-families, and genera of Angiosperms;

2. particular points of interest in item 1 are similarities or differences in the double fertilization and the development of an endosperm in Angiosperms;

3. continued research in embryology, floral anatomy, and floral ontogeny in minute details;

4. mutual relationship of genetical factors and characters;
5. chemistry of genes;
6. chemistry and physiology of morphogenesis;
7. chemistry and genetics of terata;
8. continued research on induced mutations.

As far as dynamic taxonomy is concerned, we are almost exclusively dependent on palaeobotany. Next to new finds, regarding which we have largely to wait on what chance offers, new or perfected techniques may reveal valuable data: palynology of old beds, maceration, epidermal structures, etc. Palaeobotany has in the present century very materially contributed to our knowledge of morphology (Psilophytales, Glossopteridales, Caytoniales, Pentoxylales, Cordaitales, Trichopityales, Coniferales) and the very recent find of an extremely old landplant (*Aldanophyton*, a Lycopsid of the Middle Cambrian of Siberia) revivifies the hope that more complete fossil and perhaps still older material of landplants will be found, enabling us to get a better insight into the structure of the Cormophyta as a phylum. We may also hope that in not too distant a future the earth's crust will somehow deliver a clue to the origin of the Angiosperms. Dynamic taxonomy will also have to follow closely the results of research at the static level and try to evaluate this for its purposes. It will, however, not allow static taxonomy to decide alone upon matters of a purely dynamic nature.

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A VISTA IN PLANT ANATOMY

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INTRODUCTION: A PREVIEW OF THE CONTEMPORARY SCENE

IN 1956 Professor Vernon I. Cheadle[6] of the University of California wrote these words. "To many students in elementary botany classes who must learn something about (the) structure of plants, even if only to practise use of the microscope, vascular tissues do not often excite much interest. And if one reads elementary textbooks, he recognizes that most of these do not serve very well in supporting the teaching efforts of instructors who, unhappily, are seldom very confident of their own understanding of these tissues.

"Yet a knowledge of vascular tissues is immensely important to an understanding not only of the activities of vascular plants in their present environment, but also how they must have survived and prospered through the ages. Furthermore, these tissues or products derived from them have been important items in Man's economy since the time of his arrival as a thinking organism."

This statement gives, broadly speaking, a true picture of the situation as it is often found today. The study of plant anatomy is not popular, especially with the younger botanists, it seldom receives the attention that it merits in universities, there are comparatively few botanists who take the subject seriously, and there are many who regard plant structure as a branch of knowledge on a lower intellectual plane when it is compared with the exciting developments in genetics, cytology, and plant physiology which are taking place at the present time. Many seem to think that the study of plant structure can yield nothing new, and that we already know all that it is necessary to know of this subject. This attitude of mind may partly arise because the spectacular advances in certain other branches of botany have created a lack of balance in our views on botany as a whole. This is not to decry the value of the advances that have been, and are being, made in these other fields, but rather to suggest that in these days of very specialized research it is desirable to try to advance knowledge by a synthesis or remarriage of research disciplines that are tending to become segregated or divorced. In the field of botany the form and structure of the plant should surely be restored to a more central position in plant science as a whole, since it is the point, broadly speaking, wherein all botanical disciplines should meet. In the study of plant form and structure we can find a real possibility for contact between the taxonomist, physiologist, geneticist,

biochemist and other specialists. Apart from this lack of balance in the modern approach to botany, another reason for the lack of interest in plant structure is because the study of tissues and their organization in the plant body is regarded as a mode of investigation that treats the plant as if it were solely a corpse in which all vital functions have ceased. The modern interest is in the vital activities of organisms, in their physiological responses to changed experimental conditions, in the behaviour of their chromosomes, in their reaction to pathological attack by other organisms, and in the biochemical reactions and metabolic changes that are going on in their bodies throughout their lives. It is, however, clearly evident that, important as it is to study the vital activities that make up the life of the plant, the pursuit of these lines of enquiry cannot attain their maximum value unless they are considered in relation to the form, structure and even the taxonomic position of the organisms concerned. Although the plant anatomist is so often restricted by being unable to examine living tissues, modern fixation methods are designed to cause the death of cells with the minimum distortion. Even when the anatomist has perforce to study tissues that have long since died, as in archaeological, palaeobotanical, or partially digested plant tissues, every possible action is taken to ensure that the cells are restored as far as possible to the form that they most probably presented when still alive. Furthermore, the tissues of living organisms can be fixed at any stage during their life history and at any intervals of time. The anatomist is therefore rather in the position of a member of the audience in a cinema who could cause the film to be stopped at any moment, thereby enabling him to pay particular attention to any stage in the presentation of the film in which he might be specially interested. The desire to stop a film must often have been felt during the showing of a motion picture of a biological subject. However, the point before us is that a plant anatomist should always approach his problems bearing in mind that what he sees under the microscope are carefully selected "stills" in the presentation of a motion picture of absorbing interest. So we come to realize that the line of demarcation between the disciplines that study the dead corpse and the living organism respectively is seldom so clear cut as may appear at first sight. With a little more imagination on the part of specialists this barrier could be still further demolished. However, to understand the present position of plant anatomy we must leave this brief preview and start from the beginning of our vista, and, by viewing the phases through which the subject has passed between the time of its initiation and the present day, gain some further insight into its present status.

The Historical Vista

The vista that we are about to explore begins in London on April 10th, 1672, when it is recorded that at a meeting of the Council of the Royal

Society "the Bishop of Chester proposed Dr. Grew to be a Curator to the Society for the anatomy (of) plants for a year, upon subscriptions, amounting to fifty pounds, to be made by such members as should be willing to contribute thereto. The Council approved of this proposal." We were reminded of this event by Mrs. A. Arber[3] at a meeting of the Linnean Society which she addressed in 1941 to mark the tercentenary of the birth of Nehemiah Grew (1641–1712). The tercentenary fell during the Second World War, and therefore called forth less comment than the occasion deserved, for Nehemiah Grew was a pioneer in the study of plant structure, and the work that he did was of such a high order that it was unequalled by any of his immediate successors in the field, either in England or on the Continent. As we shall see, Grew's work was no less important or far-sighted than that of his contemporary Marcello Malpighi, but the work of these two plant anatomists stands out well above that of their successors for many years that had yet to come.

Grew, the son of a schoolmaster, excluded from a university career because of his non-conforming religious views, studied medicine at Leiden, and afterwards practised at Coventry. He then came to London, and, thanks to the Royal Society, took up his appointment as Curator for the anatomy of plants and we read that "he was desired to produce some observations on that subject at the next meeting. . . . In order to which it was ordered that Mr. Hooke should deliver to him the Society's microscope." There is no need to follow Grew's career in detail, as this has already been done very fully by Mrs. Arber[1–3], but we should note that in 1677 he became one of the two Secretaries of the Royal Society, the other being Robert Hooke. We should also note that, after publishing two preliminary works on plant structure, Grew's *magnum opus The Anatomy of Plants*[12] appeared in 1682, this work being an amplified version of his previous books.

As Mrs. Arber has reminded us, the soundness of Grew's work depends on the fact that he started with naked eye observations and only resorted to the use of lenses and microscopes to observe objects that could not otherwise be seen. Indeed, Grew's conception of plant anatomy was sufficiently broad to include much of what is now known as morphology and it was not confined, as is so usual today, to the study of cells and tissues, or as one might perhaps more correctly term it, the study of histology. In this respect Grew's views are in close accord with those of the present author who regards anatomy as equivalent to micromorphology, or that branch of morphology for which a good lens or a compound microscope is required. Micromorphology is not a self-contained body of knowledge, but rather the study of morphology from a particular standpoint. Those who investigate the subject are not, and do not claim to be, magicians endowed

with superior powers of knowledge, but regard themselves rather as observers whose thoughts and mental pictures concerning the structure and physiological workings of the plant body are not based entirely on what can be seen of a plant from the outside. If this mental approach were to be more widely appreciated it would make for much greater understanding on the part of botanists whose special interests lie in other fields. The taxonomist would no longer treat anatomical evidence as "suspect" or of doubtful value if it happens to conflict with his own previously conceived views but would, in collaboration with the anatomist, explore the reasons underlying their apparently contradictory conclusions. Similarly the physiologist must listen to what the anatomist has to say if he is to construct an accurate picture of the processes that make up the life of the plant.

The main object of this digression from Grew is to show how, in his time, he was in a sense in a much stronger position than we are today, for he studied plant anatomy before there were so many specialists and specialized approaches, and he was therefore able the more easily to visualize the significance of his researches in relation to botany as a whole. Furthermore Grew was himself far from being an anatomist only, his whole approach was very broad, and, as the author was recently reminded by Dr. Hamshaw Thomas, he had a surprisingly good knowledge of plant biochemistry for the times in which he lived. For his anatomical work Grew found that three things were essential "viz., a good eye, a clear light and a Rasor wherewith to cut." How true! Even in these days we should be much better served in the field of plant anatomy if everybody concerned would learn the simple and basic requirements of his trade before worrying too much about the latest developments in phase contrast microscopy or discussing the relative merits of microscope objectives of different makes. Modern refinements in microscopy have their own rightful and useful place, but it is the man behind the instruments that counts more than the instruments themselves.

Returning once more to Grew we may note that he recommended the use of transverse sections, and was in fact the first to introduce this term. He also came to appreciate the value of tangential sections, and had the conception of serial sections although in a rather crude form when compared with modern standards. A perusal of his writings shows that he had, for his time, a very remarkable insight into plant structure, and his work was a notable achievement in view of the poor quality of the optical equipment that was available in his day. This was a factor that limited his investigations. His most notable misconception was that the cell walls consist of fibres, and that these served also to connect the cells together. Here he was not picturing his "fibres" in the modern sense at all, for he was not referring to individual fibre cells as we at present understand them but to actual components of the cell walls themselves. Did he, we might ask ourselves,

foresee the fibrillar structure of cell walls now being revealed by the electron microscope? However this may be, Grew was also aware of the existence of fibres in the modern sense, but his application of the same term to actual cells and constituents of cell walls naturally leads to confusion.

We have already referred briefly to Grew's famous Italian contemporary, Marcello Malpighi (1628–1711). Malpighi, like Grew, was a physician by training, and, like Grew, he devoted considerable attention to vegetable anatomy. His best known work on this subject consists of two handsome volumes entitled *Anatome Plantarum*, the two volumes being published in 1675 and 1679 respectively[19]. Grew and Malpighi were well known to each other by correspondence, and indeed it is interesting to note that the publications by both authors were sponsored by the Royal Society in London. It is unfortunate that Schleiden, at a later date, cast aspersions on Grew's work, asserting that he merely repeated what he had learned from Malpighi. Mrs. Arber[3], who has since studied the relationship between these two pioneer anatomists with her well-known care and perspicacity, found that Schleiden's attitude was quite unjustifiable, and concludes that "Schleiden's statement is demonstrably a tissue of errors as regards dates and facts."

Although Malpighi and Grew stand out above all their contemporaries in their knowledge of plant structure, we must not ignore the influence of Robert Hooke, Grew's co-secretary of the Royal Society, who studied a great variety of objects with the compound microscope, an instrument to which he himself added improvements. He, however, made no serious attempt to study plant structure apart from examining material of vegetable origin such as charcoal, cork, and the pith of elder and other plants. Another investigator of this period was Anton von Leeuwenhoek (1634–1723) who made scattered observations on vegetable anatomy. The contributions of Hooke and Leeuwenhoek to our knowledge of plant structure, although important, were in themselves very small compared with the achievements of Grew and Malpighi. The fact remains, however, that after the great pioneering endeavours of these early workers in the field of plant structure, no further advance was made for many years. Indeed the ensuing period was, if anything, a period of decline rather than advance, for less able investigators added incorrect information, based on inaccurate observations and interpretations, to the body of knowledge established by Grew and Malpighi. Here again Mrs. Arber expresses the position so well when she says of Grew, Malpighi, and Leeuwenhoek that they "illustrate, although belatedly, the searchlight quality of the renaissance mind which gave such brilliant but brief illumination to realms which again lapsed into darkness, and were not actually explored again until after the passage of centuries."

From the time of Grew and Malpighi onwards the student of the history

of vegetable anatomy can follow the somewhat chequered course that the subject has undergone in several admirable summaries. There is firstly the *History of Botany* by Julius von Sachs[29] of which an English translation was published in 1904. Unfortunately this carried the story forward only as far as 1860. It is brought much more up to date from the German standpoint by Schmucker and Linnemann[30] in their *Geschichte der Anatomie des Holzes.* This interesting account, which includes a portrait gallery of the leading German workers in this field, is not, as might be expected from its title, solely concerned with plant anatomy as applied to wood structure, but covers the subject from other points of view as well. The subject from the French standpoint is treated by Maurice Hocquette[14] in *Histoire de la Botanique en France* issued in 1954 on the occasion of the 8th International Botanical Congress held in Paris, and this account is also accompanied by an interesting array of portraits of some of the leading French anatomists. Since these accounts are available there is no point in discussing in detail the contributions made by each of the considerable number of German and French workers who were mainly responsible for carrying forward and amplifying our knowledge of plant structure until comparatively recent times. The English contribution to the subject during the early part of this period was small, as no successor followed immediately in the footsteps of Grew, and it has been suggested that this was mainly because Grew held no University post and therefore had no pupils. Indeed it was not really until the Jodrell Laboratory at Kew was opened in 1876 that a renewal of interest in the form and structure of plants was again aroused amongst British botanists. At that time the Jodrell Laboratory was one of the chief centres through which British workers came to know about the great strides that had by then been made in the fields of anatomy and physiology by continental botanists. This particular phase in the history of botany has been described by Bower[5]. F O Bower, D. H. Scott, and others of the younger botanists of those days, failing to find in British universities the inspiration that they felt was needed, worked in continental laboratories, particularly under Julius von Sachs at Wurzburg and Anton de Bary at Strassburg. Returning to England, these then youthful botanists inaugurated a new era in British botany. The younger botanists of today probably do not realize the key position that was then held by the Jodrell Laboratory, and, in that small building, under the inspiring leadership of D. H. Scott, who was the Honorary Keeper of the laboratory, an all-important page was written in the history of British botany, particularly in the fields of morphology and anatomy. This page shows so clearly how much can be achieved by a small band of really enthusiastic workers of first-class calibre, and the whole technique by which the workers of those days approached their problems stands out in marked contrast to that by which the large teams of

hierarchies of workers, armed with expensive equipment and housed in large buildings, attack the research problems of today. Both methods of approach have their strengths and weaknesses, but one may well ask oneself whether, even in these days, a few really first-class workers in a comparatively small department would not advance the science of plant anatomy, or indeed any branch of botany, more reliably and effectively than a large team of less able workers operating under a leader harassed by the moils of administration. Before passing judgment on this difficult problem, the reader is invited to peruse the more ample account of the early work at the Jodrell Laboratory published by the present writer elsewhere[20].

After this bold jump forward from Grew and Malpighi to Bower and Scott we must return along our vista to gain some further insight into what had been happening meanwhile, especially on the Continent. As we allow our eyes to skim through the pages in which Julius von Sachs[29] so ably records the achievements of his anatomical compatriots, and refers more briefly to the work of anatomists in other countries, all of which he does with truly teutonic thoroughness, von Wolff, Mirbel, Moldenhawer, Sprengel, Link, Rudolphi, Treviranus, and Meyen are amongst those whom we encounter. The plant anatomists of this period are referred to as "phytotomists" and their subject as "phytotomy." Mirbel's *Traité d'Anatomie*[25] and Moldenhawer's *Beyträge*[27] are passed under review. We are told how the nature of vessels came to be understood, of attempts to relate structure to physiological function, and of how this was handicapped by a belief in a doctrine of "vital force." We read of a controversy between Mirbel and Sprengel as to whether cells are interconnected by pores. And so we are led on through a maze of increasing complexity, following the gropings and strivings of the phytotomists, until we come, with a sigh of relief, to the famous von Mohl (1805–72), than whom, we are told, and may well believe, there was none greater since the days of Grew and Malpighi. Von Mohl[26] related anatomy to physiology, always remembering that "the interpretation of visible structure must not be disturbed by physiological views." He was a careful investigator, he never speculated unless very sure of his facts, and he could himself polish lenses as well as any man of his time. Before 1845 he was regarded, with good cause, as the leading phytotomist of his day. Von Mohl, unlike many of his predecessors, illustrated his work with his own drawings. There was a belief before his time that drawings should be made by draughtsmen employed for this special purpose so as to eliminate any possibility of the misinterpretation of structure through prejudice on the part of the phytotomist. What folly this must have been. Even today an anatomist who must rely on others to portray what he sees with the microscope is at a serious disadvantage. He is one who seeks to evade the responsibility of correct interpretation by

placing it on the shoulders of others, probably doing so because he is not quite clear in his own mind how the structure before him should be interpreted. Von Mohl knew all about this. To him a drawing must be not only a delineation of what is seen, but an expression of the investigator's own opinion concerning the interpretation of structure. And why not! The investigator who knows what he is about should be able to interpret what he sees more accurately than anybody else. A drawing is always a convention, some drawings are more conventional than others, and no pictorial delineation, by whatever means it is produced, can ever wholly and completely express everything that there is to be seen or understood of a natural object whether this be a landscape or a plant cell. Listen to what von Mohl has to say: "as the microscope trains the eye to scientific sight, so the careful drawing of objects makes the educated eye become the watchful adviser of the investigating mind; but this advantage is lost to the observer who has his drawings made by another hand." Von Mohl's *Principles*[26] is a fine work, illustrated with line drawings of remarkable accuracy, and is a very marked advance on the two volumes of Mirbel's *Traité*[25].

In the part of his book[29] that deals with plant anatomy during the 1840–1860 period, Julius von Sachs says: "Much as the founding of scientific periodicals has facilitated communication between professed botanists, yet this form of literature makes it more difficult to see the way clearly through the work of earlier periods and to discover historical connections in the science, not to speak of the harm that actually results from it to young and inexperienced students." Here again, in this present age, when journals become more numerous, and a large proportion of their contents so often consists of the immature writings of the inexperienced in search of early recognition, the anatomist may well pause to consider whether or not there is some wisdom in the comments of von Sachs. However this may be, the 1840–1860 period saw important advances. The quality of microscopes improved; the use of clearing agents was introduced; potassium chlorate and nitric acid came to be employed for the maceration of plant tissues. The mode of development of cells and tissues became more fully understood, and tissues of different kinds were recognized and classified It is impossible to mention all of those who played a part in these advances, but the name of Nägeli ranks very high in this connection. We may also note that an Englishman, Robert Brown, discovered the nucleus in the cells of the epidermis of orchids in 1831, and thereby inaugurated the great field of vegetable cytology—but that is another story.

It is a weakness of von Sach's history that he pays scarcely adequate tribute to those anatomists, apart from Mirbel, who published their work in French. One must confess that this may in part be due to the very discursive way in which so much anatomical information has, in the past, been imparted in

the French language. A wealth of detail has so often tended to obscure the basic truths that are being presented. There can be no more exasperating occupation than reading very discursive articles on plant structure of the type just mentioned, with a view to abstracting some particular point of information that may or may not lie concealed in their midst. For example Gravis[11] published a treatise, consisting of 285 quarto pages and illustrated with 23 plates, on the anatomy of *Urtica dioica*. The care and energy devoted to the preparation of this work are most praiseworthy, but the reader is left to wonder if this account of the structure of the Common Stinging Nettle would not have been much more useful if the essential facts had been presented more concisely. Then again Lignier[17] devoted 455 pages and numerous illustrations to the structure of the vegetative organs of the Calycanthaceae, Melastomaceae, and Myrtaceae. It is interesting to note that the pages of the copy of this book in the Kew library have never yet been cut, in spite of the fact that anatomists have been working at Kew from the date when the book was published until the present time. It is abundantly clear from Hocquette's[14] historical review that French anatomists have been much more numerous than is sometimes recognized. It is perhaps in the field of the anatomical approach to taxonomy that their maximum contribution has been made. We are generally apt to regard Radlkofer (1829–1927), of whom Solereder was a pupil, as the father of this branch of anatomy. Important as the Radlkofer-Solereder combination undoubtedly was in inaugurating this field of enquiry, the contribution from our French colleagues should not be overlooked. Hocquette prefaces his remarks on this subject with these words. "Mais en France, comme a l'étranger, le gros effort des anatomistes devait porter sur l'anatomie comparée et l'anatomie appliquée a la systematique. Ces deux genres de recherches sont intimement liés et intriqués qu'il n'est pas possible de les séparer." He then reviews the French contribution, referring to the work of Regnault, Vesque, Van Tieghem, Trécul, and other early workers, and, coming to more recent times, mentions 40 workers in the field between 1890 and 1940, stating that his list is far from complete.

Before leaving the more historical aspects of this survey, it should be noted that whereas the early stages in the development of plant anatomy took place in Europe, in recent years interest in the subject has spread to many other countries. We find wood anatomists at work in many parts of the world. There is in existence an International Association of Wood Anatomists with members from some 20 countries. We find a great interest in various branches of plant anatomy flourishing on the Indian Subcontinent, and Indian work has been comprehensively reviewed by Chowdhury, Rao, and Mitra[7]. Botanists on the Indian Subcontinent have a wonderful opportunity for developing the subject, as they have access to a

great wealth of tropical material that has hitherto received relatively little attention from anatomists. It is, however, abundantly clear from discussions and correspondence with Indian workers that they are handicapped by inadequate library facilities, and, as things are at present, it is very easy for work that has already been done to be repeated unknowingly. Furthermore, investigations on topics that really are new are unsatisfactory unless founded on the body of knowledge that already exists. Turning further eastwards we find anatomists in Japan studying the structure of a wide range of plants. It is, however, in the U.S.A. that some of the most important of the recent anatomical investigations have been undertaken, especially as a result of the stimulus provided by Irving W. Bailey, together with his pupils and colleagues. Bailey's writings inspire confidence because they are based on careful thought following thorough investigations. His long series of papers extend from 1909 until the present time. A selection of them was reprinted in 1954 with a biographical sketch of Bailey by Elso F. Barghoorn[4].

Bailey's work covers many aspects of plant anatomy and related fields, but one of his most notable contributions has been to show how the study of secondary xylem, and particularly of the nature, dimensions, and pitting of tracheal elements, is a reliable and essential tool in the study of angiosperm phylogeny. This is not the place to repeat the facts and line of reasoning on which Bailey's views are based, or the conclusions to which they lead. For further information the reader is referred to Bailey's own papers and the summaries by Metcalfe and Chalk, and Metcalfe[21–24].

Another aspect of Bailey's work that merits special attention at the present time is his insistence that the descriptive aspects of biology, and these of course include plant anatomy, are of real importance. Listen to what he has to say in his own words. "The compilation, codification and analysis of descriptive data and the formulation of valid correlations are not only of great practical significance in the development of the biological arts, but are indispensable in the visualization and definition of those fundamental problems which biology sets out to solve. Nor should it be inferred that this work when well done is of an inferior intellectual quality. The descriptive method requires capabilities and disciplines which are by no means inferior to those used in the exact sciences. In fact, the successful employment of cumulative circumstantial evidence—e.g. Darwin and the Theory of Evolution—demand qualities which are rarer and often more finely discriminating than those employed by the exact sciences."

Although there may be occasional individuals who can master modern physics and chemistry and a descriptive science, in Bailey's opinion this is an exception rather than a rule. When an individual attempts too much he so often tends to become superficial in all fields. According to Bailey "much of the so-called 'modern fundamental' biological research is unfortunately

an aimless puttering with quantitative methods and is unproductive from the point of view both of the descriptive sciences and of the basic experimental ones. The phenomena to be investigated are so complex and variable that, in many cases at least, they can be analysed accurately only through the active co-operation of a group of experts in physics, chemistry and biology."

Bailey's insistence that the descriptive approach in biology is a discipline of the utmost value should be noted. Furthermore, he has done well to emphasize that work of this type, if well done, calls for intellectual qualities of the highest order, in no way inferior to those that are necessary for the experimental approach. Bailey would have little sympathy for a Professor of Botany who advised only his second-class students to take up the descriptive approach, implying that his best students should not demean themselves by allowing their alleged superior intellectual abilities to be wasted on considering the mere form and structure of the biological material with which they have to deal. Unfortunately this type of advice is not altogether unknown, and, in consequence, there are all too few workers of first-class calibre in the morphological and anatomical fields today. No thinking botanist will want to return to the arid wastes of anatomical description without a purpose, but description undertaken with an object in view is the very life blood of plant science. For who can successfully classify plants without knowing their structure? Who can discuss phylogeny and evolution to any effect without first making himself master of a wealth of descriptive detail? Finally, who can understand the physiological working of even one species of plant, comprehend the delicate adjustment between that species and its environment, or fully appreciate what is involved in the transmission of characters from parent to offspring, without mastering the details of the form and structure of the species concerned? To draw theoretical conclusions based on the structure of plants is easy to a botanist who takes good care not to see too many "kinds" during his botanical career. Phylogenetic speculation, for example, is very easy until one has mastered a wealth of detail, and when this stage is reached the would-be phylogenist, recognizing his limitations, is less likely to broadcast theoretical views based on inadequate factual information.

Anatomical Specialization

There has been a tendency, probably inevitable, in recent years for plant anatomists to specialize in some particular field of enquiry. A perusal of the writings by some of the early anatomists already mentioned reveals how much more closely anatomy and physiology were interwoven than they often are today. This applies, for example, to Mirbel's[25] *Traité*, only a small part of which is anatomical in the strict sense. From the very beginning,

even in the time of Grew and Malpighi, attempts were made to correlate structure and function. With the interest in evolution that followed the work of Darwin and Wallace there was a change of emphasis, and those who were interested in the form and structure of plants, lacking a geological record that showed the course of plant evolution with any degree of completeness, attempted to fill the gaps in phylogenetic schemes by studying the comparative morphology and anatomy of present-day plants. Work of this kind generally involves considerable speculation, and, in the minds of many botanists, the study of morphology and anatomy has come to be associated with phylogenetic speculation rather than with physiological function. Unfortunately the phylogenetic interest led to the promulgation of conclusions which we have since come to realize were not justified by the factual information on which they were based. In consequence there has been much fruitless controversy concerning matters that can be neither proved nor disproved from the evidence of morphology and anatomy alone. Thus we find that much ingenious argument was devoted to discussing such questions as whether or not floral members are modified leaves; how far the stem consists of leaf bases; whether stems and leaves are organs of a fundamentally different character or whether leaves are shoot systems with mesophyll between the branches. The real weakness of most arguments on topics of these kinds is that, when we argue from comparative structure of present-day plants alone, there is no real evidence of the direction in which supposed phylogenetic advances have taken place. The series might just as well have progressed from *a–c* as from *c–a*. The fact is that theoretical discussions on phylogenetic topics, whilst intellectually stimulating to some minds, make little or no appeal to those who can see that argument might be continued indefinitely and prove nothing or very little. Herein lies one important reason why plant anatomy has become unpopular, for, in the minds of many, the study of form and structure is so intimately associated with unprofitable speculation. Purely conjectural reasoning of the type that we have just been discussing is a very different thing from the careful researches into angiosperm phylogeny on the lines adopted by I. W. Bailey, as we have already seen.

We must now return once more to an earlier phase in the history of plant anatomy to see how, and in what other specialized directions, the subject has developed. A good starting point for this purpose is the publication in 1877 of the first German edition of Professor A. de Bary's *Comparative Anatomy of the Vegetative Organs of the Phanerogams and Ferns*[9]. The well-known English translation of this book by F. O. Bower and D. H. Scott appeared in 1884. The publication of this great work, based largely on the researches of von Mohl, Nägeli, Sanio, Th. Hartig, and van Tieghem, can almost be regarded as the focal point for the start of the modern era of

plant anatomy. The book is essentially a descriptive work giving the solid facts of the anatomy of the Phanerogams and Ferns as they were known in de Bary's time. It contains but little theoretical discussion, and is concerned with the structure of mature plant organs rather than with the anatomical changes that they undergo during their development. Although de Bary fully recognized the importance of developmental studies, he says "It was more the object of this work to put the stage of development which is called mature to the fore, since the present overwhelming preference for the earlier stages has brought it about that in the 'voir venir,' the things themselves which are to be produced are neglected." We also find de Bary saying "From the older literature I have perhaps cited too much for many, and for others too little. But here also arose the necessity of keeping a definite limit, in order to bring something to completion. On the anatomy of plants such an indescribable amount has been written that, in a comprehensive treatise, one or many authors might be cited in reference to every word. To carry this through, even to the extent to which it is done in the section on Epidermis, makes the description exceed the bounds of convenience and overstep the limit of human power and endurance." This heartfelt cry must have been echoed in the minds of many anatomists since de Bary's time. The fact that de Bary recognized the need to condense and present as concisely as he felt it to be possible what was known of plant structure in his time is one reason why his book is so valuable. The specialized lines that we must now consider are (i) physiological anatomy, (ii) comparative anatomy, including wood anatomy, in relation to taxonomy, (iii) pathological and developmental anatomy. These aspects of plant anatomy cannot all be given equal treatment, partly because some of them have received more attention than others, and partly because the field is now so vast that an author is forced to say most about those aspects with which he has had first-hand experience.

(i) *Physiological Anatomy*

In the field of physiological anatomy we are once again indebted to a German writer for having produced a major work which was considered sufficiently important to be translated into English. This is Haberlandt's *Physiological Plant Anatomy* of which the last English edition appeared in 1914[13]. The main fault of this great work is that it was written from a standpoint that appears, to modern eyes, as too markedly teleological. In it we are told how the structure of a plant is related to the physiological activities that takes place in its various organs, and how the structure is adapted for life in specialized environments, particular attention being devoted to considering structural characters that are thought to be concerned with excessive loss of water to the atmosphere in a dry environment.

The construction of the plant is also considered from the mechanical point of view, and comparisons are made between the deposition of skeletal tissues, and girders, beams, and other units of construction employed by the engineer. In studying physiological anatomy it is often very tempting to jump to conclusions. For example it is so easy to think that stomata have become sunken in pits and that certain plants have developed a thick cuticle in response to arid conditions. This, no doubt, is true within limits, but that these conceptions are not of universal application is shown by the fact that stomata in plants from arid regions are not necessarily sunken, and the thickness of cuticle is not always proportional to dryness of habitat. Then again it is so easy to assume that the bands of large, inflated cells in the leaf epidermis of grasses—the bulliform cells—are "motor" cells concerned with the folding and unfolding or rolling and unrolling of the grass leaves in which they occur. Those who hold that the bulliform cells have a "motor" function should bear in mind that these cells often become filled with large masses of silica and that their outer walls are often thick and cutinized. Furthermore there are grasses such as *Ammophila arenaria*, of which the leaves are particularly prone to rolling and unrolling, but in which we find that the bulliform cells are not well developed. Bulliform and other translucent cells in the mesophyll are, on the whole, more developed in grasses from tropical countries than in those from temperate regions. Furthermore it has been shown, for example by De Coulon[8], that when *Nardus stricta* is grown under intense, continuous light the bulliform cells become much larger. These facts are quoted just to indicate how easy it is to jump to wrong conclusions concerning the probable physiological role of anatomical features. That some plants do show anatomical specializations by which they are fitted for life in a particular environment is undoubtedly true, but, on the whole, structural features appear to be determined by the hereditary make-up of the plants in which they are exemplified more than by responses to the rigours of environment. The author has developed this theme more fully elsewhere[23].

Since Haberlandt's time, interest in the relationship of structure to physiological function has continued, but no recent synthesis of our knowledge of this subject has been produced. In England the late Professor J. H. Priestley's school at the University of Leeds did much to develop the subject from a non-teleological standpoint. It is, however, a very great misfortune that physiological and anatomical investigations have not been more intimately associated in recent years, although there are signs in some quarters that physiologists are becoming more alive to the necessity for anatomical investigation as an aid in their studies. There is, however, still much to learn even about such basic topics as the paths and mechanisms by which water and foodstuffs move, or, as we more commonly say, are translocated

through the plant body. Do we yet really understand the mechanism by which sap ascends in a tree? Still less do we understand how the structure of phloem is related to the role of food movement, in spite of the important researches made in the U.S.A. by workers such as Alden S. Crafts and Katherine Esau to which Cheadle[6] refers in his recent review of research on xylem and phloem.

As Cheadle points out, research on the structure of phloem is very difficult because of the technical problems involved in handling phloem elements, particularly the sieve cells and sieve tubes. Elementary students often complain that they have difficulty in seeing or comprehending the structure of even the specially large sieve tubes of the Cucurbitaceae which are generally employed for class purposes. Because the Cucurbitaceae are so frequently used for introducing the student to the study of phloem structure there are comparatively few botanists who have any idea of the range of variation in the structure of sieve-conducting elements in the angiosperms alone. Still fewer can be aware of the complexities surrounding the ontogeny of sieve elements and of the parenchyma associated with them. We learn from Esau's careful and painstaking work that phloem parenchyma consists of cells of which the ontogeny is not uniform. We have known for many years that the component cells of sieve tubes—the sieve tube members—are enucleate when mature. They are also remarkable for containing cytoplasm with unusual staining properties; they have characteristic sieve areas on their walls; they appear to be relatively short-lived and become squashed when they form part of the bark and are ultimately sloughed off, often by phellogen activity. Furthermore, we find the phloem strongly supported by fibres in some plants and consisting wholly of soft tissue in others. It is clearly desirable for those who are interested in the role of phloem in the physiology of the plant to take the anatomical peculiarities of this tissue into account. The following words of Cheadle's may well be pondered by those who accept without question the generally held belief that the phloem is concerned with the translocation of foodstuffs. "In connection with the size of the lumen through which food substances presumably pass, it would be wise for students of translocation to consider the extraordinary thickness of walls of sieve elements in many species. Even after complete dehydration, many of these cells are so thick that the lumen is almost completely obstructed. This aspect of structure in relation to translocation is almost universally ignored, chiefly because such thick walls are not commonly present in the usual experimental plants. Here is a problem that needs critical attention." In this connection the author must draw attention to his own observation that the diameters of the sieve elements in certain grasses are exceptionally wide and in others quite narrow. If the diameter of a sieve element is correlated with its efficiency as a channel for the translocation of

food how is it that grasses with wide and narrow sieve elements respectively appear to thrive equally well?

We cannot here enter into further discussion of the relationship between structure and physiology. It must suffice to indicate by the few examples that have been given that we have much still to learn about plant structure before we can solve even some of the elementary problems of plant physiology.

(ii) *Anatomy and Taxonomy*

We have already noted that during the 19th and at the beginning of the 20th centuries many French anatomists recognized the important part that the microscopical structure of plants can play in studying their taxonomy. This tradition has been carried forward until the present time by a number of investigators. We cannot here review this work in any detail, but we may note that two of the earliest workers were Regnault and Vesque, the last of whom, according to Hocquette[14] wrote in 1881 "Il est possible de reconnaître la famille à laquelle appartient un végétal a l'aide des caractères anatomiques empruntés aux seuls organes de la végétation." Similar views were expressed by van Tieghem and Parmentier. By 1875 we come to Duval-Jouve's[10] *Histotaxie des feuilles des Graminées* which was a pioneer work on the comparative anatomy of grass leaves which can with profit be consulted by grass anatomists even today. We may also note the great interest in the vascular structure of the petiole as an aid to taxonomy, especially following the classical work of Petit[28]. It is a safe prediction that even now we have not heard the last word on the taxonomic value of petiole structure.

We have already noted that the subject of systematic anatomy received what was probably its greatest stimulus when Hans Solereder, Professor of Botany at Erlangen, published his famous *Systematische Pflanzenanatomie der Dikotyledonen* which was later translated into English and appeared in 1908[32]. This translation was partly undertaken by Boodle at the Jodrell Laboratory at Kew. If we may take a bold jump forward along our vista it may be noted that the author, in collaboration with Dr. L. Chalk of the Imperial Forestry Institute at Oxford, and assisted by various other workers, published a new, two-volume treatise on the anatomy of the Dicotyledons in 1950[24]. Since then the main subject under investigation at the Jodrell Laboratory has been the systematic anatomy of the Monocotyledons, which are to be covered in a book of several volumes, the first volume on the Gramineae being nearly ready for the press. The only previous book on the comparative anatomy of the Monocotyledons is the important but incomplete treatise by Solereder and Meyer[33].

The anatomical approach to taxonomy has at all stages been stimulated by the practical necessity of maintaining standards of quality and detecting

adulteration or substitution in economic products of vegetable origin. The traditional methods of the herbarium botanist cannot be employed to identify a timber or to detect adulterants in powdered herbs. The anatomical method also finds applications in assisting archaeologists to establish the botanical origin of manufactured articles and other materials obtained during their excavations. It is also, in certain circumstances, possible to identify the partially digested remains of vegetable foodstuffs taken from the bodies of dead animals when it is suspected that their death may have been caused by poisoning. The feeding habits of animals such as foxes and rabbits can be studied by identifying particles of vegetable matter in their excreta. The solution of problems such as these, and even to give anatomical assistance in the detection of crime, have, for many years, been everyday activities at the Jodrell Laboratory. It is surprising how infrequently the attention of botany students at universities is drawn to these applications of plant anatomy. This would surely increase their interest in plant structure and also broaden their outlook.

We must, however, content ourselves with noting that these important practical applications exist and pass on to discuss some more fundamental issues raised by the impact of anatomical studies on the field of taxonomy. Here we may first note that if our systems of classification are to be something more fundamental than aids to the accurate identification of the species that exist in the world today they must take the geological record into account. The integration of palaeobotanical discoveries into taxonomy is of fundamental importance, and the closer the link between palaeobotany and taxonomy the better. Since many palaeobotanical specimens are known only as remains of vegetative organs it is clearly evident that an intimate knowledge of the structure of both palaeobotanical and present-day plants is a necessary preliminary to strengthening the link between these two branches of knowledge.

Although taxonomists are coming more and more to recognize the value of the anatomist's contribution to their subject, there are still some who would enquire whether anatomy is really necessary. Here we must first reiterate that classification should be based on as many attributes of living organisms as can be conveniently studied if it is in any degree to reflect the true affinities of the organisms concerned. As is only to be expected the external form of a plant generally provides the most essential characters in taxonomy, and no anatomist should aim at basing a classification solely on internal or microscopical characters. It has, however, repeatedly been shown that anatomical characters serve as a key to the affinities of a plant when other methods fail. For example, much confusion and doubt in the classification of the Gramineae is being eliminated by the intelligent use of microscopical characters of their leaves.

It is often difficult for a taxonomist whose knowledge of plant anatomy is limited to realize just wherein the strengths and weaknesses of the microscopical approach are to be found. The author has frequently been asked by taxonomic colleagues to help them to solve specific taxonomic problems and has been unable to do so. Why should this be? Firstly, the difficulty arises when the habit or general form of the plant is such that it does not yield much in the way of anatomical data of taxonomic significance. This applies, for example, to slender herbs without any very distinctive microscopical characters. One can learn very little about the affinity of *Adoxa moschatellina* from a study of its anatomy. This type of difficulty is, however, very small compared with that which is due to the incompleteness of our knowledge of the vegetative organs of a large proportion of the plant kingdom. During the last 28 years we have, at the Jodrell Laboratory, built up a reference collection of over 20,000 microscope slides, and, with the aid of this collection, and what we know of the structure of plants from the literature, it is possible to solve a great many taxonomic problems, but we repeatedly find ourselves at a standstill just because the necessary microscope slides are not available. It is always possible to prepare more slides and solve many problems that are at present beyond us, and this is in fact being done. However, the problems are numerous and it takes time to make the slides, especially when, as so often happens, the only material available consists of herbarium specimens in which the structure is so distorted that reliable observations are impossible. Meanwhile the hard-pressed taxonomist is apt to lose interest unless the necessary information can be made available at short notice and the matter drops. The present position of a systematic anatomist is, therefore, like that in which a herbarium botanist would find himself if he had to work in an inadequately stocked herbarium. It is a safe prediction that as more anatomical knowledge is made quickly and easily accessible by building up reference collections of slides, and the publication of more data in reference books or on index cards, we shall be forging a tool that will place the anatomist in a much stronger position to aid his taxonomic colleagues.

Another current difficulty is that qualified anatomists are so few that they can scarcely keep pace with the great output of taxonomic work that is being produced by a very much greater number of taxonomists in various parts of the world. The mere problem of trying to keep up to date with taxonomic revisions and changes of names adds considerably to the burden of the systematic anatomist. Difficulties of these kinds are inevitable, but they could be reduced, and it would be to the mutual advantage of all concerned if there were more widespread collaboration between herbarium taxonomists and systematic anatomists. What seems to be needed is a better balance between the work of herbarium botanists and those who approach

taxonomic problems along lines other than that which is traditional amongst herbarium workers. Taxonomic revisions which incorporate the outcome of several different lines of investigation would take longer to complete, but the results would tend to be more balanced and as scientifically accurate as it is possible to make them. There has, in recent years, been a tendency for taxonomists and wood anatomists to work in close collaboration, but, valuable as this collaboration undoubtedly is, something more is wanted. Wood is only one part of the plant body. Nevertheless there is sometimes an unfortunate tendency to treat wood anatomy and systematic anatomy as being synonymous, ignoring the fact that important taxonomic evidence can also be obtained from studying the leaf, young shoots, and other parts of the plant body, including the microscopy of the flower and fruit. Furthermore, the evidence provided by wood structure is of comparatively little value when dealing with herbs.

(iii) *Pathological Anatomy and Developmental Studies*

Curiously enough the study of abnormal structure induced by pathological organisms has seldom been treated as an aspect of plant anatomy that is worthy of investigation in its own right. The subject was dealt with by Dr. Ernst Küster in his *Pathologische Pflanzenanatomie*[16], a comparatively rare book with which many present-day anatomists are probably unfamiliar. Nevertheless this aspect of plant anatomy merits renewed attention, not, as so frequently happens, just as a sideline to investigating the ravages caused by plant pathogens. It would seem that a more intimate knowledge of the morphological and anatomical changes induced by pathogenic organisms, and of the mechanisms by which they are produced, apart from being of great interest in themselves, might help to throw further light on the causes that control the normal differentiation of plant tissues. This would serve to connect the study of pathological anatomy to the active research into the study of tissue differentiation and developmental anatomy which is already in progress.

The changes by which the fertilized egg of the higher plants becomes gradually transformed, first into an embryo and then into a seedling, have been investigated over a long period of years by a considerable number of botanists. The earlier work on descriptive embryology has been exhaustively summarized by Schnarf[31]. Also the very detailed work by Souèges[34], is especially worthy of note, for the care with which he has studied the course of the cell divisions in plant embryos can seldom have been equalled. In recent years a vigorous school of plant embryologists has grown up in India under the influence of Professor P. Maheshwari, who has provided us with a well-known textbook on the subject[18]. D. A. Johansen's[15] book on plant embryology is also a noteworthy

contribution to the literature. In England, Professor Wardlaw, the most recent of whose well-known books deals with embryogenesis[35], besides adding to our knowledge of plant embryology and tissue differentiation from the descriptive standpoint, has also approached these subjects from the all-important experimental angle. At the present time, so much interest has been aroused in the experimental approach that it seems likely that this is one of the lines of investigation from which much useful knowledge is yet to be expected. From this point we are led on to the study of the growth of detached tissues in aseptic cultures, but we must content ourselves here by merely drawing attention to this line of enquiry.

Although we are familiar with the micro-morphological changes involved in the development of tissues and organs, we must face the fact that we know practically nothing of the underlying causes of the changes that are involved. We can rightly take a pride in the great strides forward in biological thought and discovery that have been made in recent years and which are still continuing. The border where physics, chemistry, and biology meet is being explored, and it would be rash to predict where these investigations will ultimately lead us. The enormous magnifications that are now obtainable with the electron microscope help us on the one hand to understand something more of the structure of large molecules and the submicroscopical structure of cell walls. Indeed the electron microscope enables us to contemplate the structure of plants from a new point of view, and it may well become a major task in the future to reinterpret all that we know of plant structure in terms of what the electron microscope is beginning to reveal. In our pride at these achievements we should, however, remember that these investigations are taking us farther and farther away from the study of whole plants, and, after all, the whole plant should remain the botanist's chief interest. We must, indeed, take the utmost care not to lose our sense of proportion and perspective.

We are all aware that a cambium cell in a young dicotyledonous stem divides repeatedly, and that the derivatives cut off from it on one side turn into xylem elements and that those cut off from it on the other develop into phloem. Furthermore we know that phloem and xylem are complex tissues made up of cells of entirely different types with specialized roles to play in the metabolic economy of the plant. Our very familiarity with the fact that these totally different and complex tissues are derived from the same cambium cells blinds us to the wonder and apparently almost miraculous nature of the changes involved. Our wonder should be increased still further when we consider the deviations from the normal behaviour of cambium that are to be seen in stems whose girth increases by histological changes that are termed "anomalous." We may well ask ourselves what has caused these subtle deviations from the normal to have taken place.

Marvellous as they are, the changes involved in the transformation of the derivatives of cambial cells into the various forms that they assume when they are mature are far less remarkable than those involved in the transformation of a fertilized egg cell into a giant forest tree. The understanding of these changes is worthy of investigation by all of the scientific methods at our disposal. It remains to be seen, however, whether scientific methods, as we know them at present, will lead to a complete understanding of these questions. Is there, in fact, a limit to what can be comprehended or revealed by scientific investigation alone?

CONCLUSION

At the outset of this review attention was drawn to the comparative unpopularity of the anatomical approach to botany. We then started along our vista, and, during our passage along it, we have seen something of the historical development of the study of plant structure. This vista is only one of many that might have been drawn. We might, for example, have considered more carefully the important subject of floral anatomy; we might have delved more fully into the details of recent histological techniques; we might have considered more fully how important it is for studies in systematic anatomy to be accompanied by investigations in cytotaxonomy or even in biochemistry, for the plant body is, after all, a more or less stabilized system of the products of metabolism and biochemical reaction. All vistas must, however, have an ending and ours is already quite long enough. In passing to and fro along it in the course of our discussion we have paused here and there to look to the right and left up side alleys, to catch glimpses of distant panoramas, and to see how our vista is related to some of the others of which botanical science is composed, noting how close is the connection between anatomical investigation and many other lines of botanical enquiry. In the course of our travels we have seen how many directions there are in which exciting and useful anatomical discoveries have yet to be made.

To the author it seems that, besides the reasons already mentioned, the comparative lack of interest in plant anatomy is partly due to the singularly dull way in which the subject is so often presented to students. The spirit of adventure and enquiry is so often lacking. The subject is presented in the form of a mass of dull facts, the student is left with little idea of how much has yet to be discovered, furthermore many of the items that he is told that he "must see" under the microscope are often obscure. Then again he is asked to work with microscope slides prepared by a technician from material that the student himself has not seen or handled. The author had the great good fortune, at the outset of his botanical career, to be introduced to the study of plant structure along quite different lines, for he was encouraged to

study the structure of plants that he himself had collected, in microscope slides prepared by himself. The spirit of enquiry formed the very basis of these activities, which were purely voluntary and did not form any part of the official school curriculum. It was so stimulating to be asked to discover in what respects the stem of one plant differed from that of another, or to try to find out how the structure of plants was related to the habitats in which they were growing. Even such common, everyday objects as a banana skin or orange peel acquired a new interest when their structure came to be examined. Once a beginner's interest has been aroused by simple enquiries such as these, it is only a question of time before he can be led to more complex investigations, and, with his enthusiasm aroused, to follow them through with intelligence and zeal. How different this is from memorizing a mass of facts as a preliminary to sitting for an examination! Memorizing is necessary, however, but after a time this becomes a pleasure rather than a curse. It is an invaluable exercise to picture to oneself the histological details of the plants encountered on a country walk, in a garden, or wherever one may happen to be. What, one may ask oneself, are the diagnostic characters of the wood of this birch tree; why has this buttercup flower such glossy petals; what will be the appearance of this grass leaf in transverse section. On an autumn day the slipperiness of the wet leaves that have recently fallen from the lime trees in a suburban avenue should serve as a reminder that the leaves contain cells that are filled with mucilage. Nobody can memorize the answers to all of the many questions that present themselves, but the mental exercise of trying to do so can be a most valuable discipline. It should also be remembered that the old-fashioned habit of making accurate drawings of objects under the microscope is one of the greatest aids in building correct mental pictures of plant structure. It is amazing how much can be learned if one be armed, like Nehemiah Grew, with "a good eye, a clear light and a Rasor wherewith to cut." It might be added that a sharp knife, a safety razor blade and a really good hand lens are the most useful tools in the field in modern times. Supplementary studies can be made later in the laboratory.

To many readers much of what has just been said may appear very elementary and self-evident. To the author, however, it seems that the current tendency to replace what is simple and obvious by what is complex and difficult is a serious barrier to further progress. We are so apt to learn the latest views concerning the molecular structure of the cell wall before we know very much about the cells themselves and the way they are arranged in the plant. We must also remember that it is the duty of the anatomist to carry forward our present knowledge as well as to add to it.

It is hoped that the experience of passing through this anatomical vista may provide some stimulus to those whose interests already lie in the field

of plant structure. Perhaps it may help them here and there to see their own studies in a new or broader perspective. Furthermore it is hoped that all who study plant anatomy may come to realize that they are taking part in an exciting adventure, a voyage of exploration in miniature. Finally, it is hoped that perhaps even those who may regard plant anatomy as a dull, outmoded discipline may pause, and come to realize that the anatomist is able, after all, to add something that is valuable to our rapidly expanding body of botanical knowledge.

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PLANT BIOCHEMISTRY

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INTRODUCTION

IT was F. G. Hopkins who first recognized a distinction between the static and the dynamic aspects of biochemistry, later developed by E. Baldwin, one of his many distinguished pupils, in his well-known book *Dynamic Aspects of Biochemistry*[3]. Sinnott and Wilson[51] take a similar view of the subject of botany itself when they write: "Modern botany is concerned with the plant not so much as a static structure, to be cut up, picked apart, and described, but as a dynamic living system—functioning, growing, and reproducing itself." This dichotomy is especially valuable when one is faced with the task of attempting to discern trends in Plant Biochemistry, and where the great opportunities for progress appear to lie. As Baldwin points out, a "static" phase—the discovery of the nature of the building stones of which living organisms are composed—must necessarily precede the "dynamic"—the discovery of the interrelationships of the different constituents and the way in which they interact to produce the manifestations of life. Much—very much—has still to be done in identifying the building-materials themselves. The plant biochemist is continually made aware of the diversity of form and content in the individuals and species he is called upon to study; to the animal biochemist, mainly concerned as he is with the human subject or a few closely related mammalian species, this is a less compelling consideration. Much of plant biochemistry is therefore still concerned with straightforward isolation, identification, and analysis, and the dynamic aspects, with a few striking exceptions which fall within the province of plant physiology, are for the most part concerned with attempts to discover to what extent processes analogous to those first found to operate in animal tissue can be discerned in the plant.

A reviewer of the present state and future prospects of plant biochemistry must necessarily find himself preoccupied, therefore, with the question of form: how it is reflected in the chemistry of the plant; how it can be depicted or explained in terms of chemistry; and by what chemical processes it might be mediated. The logical treatment of the theme is, therefore, from a consideration of the chemical constituents of plants to the variations of these constituents in different plant forms and thence to a consideration of the processes by which diversity of form might arise.

I. THE CONSTITUENTS OF PLANTS

It is in this department, more than any other, that spectacular advances have recently been made, due to the introduction of chromatographic methods. Paper chromatography, which enables substances of low molecular weight to be separated and isolated in amounts sufficient for their structure to be ascertained, or to be immediately recognized by simple chemical tests, is the best known and most widely used of these methods. It is doubtful, however, whether even now the potentialities of this method in plant biochemistry have been fully realized and exploited. Equally valuable, but still further from full exploitation, are the methods of separation of substances of high molecular weight such as proteins and polysaccharides. In this case electrophoresis is an even more powerful tool than partition, ion-exchange, and absorption chromatography, which come into play when the smaller units from which the large molecules are built up are separated and analysed.

The constituents of plants can be conveniently divided for discussion into high-molecular and low-molecular groups; and the former divided again firstly into proteins and polysaccharides, and secondly into other less well-defined classes of constituents.

(a) *Proteins and Polysaccharides*

The customary procedure for the examination of these constituents is to fractionate the complex mixtures in which they usually occur by methods depending on differential solubility or differential reactivity, and to establish the homogeneity of the product by every available and relevant criterion. Centrifugal sedimentation and electrophoresis are powerful tools in the separation of soluble high-molecular constituents, and the removal of unwanted contaminants by the action of selective enzymes is equally valuable in the isolation and purification of the insoluble structural constituents. Often, and especially in the case of enzymes, the gradual enrichment of a specific functional property is employed as a criterion of increasing purity or homogeneity of a particular constituent; or the gradual impoverishment of a suspected contaminant may be the best criterion of improvement in purity. In the case of enzymes, care has always to be taken to avoid the removal of, or to replace, essential co-factors, and care has always of course to be taken to prevent changes such as denaturation which may alter not only the physical but also the chemical properties of the constituent.

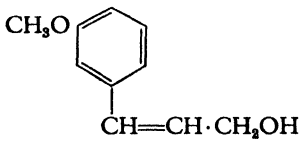
The progress that is being made in isolating and characterizing individual proteins is illustrated by the number of crystalline enzymes listed by Dixon and Webb[18]. In 1957, when their book was written, there were already more than 120 such preparations recorded, about a score of them from the tissues of higher plants. The first crystalline enzyme to be prepared was, in

fact, a plant enzyme, jack bean urease (Sumner[53]). Dixon and Webb's book is so recent and comprehensive in its account of the methods now being used for the preparation and purification of proteins that no more is required here than to refer the reader to it.

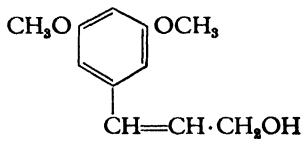
Of the plant polysaccharides, starch and cellulose have received the most attention in detail. These are relatively easy to isolate, from favourable sources, in a state of purity. It is the great variety of lesser-known polysaccharides, usually present in complex mixtures, which constitute a difficult problem for the plant biochemist. Insight is being gained here from a combination of physical with biochemical methods, and a good example of the use of these methods is provided by the work of R. D. Preston and his school on algal cell wall[48, 17]. The cell-wall material is fractionated into fibrous, sub-crystalline elements and amorphous ground substance by step-wise extraction and oxidation procedures, the progress of degradation being followed by X-ray analysis and electron microscopy. The several fractions are then further degraded to the component simple sugar residues, and these, like the amino-acid residues of the proteins, are identified and determined by the chromatographic methods which will be described later.

(b) *Other High-molecular Constituents*

Some of these have provided unprofitable puzzles for many generations of chemists. Lignin, many tannins, and resins, for instance, have proved unsusceptible to the methods which have yielded answers in the case of proteins and polysaccharides because they do not fall apart into their primary building-stones when they are digested with acids, alkalis, or enzymes; the precursor molecules, whatever they may be, are altered in the process of condensation and the products resemble the huge molecular complexes formed in the polymerization of plastics. Nevertheless, these problems are also yielding to a combination of analysis of degradation products and inference from the behaviour of likely precursor molecules when these are administered to the plant. The name of Freudenberg will always be associated with these studies. So far as lignin is concerned, it is not yet possible to say how far his hypothesis of the origin of this constituent from coniferyl (I) and syringyl (II) alcohols will be justified, but it is already



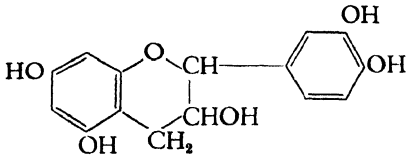
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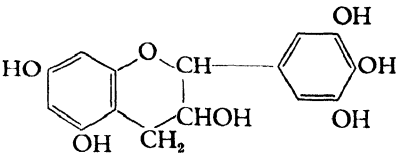
(II)

fairly certain that the precursor molecules are substances containing nine carbon atoms in the same phenylpropane configuration and with the same

pattern of hydroxyl and methoxyl group substitution. The probable nature of the condensed tannins has, however, recently been elucidated, largely with the help of chromatographic methods. The elementary analysis of these tannins, and the properties of the catechins (III, catechin, IV, gallo-

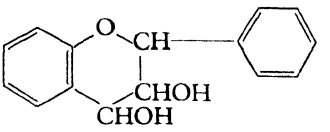


(III)



(IV)

catechin) had suggested these as likely constituents of the condensation product responsible for the tanning action of many commercial tanning materials, but it was only with the recognition of the presence of leucoanthocyanins in these materials (Hillis[36, 37]; Roux[50]) and of the tannin-like properties of their condensation products (Bate-Smith and Swain[9, 10]) that the probable origin and constitution of these substances has been revealed. The monomeric precursors of these tannins are, in fact, hydroxycatechins of the general configuration V:



(V)

They are most commonly substituted by hydroxyl groups in the configurations corresponding with catechin (leucocyanidin) and gallocatechin (leucodelphinidin) (Bate-Smith and Metcalfe[8]).

(c) *Low-molecular Constituents*

It is sometimes said that almost every substance mentioned in Beilstein's *Handbook of Organic Chemistry* is to be found somewhere in the plant world. But to regard this as occasion for despair is to overlook the fact that some are universally present, the presence of many is causally related to metabolic processes which are well understood, and many others are restricted in their occurrence to obviously related species of plants and can therefore be employed as signposts to affinity between species.

Historically, the sugars and the plant acids were among the first of the low-molecular constituents to be isolated, studied in detail, and analysed. The simpler alkaloids and the esters and terpenes (as the constituents of essential oils) followed, and then plant dyestuffs and amino-acids. In these instances the powerful influence of medicine and industry can be discerned, but in the case of the anthocyanin pigments of flowers, it was the opportunity

for the skill of the chemist and the enquiring mind which provided the driving force. Structures of ever-increasing complexity could now be tackled, and the most complex alkaloids, the carotenoids, the sterols, and finally chlorophyll itself have fallen before the chemists' attack.

The task of recognizing and estimating these and most other constituents of plant tissues has been made incomparably easier with the aid of chromatography. Many new constituents have been revealed—many, in fact, still awaiting the assignment of a chemical structure. And, above all, it is now possible to see at a glance constituents which are consistently present, and presumably, therefore, implicated in essential metabolic processes.

Apart from the recognition of already known substances, paper chromatography is proving of the utmost assistance in establishing the structure of newly isolated compounds. There are three ways especially in which this method can afford guidance in identification. The first is the application of "spot tests" such as ninhydrin for amino-acids, ammoniacal silver nitrate for phenols and sugars, aniline phthalate and naphthoresorcinol for sugars, diazo reagents and ferric-ferricyanide for phenols, bromthymol blue for acids, and so on almost indefinitely.

The second is the R_f value in a diversity of solvents. These can be aqueous, alcoholic, or phenolic; acid or alkaline; various hydrocarbon or chlorohydrocarbon solvents, aided by buffering or chelating treatments of the paper with such substances as borax, potassium phosphate, or aluminium hydroxide. The R_f is characteristic of a particular substance, and the direction and extent to which the R_f differs for a substance of the same chemical class gives a valuable indication of the nature of the difference between an unknown and a known compound. Thus a hydroxyl group will lower the R_f in an alcoholic solvent whereas an alkyl group will increase it; a phenolic hydroxyl group will lower the R_f in an aqueous solvent while an alcoholic group will increase it. The sugars afford an exceptionally good example of the way such principles as these can be used to predict the constitution of an unknown member of the class. Pentoses, hexoses, disaccharides, trisaccharides, fall each within a particular range of R_f values in any one of a number of solvents. A selection of solvents will soon show to which class it belongs, and an accurate measurement of the R_f interval between the unknown and one or more known members of its class will often narrow down the possibilities of its identity to a point approaching certainty (cf. Jermyn and Isherwood[39]; Isherwood[38]).

The third way in which paper chromatography can be of value in the elucidation of structure is in the identification of degradation products, especially if the course of reaction is followed by examining samples taken at intervals from the reaction mixtures. If, for instance, a peptide is being studied, not only can the individual amino-acids be identified in the

completely hydrolysed end-product, but the partially hydrolysed fragments can be displayed and characterized giving information about the number and sequence of the component amino-acids. Another useful application is in following the removal of methyl groups from methoxy compounds, when more than one of these groups is present. The number of different intermediates that might be formed in the course of demethylation of a trimethoxy compound, for instance, would be six, and if some of the intermediates as well as the end-product were known and recognizable, much useful information could be gained regarding the configuration of the original compound.

Some recent work in which all three of these methods are invoked is of especial interest to plant geneticists. This is by J. B. Harborne[31], and concerns the identification of the anthocyanins present in flower petals. Quite remarkable uniformities are recorded in the chromatographic behaviour of the corresponding glycosides (e.g. the 3, 5-diglucosides or the rhamnosides, rhamnoglucosides, galactosides, arabinosides, etc.) of the six principal anthocyanidins.

These are by no means the only new methods that are now available to the biochemist. The wealth of information so rapidly accumulating as a result of the application of such methods imposes a corresponding requirement for codification and regimentation. This requirement was well appreciated by the late K. Paech, and he had already, in his book on the biochemistry and physiology of the secondary plant compounds[45], published in 1950, provided a masterly summary of the existing information. The larger work edited by Paech and Tracey[46] expands this information into the scope of a work of reference. As is clearly stated in the introductions to these works, it would have been Paech's aim and endeavour, in due course, to complete the codification of the constituents of plants, and to illuminate the significance of the immense diversity of these constituents by generalizations as to their biosynthesis and specific functions.

II. THE ARCHITECTURE OF PLANTS

The constituents considered in the preceding section are differentially distributed. In unicellular plants, and within the cells of higher plants, perceptible differences in structure at the microscopic and submicroscopic level can be translated into chemical terms by histochemical procedures and biophysical techniques of separation. In multicellular plants there is usually a separation of function from one part of the plant to another and usually also there are distinct supporting elements often composed of, or containing, dead cells and incrusting materials. The interpretation of these features of the architecture of a plant in chemical terms is an essential element in

biochemistry, and one which must be interposed between the static phase of descriptive chemistry and the dynamic phase of physiology.

In this aspect of plant biochemistry a difficulty is accentuated which always confronts the chemist investigating natural products—that of separating the wanted substances from the unwanted. The "wanted" material may be a particular kind of cells associated anatomically with other cells of an entirely different kind, and the biochemist is often faced with a choice between, on the one hand, a whole lot of tedious dissection, and on the other hand, the task of coping with a generalized homogenate. These problems are particularly met with in the study of cell-wall and incrusting materials, and provide the main reason for the intractability of these materials to chemical elucidation. Advances are, however, being made: a combination of refined histochemical studies alongside relatively gross chemical treatments will solve one problem; a "trick" may be found to prepare single-cell suspensions or to strip off uniform cellular layers of, for example, epidermal cells. Another ingenious "trick" has been devised which enables the sieve-tube fluid of the stem of a plant to be analysed. This consists in allowing an aphis to start feeding (its mouth parts being accurately positioned in a sieve-tube cell), then to cut off the stylet and collect the droplets of fluid exuding therefrom (see later, p. 110). In this way a localized chemistry of plant tissues is gradually being built up, as well as a knowledge of the variability of composition from one discrete organ to another. Much information is being obtained, for instance, of the chemistry of pollen, of flower-petals, of seeds (especially of the different anatomical fractions of the wheat grain), and of the relatively homogeneous parenchymatous tissue of such large organs as apple fruits and potato tubers. Mention must also be made of the microchemical studies of apical meristems.

(a) *Macrostructure*

In terrestrial plants architectural problems are mainly concerned with the mechanical stresses and strains which have to be supported. In the higher plants, therefore, particular interest attaches to the structural devices and materials employed in providing for these requirements. The "fabric" is always of an essentially carbohydrate nature—cellulose, pectin, chitin, and so on, but the cementing and incrusting materials employed for imparting strength and rigidity are fascinating in their variety. Most are organic, but some, such as lime and silica, are inorganic. The means employed for these purposes are highly characteristic of the class of organism, often characteristic of smaller divisions even down to the species level, so that they may be used in taxonomy and as a help to identification. In the vascular plants the most widespread and characteristic are the structures employing aromatic compounds in the process of lignification. It is now becoming apparent that not

only the complex substance known as lignin, but also tannins and extractives nearly related to the tannins in their chemical nature are concerned in this process, and that the composition both of lignin itself and of these other incrusting substances varies characteristically from one taxonomic group to another.

(b) *Microstructure*

The architecture of the single cell is just as important in its own way as that of the complete organism. The diagrammatic representation in fig. 1 gives

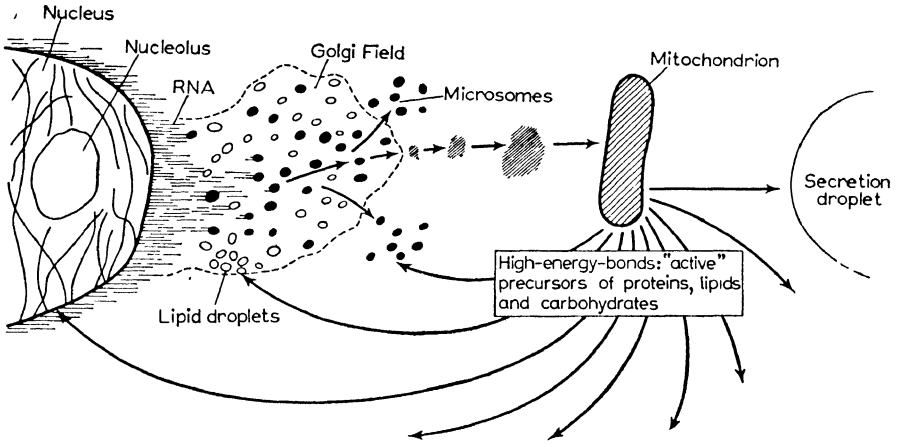


Fig. 1. Diagram of the formation of cytoplasmic particles and their interaction with other elements (after Lindberg and Ernster). (Oparin[44].)

a good idea of the kinds of structure that can now be recognized within typical cells of both plants and animals. Definite functions can be assigned to the different cytoplasmic particles: microsomes are associated with protein synthesis, mitochondria with intermediary metabolism and cytoplasmic secretion (Hackett[30]). In plants, mature cells contain a vacuole, often very large relatively to the protoplasm, the origin of which is obscure, but which probably arises from the enlargement or fusion of secretion droplets (Küster[40]). This constitutes an internal aqueous environment very different in composition from the aqueous phase of the cytoplasm, but providing a regulating mechanism for the ionic composition of the cytoplasm against changes in the external environment (see e.g. Briggs and Robertson[14]). Recognition of the spatial distribution of constituents between the protoplast and the vacuole is a highly important aspect of biochemistry, and of course immensely important also to the physiologist. Furthermore, the constituents of the vacuolar sap are, often, highly distinctive of the classes and lower taxonomic ranks of plants, and great strides are being made at the present time in recognizing and classifying these varied and distinctive materials.

Apart from the regularly formed elements common to most living cells, there are in plant cells specific bodies such as chloroplasts and other plastids. These are being examined in finer and finer detail by the biochemist, the chloroplast especially in relation to the process of photosynthesis (see p. 109). Other important inclusions are tannin bodies, starch and aleurone grains, and crystals of various kinds, which are of considerable diagnostic importance to the plant anatomist (Metcalfe and Chalk[42], pp. xvii–xix). These, and the distinctive contents of the vacuoles of many plants are dealt with comprehensively by Küster[40]. It is clear, however, that most of the data of this kind are at present descriptive rather than analytical, and their diagnostic value would be even greater if the chemical nature of these cellular inclusions were better known and more easily ascertained.

III. SOME PLANT PROCESSES

Many of the events taking place in plant tissues are similar, at the biochemical level, to those taking place in the cells of other living organisms. In considering plant biochemistry specifically, therefore, we need pay attention only to processes which are peculiar to plants, those indispensable to plant life specifically. We are, here, in territory common to biochemistry and physiology, and it is permissible therefore to select only a few aspects of particular biochemical interest from the many aspects of the physiology of plants into which biochemistry enters.

(a) *Photosynthesis*

The biochemical aspects of photosynthesis are at the moment subordinate to the biophysical; the essential unknown is the precise way in which radiant energy is converted into chemical. (The state of this problem is very like, in fact, that of the conversion of chemical into mechanical energy in muscular contraction.) The main biochemical pathways of photosynthesis are now, especially as the result of Calvin's[4] work with radioactive carbon, well established; the chemistry of the substances participating is becoming increasingly known; and it is now for the biophysicist, with the aid of the electron microscope and by the analysis of the interchanges of molecular energy, to elucidate the molecular fine structure and the mode of transfer of one form of energy into another.

The first step in the conversion of carbon dioxide into carbohydrate is the linkage of CO_2 to ribulose diphosphate to form two molecules of phosphoglyceric acid, thence through a 3-carbon sugar stage to hexose, pentose, or a 7-carbon sugar sedoheptulose, all of which link up directly with the processes of intermediary metabolism common to many forms of life. This first step is carried out in a highly ordered complex of chlorophyll, protein and lipid having a lamellar structure, organized in the higher plants into small bodies

of approximately spherical form known as grana, many of which are present in each chloroplast. The arrangement of electron-dense material, after staining with osmium tetroxide, within and between the grana is shown diagrammatically in fig. 2. The distances and optical properties are consistent with the view that the structure is that of a double protein layer with lipoid between, a structure reminiscent of the retinal rods, the light-absorbing elements of the vertebrate eye.

This analogy may be even closer when we consider the presence in chloroplasts of various accessory pigments. In diatoms the carotenoid pigment fucoxanthin is present, in the red algae the haem pigment phycobilin, in

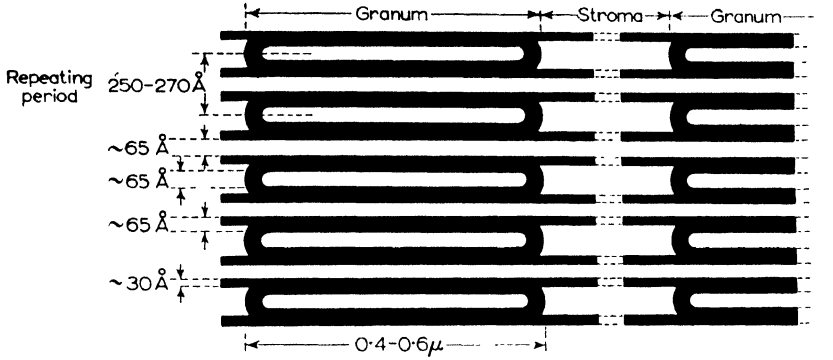


Fig. 2. Diagram of chloroplast structure according to Steinmann and Sjostrand (1955). (Whittingham[57].)

higher plants xanthophyll and β-carotene. The precise function of these pigments is unknown but it is significant that in each case the wave-length of the fluorescent light emitted by the primary pigment is within the range of absorption of the secondary pigment. "It is probable that chlorophyll *a* is the pigment most directly concerned in the photosynthetic process, the other pigments thus serving to extend the range of wave-lengths which may be utilized by the plant" (Whittingham[57], p. 323).

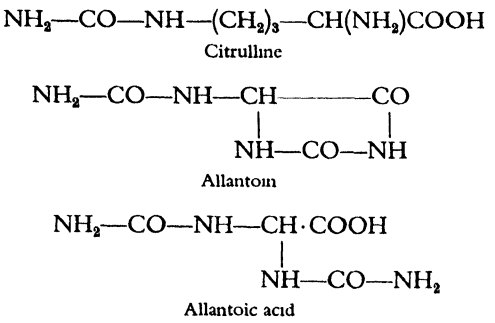
It does seem that the operative parts and the structure of the photosynthetic machinery are fairly well known, and that advance in knowledge of the way the machine works will continue to be rapid.

(b) *Transport of Nutrients*

Plant cells other than those endowed with the ability to utilize solar energy have to be supported by nutrients translocated from the areas of photosynthesis. In vascular plants the route for such translocation is, presumably, through the tubes of the phloem. The question is: What is translocated? Attempts to answer this by analysis of the exudates from cut surfaces have always been frustrated by the uncertainty as to the precise origin of the

exudation, but it now seems possible that the exudate draining from the stylets of aphids may represent the contents of the sieve-tubes, uncontaminated by any contribution from neighbouring tissues. This method, studied in detail by Kennedy and Mittler (see Mittler[43]), is now being applied by P. E. Weatherley and his students to the analysis of the sieve-tube fluid of willow stems[56]. It appears that this fluid contains sucrose and amino-acids as its main organic constituents, but other classes of substances have not yet been examined and it will be interesting to learn whether organic acids, phenolic compounds, and the like are also translocated from the sites of photosynthesis to the actively-growing and differentiating tissues.

As regards transport of nutrients from the root system via the xylem, Bollard[13] has observed that nitrogen is translocated in various forms in different species of plants. Glutamine and asparagine are quantitatively the most important, but some saps contain citrulline, allantoin or allantoic acid as a major constituent. The last three are derivatives of urea:



All these organic nitrogenous compounds are formed in the root from inorganic nitrogen assimilated from the soil. A question one would like to have answered is whether in such species nitrogen is translocated from the leaves in the same form as that in which it is translocated from the roots. The aphid stylet technique should be able to supply the answer to this question. As Bollard[12] points out, we do not know whether the shoot requires nitrogen in some specific organic form for its development, or whether all it requires is a bulk supply of organic or inorganic nitrogen.

(c) *Transport of Growth Factors*

It is generally accepted that auxins synthesized in the leaves are translocated throughout the plant and initiate the development of roots, vegetative buds, and flowers. These growth factors, some of them of known constitution must be only a few of the low-molecular substances transported in the sap, and exerting an influence on tissues widely separated from the organs in which they are synthesized. It is not unreasonable to suppose that ascorbic

acid and nicotinic acid, for instance, might be so transported, and hypothetical substances such as florigen and vernalin have been postulated in order to account for the facts of flower induction and vernalization. Heslop-Harrison[35] speculates that the agent initiating flowering might be nucleo-protein in nature, possessing powers of self-duplication which are limited by the conditions prevailing, of which the auxin balance is most critical. This suggestion requires that nucleo-protein should be transported from one organ to another in the plant, but as we have seen there is no indication from the analysis of either phloem or tracheal sap that nitrogen is transported in molecules larger than peptides (Bollard[12, 13]; Mittler[43]).

Thimann[54] and others see no reason why the known growth substances should not account for all the demonstrated effects of auxins, including the initiation of flowering, bud inhibition, the initiation of roots on stems, and the promotion of cell division in the cambium. Consideration of the apparently contradictory effects of auxin in the phenomena of fruit set and fruit drop has "brought out one rather general principle, namely production of auxin is a transient activity of developing tissues," which is soon given up and taken over, in time, by other tissues; and "it seems probable that some kind of balance is involved between auxin and other factors, and that buds of fruits continue to develop only when this balance is maintained, while excess of either one inhibits."

The naturally-occurring auxins that have been identified so far are indoleacetic acid $(C_7H_7N)CH_2{\cdot}COOH$ and its nitrile, $(C_7H_7N)CH_2CN$. Many synthetic growth-promoting substances are known, and these are almost all simple aromatic derivatives of acetic acid, or able to give rise to such compounds in the plant. As Thimann remarks "the greatest puzzle of all is the mechanism whereby traces of auxin, a relatively simple organic acid, can so dramatically bring about growth or cellular enlargement." The interest and importance of this problem, stimulated by the recent work on gibberellic acid, a growth substance produced by certain fungi, can be expected to produce many useful discoveries in the whole field of plant biochemistry in the near future. Among these, we may hope, will be more definite information as to the route and mechanism of transport of smaller molecules throughout the body of the plant.

IV. BIOCHEMISTRY OF THE SPECIES

A botanic garden is the place, above all others, where the species dominates the scene. Underlying and determining the features of the plant, which serve as a means of distinguishing it from plants of other species, are chemical processes some of which, individually or in concert, are peculiar to that plant. It is of interest to discover what biochemistry has to say concerning the way in which such distinctive chemical processes may have arisen.

A prevalent view of the origin of living things is that life emerged in an "ocean" containing the essential elementary ingredients, through simpler organic substances, under the influence of irradiation from extra-terrestrial sources. Life, as defined by Engels[11], is "the mode of existence of albuminous substances" and entails "uninterrupted self-preservation and self-reproduction of the living system as a whole" (Oparin[44], p. 350). (The "albuminous substances"—*Eiweisskörper*—of Engels have a broader significance than "proteins," a term usually nowadays restricted to individual chemical compounds of precise configuration.) The simplest living things can be conceived as existing in such an "ocean" provided with an unlimited supply of all the elementary ingredients needed for the self-preservation and self-reproduction of "albuminous substances." Differentiation in the evolutionary sense emerged when the proliferation of life led to the exhaustion of any of these elementary ingredients. Survival then depended upon the ability of the life-form to improvise the synthesis of the missing ingredient, and it is this capacity to improvise which has led to the persistence and success of the forms now in existence. The diversity of forms corresponds with the diversity of problems encountered and surmounted. In the continually varying circumstances of poverty and enrichment, some forms survive, some are modified and supersede their progenitors, strikingly new ones intermittently emerge.

New faculties acquired do not necessarily mean that earlier ones are lost. On the contrary, there is ample evidence that primitive life processes can be retained side-by-side with those later acquired. As an example, anaerobic metabolic processes must have been the earliest source of energy, aerobic processes only having been acquired when an atmosphere containing oxygen became available to support them. Anaerobic processes still survive, however, in all aerobic organisms, and can be invoked when the supply of oxygen falls below that needed for aerobiosis.

The idea of faculty being added to faculty in the evolution of species is supported by the study of nutritional mutants of such organisms as *Neurospora crassa*. It can be seen in many such cases that the ability to synthesize an essential primary nutrient such as an amino-acid from simple carbon and nitrogen sources requires the ability to perform a sequence of separate operations. Depending on which step is affected in the mutant form, an intermediate of a particular degree of elaboration must be supplied from which the synthesis of the required amino-acid can proceed. Back-mutation to a fully-equipped form is frequently observed, and this can perhaps be likened to the acquisition of the original faculty in the evolutionary development of the organism. Such examples as this show, if nothing else, the extraordinary multiplicity of unit operations which living organisms are equipped to carry out; but so long as every observed process can be accounted

for in a sequence of simple steps, mere number of such steps does not constitute a barrier to the acceptance of the concept.

In spite of all the opportunities for diversity that are seemingly provided by such mechanisms as these, what most impresses the biochemist is the uniformity of biochemical processes over the whole range of living matter. "Not only are all living cells made of much the same type of material, but one finds the same cofactors and prosthetic groups, and essentially the same enzymes, in the most diverse organisms" (Dixon and Webb[18], p. 666). If we are to discern the nature and causation of diversity in plants, we have therefore to consider the major advances that have been made in the life-habit of these forms, which enable us to distinguish them from forms which are not recognizable as plants.

The first significant advance is, of course, the capacity for photosynthesis allowing the formation of complex organic substances from simple inorganic carbon dioxide and water. It is not necessary to suppose that this ability arose uniquely, for the porphyrins, to which class of substances chlorophyll belongs, are universally present in living matter in such forms as cytochrome, catalase, and haemoglobin. Chlorophyll itself is, however, except for a few bacteria, restricted to green plants; and the chloroplast, as a highly organized system of enzymes, coenzymes and accessory substances subserving the function of photosynthesis, is found only in the Algae, Bryophyta, Pteridophyta, and Spermatophyta. The possession of chloroplasts is, therefore, a feature which distinguishes green plants from all other forms of life.

The second significant advance is that represented by the translation from an aquatic to a terrestrial habitat. In this translation two main obstacles had to be surmounted: overcoming gravity, and the mechanical forces of air movement; and overcoming drought. The considerations involved in the second of these have been vividly reconstructed by Church[15] in his "Thalassiophyta." Both obstacles were most successfully overcome by plants which possessed or developed, a vascular system, and especially those in which the soma was divided into a root for water absorption and an aerial shoot with stem and leaves.

Further diversification arises from the means which are employed to fulfil the two primary requirements of self-preservation and self-reproduction in the endless variety of circumstances which the environment imposes. Besides contending with adverse physical circumstances self-preservation implies protection against attack by predators. The vascular plant, which achieves the mechanical strength required by its terrestrial mode of life by the deposition of incrusting materials in the walls of the vascular system, possesses among those incrusting materials substances which afford protection against many forms of attack and injury. If the ancestral precursor of the vascular plant still survives among the lower forms of plant life, it must

be sought in those forms which produce substances, namely the flavonoid compounds and the hydroxy- or hydroxymethoxycinnamic acids, of a like nature to these incrusting substances. So far, however, these have been found exclusively in the vascular plants.

This gives us a first clue as to the direction in which biochemical specificity, or conversely specific biochemistry, is to be looked for: it is in the secondary products common to a particular group of plants and closely restricted to that group. Substances occurring uniquely in one species, or those occurring commonly over a wide range of species are of little use in clarifying the biochemical processes associated with specificity in living organisms. So far only a few classes of chemical constituents show promise of usefulness in this respect. These will be discussed in the next section.

Differentiation is necessarily detected in the first place by differences in outward form. It will be a long while before the chemical mechanisms underlying such gross differences as the branching habits of the higher plants, and the forms of leaves, flowers, and other organs will be completely uncovered, but already some of the agents concerned, in the shape of auxins, have been isolated and characterized. Smaller differences involving the presence or absence of one or a few constituents, such as differences in flower colour can, however, be accurately described in terms of chemistry, and mechanisms can be envisaged by which such differences are brought about. In every such instance the difference in question is under gene control; often only a single gene is concerned, and a chain of causation from the chromosomic apparatus in the nucleus, through the enzyme system in the cytoplasm, to the formation or non-formation of the specific pigment substances in the cell-sap can be confidently presumed. It must be borne in mind, however, that while the action of a particular gene may be expressed solely in the one character of petal colour, every cell in the plant possesses the same genic constitution, and the action of that gene may be capable of expression in a number of less obvious ways. It has been observed, for instance, that genotypes possessing a large number of recessive alleles for flower colour are frequently relatively weak in constitution, indicating deeper-seated biochemical disturbances than that concerned only with the development of colour in the petal.

The concept of units of inheritance, multiplied indefinitely to comprehend all the characters by which plants may differ from each other, gives us a picture of the way in which specificity, morphologically and biochemically, is achieved. Bearing in mind the number of processes which living organisms possess in common (p. 112) the picture is presented of a "gene pool" out of which each species draws its limited, particular complement. For any individual, the complement is determined by the joint holding of its parents, except for the occasional mutation which takes place, either from the

inherent mutability of the gene or by outside influences such as radiation or the action of mutagenic substances. Mutant genes, if viable, are added to the pool. The total number of genes carried and transmitted by the nuclear material of an individual organism is enormous—the number of nucleotide pairs (each of which can be likened to a letter in the message conveying genetic information) even in so minute an organism as a bacteriophage has been estimated at half a million and that in a mammalian cell at three thousand million (Perutz[47])—so that the biochemical information transmitted to each successive generation is commensurate to the task which it is called upon to perform.

Some of this information determines the production of protein molecules able to induce the formation of antibodies in mammalian blood serum. These antibodies are specific, or nearly so, against the protein which gave rise to them, and it is thus possible to identify this protein, or closely similar ones, in an extract of a plant containing them. Gell, Hawkes and Wright[24] have used this property to detect "blood" relationship between different species of *Solanum*, affinity being judged by the number of proteins common to two or more species. The biochemistry of species might be narrowed down in this way to the presence of proteins of specific configuration possessed only by this species and its nearest relatives.

Specific identity in the higher plants is most often determined by analysis of floral morphology. This is perhaps the least studied of any aspect of plant biochemistry, in so far as the chemistry of flowers is of little importance economically and of no immediate value diagnostically. Nevertheless modification in the flower, especially in response to changing opportunities for fertilization and dispersal, is one of the most significant causes of diversification of the higher plants, and should richly repay increased attention to the chemical foundations of the diversity which has been intensively studied in the chemistry of flower-petal pigmentation, though mainly from the viewpoint of the causes of variation *within* species. This line of approach offers one of the best opportunities for studying gene action in the higher plants, an opportunity which was so well appreciated by Lawrence and Scott-Moncrieff in their classical work on the chemistry of flower colour in *Dahlia variabilis* and other ornamental plants. This work is being continued by Harborne (cf. p. 105) with all the advantages provided by the newer methods of chemical analysis. Another study of equal promise is that by Feenstra[23] of the variation of seed-coat pigmentation in *Phaseolus vulgaris*. These researches, it will be remarked, are all concerned with pigments, which are especially appropriate for such studies because so much of the essential genetic work can be done by visual inspection alone. Moreover the end-products of the synthetic process are frequently unique—gene action seems to be confined to one single chemical event, and that is

invaluable in the interpretation of the mechanism of the processes affected by the presence or absence of that particular gene. It can be confidently predicted that extension of such studies as these to include the other differentiated tissues of the flower and the vegetative organs of a single subject will answer many of the problems concerning the differentiation of species which are at present so puzzling to the plant biochemist.

V. BIOCHEMISTRY AND TAXONOMY

The idea that fields other than morphology may have a contribution to make to systematic botany is becoming increasingly more acceptable to the taxonomist. Chemistry is more reluctantly admitted than some other subjects. It is a complex subject with a complicated language of words and symbols which demands much application to master. Another reason is, of course, that chemistry has failed, hitherto, to provide any substantial guidance to the botanist in his efforts towards a truly natural classification of plants. Constance[16] summarizes the situation by saying "we may have to await the establishment of adequate classifications of biochemical substances and processes before we can hope to utilize them freely in systematic botany, but we should not forget their great potentialities."

We have to remember that chemists do not classify their substances with the idea foremost in their minds that the classification adopted should be that of greatest value to the taxonomist. To be of taxonomic value, therefore, the chemist's classes are likely to have to undergo some re-sorting. There is, to the pure chemist, no particular virtue attaching to the fact that a substance does or does not occur in Nature, but to the taxonomist that distinction is paramount. We have, therefore, to examine such classes of substances as, for instance, the alkaloids or the glucosides, to see whether finer distinctions should be made before seeking to draw conclusions from their systematic distribution; and we very soon find, in fact, that quite useful conclusions can be drawn, once distinctions are made between the very heterogeneous members of these classes of substances.

It has already been pointed out (p. 114) that substances too narrowly restricted in their distribution, or those too generally present can be of little use as taxonomic indices. Within these limits, and especially among the secondary products of metabolism, there are many opportunities for consideration with regard to significance of distribution. "Consideration" implies in the first place extensive survey, and in the second place intensive research in order to establish and confirm consistencies or inconsistencies revealed by the preliminary reconnaissance. We find that contributions towards biochemical systematics tend, therefore, to be of these two kinds—broad surveys employing indicative reactions; or detailed studies of restricted groups of plants with reference to specific, identified constituents.

Studies of Restricted Groups

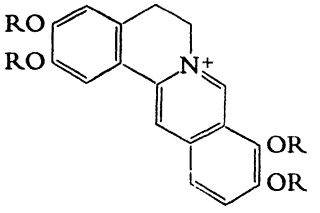
Of the second kind of investigation, by far the most substantial is that of Erdtman and his school dealing with the distribution of phenolic compounds in the wood of conifers (cf. e.g. Erdtman[21, 22]). This work is notable for the scrupulous identification both of the chemical constituents and the botanical material, and it is obvious that only such evidence can be used for drawing rigorous taxonomical conclusions. Furthermore, as Erdtman points out, the conifer field is particularly well adapted to studies of this kind because it comprises a very old, isolated group of convenient size, consisting as it does of about 600 species distributed among a small number of families and a rather large number of genera. The only defect of the work is that it is restricted to heartwood constituents, and does not lend itself to inclusion in overall taxonomic surveys which must, of necessity, comprehend non-woody as well as woody species. For such surveys leaves, or leaf-like organs—the photosynthetic lamina—are probably the best tissues to examine. From his survey, Erdtman concludes that the Pinaceae and Cupressaceae seem to be, on the whole, well differentiated. Some genera prove to be homogeneous chemically as well as morphologically, while others are chemically heterogeneous. In *Pinus*, even the subgenera can be differentiated chemically.

A similar survey of *Prunus* woods by Hasegawa and his collaborators has recently been summarized[32]. Each of the five sections of the genus has a particular flavonoid pattern, coinciding with the taxonomical classification excepting two species in the subsections Eucerasus and Euprunus.

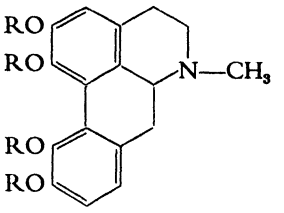
Another outstanding instance of chemical constitution supporting taxonomical classification is that of the distribution of nitrogenous anthocyanins. These are confined to the Centrospermae (Caryophyllaceae excepted) and the Cactaceae (Lawrence *et al.*[41], Reznik[49]). The anthocyanins themselves have, so far, provided little guidance to the taxonomist.

As an example of the necessity for a narrower chemical classification before useful taxonomic conclusions can be drawn, the alkaloids are outstanding. Any naturally-occurring nitrogenous substance with predominantly basic properties qualifies for this description. Understandably, it is a chemically heterogeneous class, and it is only within recent years, when the constitution of all the important alkaloids and many of lesser importance has been established, that a finer classification on chemical grounds has become possible. With the help of such a classification, Hegnauer[34] has analysed their systematic distribution and has been able to show how much information of use to the taxonomist can be gained from such an analysis. The phenyl*iso*quinoline alkaloids especially (derived biosynthetically from two dihydroxyphenylalanine residues) are highly indicative in their

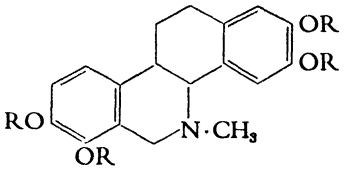
distribution of taxonomic and phylogenetic relationships. Examples of the basic formulation of these alkaloids are shown in VI to VIII below:



VI



VII



VIII

R being H, CH_3 or $-CH_2-$ (in the form of a methylene group linking two phenolic hydroxyls). These types are limited to about twelve families of the dicotyledons, those of each particular formulation being more narrowly restricted. They are, in fact, rarely found outside the orders Ranales–Rhoeadales, and where they do occur, as for instance in the Rutaceae, there is good reason to look for indications of relationship with the families in these orders. Hegnauer, with some justification, concludes that there is sufficient factual material for the establishment of a phylogenetic system in terms of phytochemistry to be attempted.

Hegnauer has also carried out a number of surveys of the chemical features of certain families, e.g. the Leguminosae[33], and these also have a taxonomic value especially if they point to relationships within the family and to possible relationships with other families. Recently, too, Enslin and Rehm[20] have analysed the triterpenes responsible for bitterness in the Cucurbitaceae, and have found the individual representatives distributed to only a limited extent in accordance with the recognized taxonomic divisions of the family. This is a fairly common experience with constituents of this kind—the essential oils (cf. Baker and Smith[1] in *Eucalyptus*), but occasionally, as with the acetylenic fatty acids in the Compositae–Umbelliferae, and Basidiomycetae; the cyclopropene fatty acids in the Malvaceae and Sterculiaceae; and chaulmoogric acids in the Flacourtiaceae, there are narrow limitations in distribution which support already well-recognized taxonomic divisions.

Wider Surveys

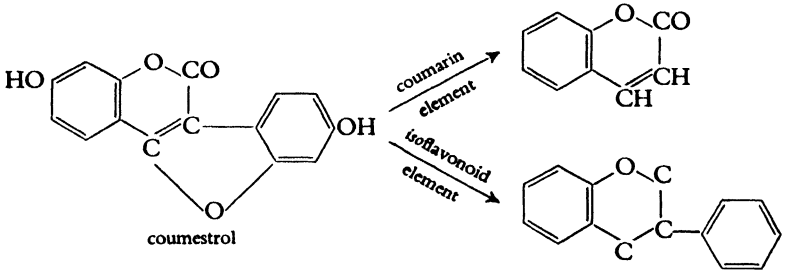
Of the surveys covering a wider range of plants, and employing tests of an indicative nature rather than isolation and identification of specific constituents, those carried out by R. D. Gibbs come first to mind. In his first

survey Gibbs[25] discussed the nitrogenous anthocyanins, the anthocyanins of *Tulipa*, the fatty acids of the Flacoutiaceae, and the chemistry of the Cupressaceae. With Towers[55] he tested the lignins of a wide range of plants for syringaldehyde, vanillin, and *p*-hydroxybenzaldehyde groups, and found differences, both qualitative and quantitative, in the occurrence of these groups in the lignins prepared from different classes of plants. More recently[26, 27, 28] Gibbs has applied five tests to the wood of numerous species in eleven families of the dicotyledons, some of which had been indicated (Gundersen[29]) as deserving of further systematic study. The tests Gibbs used reveal the presence or absence of (probably) catechol tannins, leuco-anthocyanins, cyanogenetic glycosides, raphides (calcium oxalate crystals of a particular type) and syringin (glucoside of syringyl alcohol), and were therefore fairly broad in their coverage from the chemical point of view. The systematic inferences of the results are closely argued, especially as regards the homogeneity of the families Rubiaceae, Caprifoliaceae, and Loganiaceae and the affinities of the subdivisions which can be justified on morphological as well as chemical grounds. This is, perhaps, the most determined attempt to date to bring chemical considerations to bear upon the taxonomic situation.

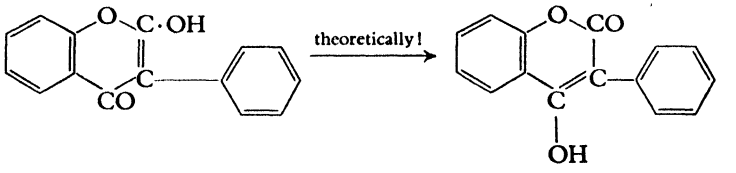
As so well exemplified by Erdtman in the case of the Coniferae, it is the phenolic constituents of plants which hold out most promise of affording assistance to the taxonomic botanist, especially in vascular plants which employ lignin as strengthening material. Not only do the lignins of these plants differ in composition, but the "accessory" phenolic constituents—the leuco-anthocyanins, catechins, flavonols, hydroxy-methoxy-cinnamic acids, and the innumerable related or vicariant substances which are found in the leaves and wood of these plants—vary in a regular and often systematic manner. So far as this new territory has been mapped (Bate-Smith and Lerner[7]; Bate-Smith and Metcalfe[8]; Bate-Smith[5, 6]) little reason has been found to dissent from the generally-held views of systematic botanists as to the classification of the vascular plants, and there are indications that useful information will be provided for the solution of many outstanding taxonomic problems. There is no reason whatever to fear that biochemistry will disturb the foundations of systematic botany, or to imagine that a "chemical systematics" will be set up to rival the established systems founded on morphological characters.

So far we have been concerned only with the contribution that advances in biochemistry might make to taxonomy. It is equally important to the chemist and biochemist to consider also the value of establishing links between taxonomy and chemistry. The fact that related plants contain similar constituents can often act as a guide to the nature of an unknown isolated compound. A working knowledge of one of the familiar systems,

with automatic mental "registering" of a plant, as it arises for consideration, to a position in the system, is immensely helpful both as a mnemonic and as a means of building up, for the individual concerned, a scaffolding of taxonomic chemistry of ever-growing usefulness and meaning. In this context the remarks of Constance quoted earlier are especially pertinent; it is no use having the chemical constituents so classified that they cannot be logically related to the classification of the plants in which they occur. It is worth while citing here a case in point. A new oestrogenic substance, named coumestrol, deriving structurally from coumarin, has recently been isolated from some clovers (Bickoff *et al.*[11]). Leguminous fodder plants have been known for some time to contain oestrogens belonging to the class of *iso*-flavones. Consideration of the structure of coumestrol shows that it is not only a coumarin, but also an *iso*flavonoid derivative:



and the structure of coumestrol is, in fact, readily derivable from the *iso*-flavon*ol* (not known to occur in Nature) corresponding to the *iso*flavone daidzein, one of the known oestrogenic substances of the Leguminosae.



As a *coumarin*, coumestrol gives rise to no association of ideas, but as an iso*flavonol* it immediately falls into place in a taxonomic-chemical continuum.

Biochemistry and Phylogeny

Phylogeny, implicitly or explicitly, enters into all the modern systems from Engler and Prantl onwards. Assumptions have to be made because lines of descent can only be traced with certainty for a very short distance backward in time. Biochemistry has had scarcely anything to say so far in support of one or another concept of what are primitive characters in plants, but the increase in chemical knowledge resulting from the application of newer methods in plant biochemistry is bound to provide material of

assistance to the phylogenist. Again it is from among the secondary products that such assistance is more likely to be forthcoming. Already one hint seems to be provided from an examination of the phenolic constituents: leuco-anthocyanins are constantly associated with those vascular plants which are regarded as the most primitive, such as the Schizaeaceae and the majority of the Pteridophyta; *Ginkgo biloba* and the majority of the Gymnosperms; and the more primitive families of the Dicotyledons. In the latter, the correlation of presence of leuco-anthocyanins in the leaves (Bate-Smith and Metcalfe[8]) with low "advancement index" and absence with high "advancement index" (Sporne[52]) is remarkably close (Sporne, personal communication). They are quite absent from mosses and algae, and in fact the only group of the lower plants in which any of the phenolic constituents commonly present in vascular plants has been reported is that of the Chlorophyceae. The report that flavonols and anthocyanins occur in *Chlamydomonas eugametos* is almost certainly erroneous. In *Spirogyra* spp. gallic acid and ellagic acid do, however, occur, and this represents a tenuous biochemical thread connecting these green algae with the vascular plants.

If biochemical processes are to throw light on phylogeny, they must be of a kind which are present in a continuous series of living forms and, when lost, are not readily regained. Some of the processes we have been considering seem to be of such a kind—those, for instance, leading to the formation of nitrogenous anthocyanins in the Centrospermae. In making phylogenetic use of the information about leuco-anthocyanins, the assumption has to be made that their formation originated in an ancestral vascular plant and, when lost from a line, no successor in that line will be found to possess leuco-anthocyanins. There is obviously a long way to go before such an assumption can be regarded as justified even in this one particular case. The conclusion reached by Baldwin in 1937 in his article on phylogeny in the animal kingdom is equally valid for plants today: "only a vast extension of our knowledge of facts in comparative biochemistry will permit of our answering the kind of question here raised about the relations between the genetic and spatial hierarchies" (Baldwin[2], p. 106). Extension of such knowledge is now more readily obtainable than it was twenty years ago, and we can look forward to increasing usefulness of biochemical information in solving problems of taxonomy and phylogeny in the botanical field.

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CAUSAL PLANT ECOLOGY

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THE relation of organisms and their processes individually to the physical conditions of their internal and external environments is the especial province of the plant physiologist but that of the plant ecologist is to study the integrated effects of the interaction of these physical conditions and the organisms they support, having due regard to the important part played by what we comprehensively term competition.

It is the purpose of this article to present some of the salient trends in the study of the causal factors which influence the character and composition of plant communities. Often in the past it has been found convenient to consider the habitat factors in separate categories, the historic, the climatic, the edaphic and the biotic, but there is an inevitable danger in such abstraction that we underrate the degree to which these interact to affect their influence on plant life.

Those influences which have operated in the past to produce the conditions of the present can be classed as historic factors and these, it is manifest, must often have been secular in character. The replacement of the prevailingly Pteridophytic and Pteridospermous flora of the Coal-measure Period by the predominantly Gymnospermous vegetation of the succeeding epochs, must have depended upon prolonged changes in the environment, both physical and biotic, as also, no doubt, the transition to the predominantly Phanerogamic vegetation of the present era. The persistence or survival of any one group that marked the facies of plant communities may well reflect, not so much the inherent capacity of the gene complexes involved, to provide organisms of survival value, as their capacity, relative to those of other organisms, to change with sufficient rapidity. The distinction is important since the one implies an intrinsic lack of physiological plasticity, the other a genetic complex that is merely resistant to adjustment. The one would lead to complete extinction under changing conditions, as with the Pteridosperms, the other to a rare persistence as exemplified by the Royal Fern (*Osmunda*) and the Quill-wort (*Isoetes*) alike survivals of very ancient lineage. Though very remote in the time of their initiation these secular changes are probably still operative in their effects. Indeed the vegetation of the Earth's surface today has, we all recognize, been profoundly modified by the age of steam and the internal combustion engine which alike depend for their source of power on our

heritage of fossil fuel from the extinct floras and faunas of the past; their exploitation has accelerated the progressive replacement of natural plant communities by the semi-natural and the quasi-artificial, a transition that the geometrically increasing population of the world is continually augmenting.

If the effects of the remote, and even of the immediate, past are often difficult to evaluate that in no degree denigrates their significance. In our own time man's influence in changing the protective cover of vegetation has disastrously accelerated erosion in many areas. By regulating waterways and creating hard road surfaces he has speeded up drainage and lowered water tables in an ever increasing area, whilst through forest destruction on catchment areas the regulatory influence of the organic sponge has been reduced so that floods are liable to alternate with drought and bring changes far beyond the extent of obvious interference. Anti-erosion measures have recognized the important role that vegetation has to play and the time must one day come when foresters, agriculturists, water engineers and others will recognize a common interest and responsibility in initiating changes in the ecology of the plant cover which they severally exploit. From the nature of evidences of the past and their often fragmentary character it is only in relation to the most recent events that it is possible to do more than note the contemporaneous occurrence of vegetation changes and physical alterations so that historical ecology is more often descriptive than causal and so outside the scope of this present consideration.

The more obvious climatic influences of wind, precipitation, humidity, temperature, and illumination were, in the earlier ecological studies, considered far too much in isolation from the point of view of the average conditions and with little regard either to their interaction or their indirect effects. Furthermore, it was not till attempts were made to correlate vegetation with the climatic pattern that it was realized how complicated this pattern might be. The effect of orographic factors in modifying the local climate was soon appreciated and the numerous studies in montane areas, such as Switzerland, showed clearly the importance of aspect and of the general level of the mountain massif on altitudinal limits of communities and species. This rapidly led to the recognition of what has been termed cold-air drainage[45] and the existence of frost pockets which could result in temperature inversions and accompanying inversions of altitudinal limits, features that have been closely studied by fruit growers for obvious economic reasons[11].

Our knowledge of the more detailed pattern of climatic features as they affect plant life is, in many areas, inadequate despite the broad correlation between vegetation types and saturation deficits that may obtain in some regions or with length of frost-free periods in others. Moreover our

knowledge of the microclimate of the various strata of plant communities and its seasonal variations is generally meagre whilst any concept of the microclimate within the soil is commonly wanting. So, even though we may know the climatic environment of the shoots with some degree of accuracy, we are often quite ignorant as to the significant environment of the root systems. During prolonged cold spells the depth to which the soil is frozen solid, for example, can vary widely in different plant communities growing on the same type of sub-soil. In one instance bare soil was frozen to a depth 2 to 3½ in., under rough grass to between 1 and 1½ in. and in a hazel copse to only ⅜ in., or not at all, according to the depth of the leaf litter[42].

The long term operation of climatic factors may clearly limit the capacity of a species to flourish and compete with others or it may even impair or inhibit its power of reproduction. The detailed studies on frost resistance of Apple varieties have, for instance, revealed the diverse times at which temperature-sensitive crises may supervene in the life-history so that if this obtains also in wild populations climatic differentiation in the occurrence of strains as well as species may obtain. But the elucidation of such relations demands a knowledge, for each species, of these critical periods, such as flower initiation, pollen-tube development, fertilization, etc., and the temperature tolerances of each.

The success of any type of plant in the wild state will depend upon its capacity to flourish and reproduce under the local climate which the plant itself in part creates. The determining conditions are not, however, the average but the extremes to which it is subjected and hence the need for continuous records of the climatic factors within the community itself not forgetting the steep vertical gradients that may obtain between different levels, of the same vegetation unit, and the interference effects of the different species with respect to the penetration of light and rainfall. The climatic pattern is often conditioned by the structure of the community and the physiognomic character of its constituent members no less than these are themselves determined by the climatic pattern which they can modify and endure.

We have referred to the fundamental principle that it is the most severe conditions of habitat, rather than the average, that mainly determine the characteristics of communities. But this, which we may term "the *Principle of Extremes*," must not be over-simplified and regarded as being in the nature of so many sieves of lethal conditions. Species that will survive a low temperature during a single winter may succumb to two successive winters of no greater severity. Again, it is commonly the extreme conditions, that are not lethal, but sub-lethal, operating from season to season that undermine the vigour of a species and give advantage to the more tolerant vegetation over the less tolerant.

The crude early concepts as to the relationship of plants to low temperature

gave place when subjected to experimental tests to the recognition that resistance of a plant or its parts was largely conditioned by its water content and that the capacity of seeds to survive storage in liquid air was only true so long as their water content was negligible[2]. The degree of toleration of low temperature is well known as a specific character that limits the range of many plants but the complexity of the phenomenon of frost resistance has only been appreciated in the light of recent observations and experiments which have shown that the low temperature toleration of a species varies seasonally[24] and that capacity to endure a certain amount of frost is no guarantee that the same species will not succumb to far less severe conditions if the temperatures be fluctuating.

Similarly with respect to drought tolerance the capacity to endure desiccation is one that is partly inherent, partly dependent upon the time of the year and partly on the manner in which the desiccation comes about. Both with respect to desiccation by drought and by low temperature, the mode and rate of recovery are operative factors in determining survival since rapid expansion of a contracted protoplast, unsupported by the cell wall from which it has shrunk, may involve lethal rupture. A detailed consideration of the general topic of plant hardiness has been furnished by J. Levitt[28] which emphasizes the diverse qualities that render the protoplasm resistant to disorganization but the particular aspect we would here stress is that the precise pattern of climatic change in a particular habitat or partial habitat, often referred to as the microclimate, can alone provide a clue to the climatic factors as they affect the constituents of a natural community. Thus the seasonal incidence of precipitation if confined to a few thunderstorms in the hottest months may scarcely support a desert type of vegetation whilst the same average rainfall spread evenly over the cooler period may suffice for a plant community which evades the waterless period by shedding its leaves. We must not lose sight of the fact that the precipitation itself may vary to a significant degree in kind as well as in amount. For example, rain contains chloride corresponding in amount to the proximity of an area to the sea. Dr. Miller of Rothamsted, half a century ago recorded the chloride content as ranging from 218 p.p.m., near the coast, to between 2 and 3·4 p.p.m. fifty miles inland, whilst for sulphur a range of from 0·6 to over ten times that amount has been determined in open country and much higher values in the polluted atmosphere near industrial areas. Calcium would appear to be present in amounts ranging from one to six parts per million[17] and though such amounts be small their repeated addition to the soil whenever there is a fall of rain does not permit their being ignored. It would, however, seem that variations in the amounts of micronutrients present in rainfall is likely to have but a negligible influence upon plant distribution[17].

The advances in our knowledge of climatic conditions have emphasized the importance of detailed studies, both spatial and temporal, that take cognizance of all types of humidity and precipitation both above and within the soil. The clue to the presence of vegetation in so-called rainless deserts has been found to rest in the dew formation that even in temperate communities may play an important role[44].

Quite recently the probable importance of high humidity under exceptional environmental conditions has been further emphasized through the experimental proof by Breazeale *et al.*[5] that plants can absorb water through their leaves from a saturated atmosphere and that this together with contained solutes can exude through the roots into the soil which may thereby attain field capacity.

To descriptive ecology we owe the recognition of a number of major vegetation types that are associated with particular climatic conditions, as for example the occurrence of the deciduous forests in areas where a favourable climate alternates with an unfavourable, due to low temperature or inadequate humidity. Another example is the association of evergreen coniferous forests with areas where the length of the growing season is restricted. But now that the broader features of the relations of plant communities with climatic types have come to be recognized the unexplored areas of the world's surface, though likely to provide further examples and interesting variants, are unlikely to contribute materially to our real understanding of the causal factors of distribution unless investigated in considerable detail. Further progress demands a detailed analysis of climatic and other habitat conditions throughout the seasonal cycle and experimental studies of individual species to determine their tolerances and the critical phases in their development which climatic conditions may promote or inhibit and the temperature and humidity limits these demand.

Other features of the climatic complex that call for more detailed analysis are the responses of individual species to direct and indirect effects of wind action and the influence of radiation of different intensities and wave lengths. The comprehensive work edited by Professor Duggar[10] constitutes a valuable summary of the position attained at that period, since when the amount of research, especially upon photoperiodism, to which we shall revert, has been both extensive and significant.

In the competition for radiant energy potential heights and spread are morphological features that determine the degree to which one kind of plant or individual can become a sunshade to another but clearly the time factor is here significant and in a population of seedlings, for example, those individuals that germinate first will have an advantage over those germinating later which emphasizes the survival value of what has been termed germination energy.

The more continuous the light screen provided by the foliage of a species the more effective will be its suppression of the plants in its shade though the mechanical vulnerability to wind imposes on leaf area the compromise presented by the compound character of most large leaves, although the rosette-leaves of many biennials which have the support of the soil or other vegetation beneath are immune from this type of injury and are often large and quite entire. We can, indeed, in many morphological features discern indications of this struggle for light. The dominance of the tree habit in the climax phase where habitat conditions can support forest is but an expression of the fact that in the struggle for light the tallest members tend to survive. The wane of the arboreal vegetation is probably an accompaniment of man's increasing interference with nature making ever-augmented inroads upon woody vegetation so that today, almost throughout the world, herbaceous communities are becoming more conspicuous.

It is, perhaps, due to the importance of the time factor that the more successful species are in general those that have the potentiality of large seed-output[43] and the marked association of average seed size with the shadiness of the plant community that a species normally colonizes[43] is a further emphasis on the importance of the light factor in competition at the juvenile phases of developments.

In the competition for nutrients the extent and rate of development of the root system to which we have already referred, is manifestly correlated with the success of the assimilating organs and the mode of spread of a species whether by seed or vegetatively will mainly determine the habitat conditions that it can invade.

From experiments with Barley growing in competition with *Holcus mollis* H. H. Mann and T. W. Barnes[29A] concluded that though the root space and supply of plant food was apparently ample for both they reduced the growth of each other and the dominant appeared to be determined by the *time of development* as well as by the density. One could multiply examples but it is clear that temporal factors play an appreciable part in the competition both for light and nutrients and emphasize the need for a much more detailed knowledge than we at present possess concerning the life histories of the chief species contributing to plant communities and the conditions that modify them.

An interesting example of the differential effect of species upon one another was exhibited by some experiments carried out with *Juncus effusus*. A. Lazenby found[25] that the number of seeds of this Rush which germinated and the subsequent growth differed strikingly according to the other species of seeds sown with them. Thus when sown with Bent (*Agrostis tenuis*) and White Clover (*Trifolium repens*) only about one-tenth of the population of

Rush plants was obtained as when the accompanying species were Rye-grass (*Lolium perenne*) and White Clover.

It is only natural that the visible, overground, parts of the plant should have received major attention from both morphologists and ecologists though it is perhaps remarkable, having regard to the early recognition of the importance of the root-system, from the nutritional as well as the mechanical aspect, that its nature, extent and mode of development should have so long been neglected. Such neglect is perhaps partially to be explained by the difficulty of exhuming the entire root system, in most soils, as a consequence of which their extent has often been underestimated.

The valuable researches of Weaver and his associates in America have served to call attention to this neglected field of study[50, 51]. From these the considerable labour involved in such studies can be appreciated but also the great diversity and significant distinctions that obtain. Sandy soils afford an especially favourable medium for such investigations since by blowing away the sand from a working face as it dries entire root systems can be excavated without risk of losing the finer ramifications and by appropriate means these can be supported in their original positions as they emerge from the matrix. The present writer's own studies on the root systems of plants characteristic of various phases of dune development[44] have shown how varied these can be not merely between different species but also between different individuals of the same species when growing in conditions of diverse water supply and aeration.

Root studies have emphasized the distinction between those that exhibit a restricted but richly branched system, which exploit a relatively small volume of soil intensively, and those in which the root system is extensive but the large soil volume is much less completely interpenetrated.

Modern studies of economic plants have shown what marked differences in this respect may obtain between cultivars of the same species as, for example, the root systems of the "Wealthy" and "Doucin" apples or the various East Malling Apple stocks, and there is no reason to suppose that similar differences both interspecific and intraspecific, do not occur with respect to the root systems of wild plants and that they play an important role in their competitive equipment.

The recognition of the fundamental importance of a number of trace elements and their frequent presence in inadequate amounts, or in more or less non-available condition, has brought into prominence the great significance that may well attach to the type and degree of root exploitation.

Furthermore it has been shown that the availability of some trace elements, such as zinc, in the early stage of development of a species, can be decisive for the subsequent healthy growth and its early supply will differentiate between failure and success. The importance therefore of the *rate* of development

of the root systems of different kinds of plants in what we may perhaps be permitted to describe as their race for the necessary nutrients which are in short supply, scarcely requires emphasis. The great success of the grasses may be in no small degree due to the extent and rapidity of their root development. Weaver showed[51] that the latter is frequently more than 12 mm in a day whilst the root of a maize plant may extend more than 50–60 mm in the same period.

With uniform genetic material the extent of the root system is very susceptible to the influence of water soluble substances, for example the calcium ion is known markedly to affect root growth. The extent of the root surface in the presence of calcium was several times that in its absence and the volume of soil that can be exploited is probably proportionately increased[44]. The extent of the root system is also affected by the soil texture and indeed one aspect of cultivation is that it reduces the resistance that the growing root has to overcome in its penetration of the soil. Again, optimum moisture content and above all good aeration promote not merely the extent of the root system but in particular the development of root hairs. One may note that root hairs can augment the absorbtive surface sevenfold, so that factors affecting their production and growth may be of great significance. All these conditions affecting the size and efficiency of the absorbing structures stress the importance of the morphological-physiological relations and one may expect that future ecological studies will tend to integrate still further the two angles of approach, but if this is to be achieved it is essential that the physiologist should be apprehensive of the extent to which field competition is likely to modify the laboratory indications and the ecologist must be alert to appreciate the field significance of the controlled experiments which, however oversimplified they may be from the point of view of their translation to the plant community, can rarely fail to make their contribution to our understanding of the more complex conditions.

In 1929 I called attention to the striking reduction in the extent of the root system of a species when subjected to the competitive influence of the root systems of other plants[40]. Eight years later Pavlychenko furnished remarkable quantitative data respecting the magnitude of this effect[34] as exhibited by cereals in competition with weeds and with one another.

The importance of the competition factors in natural communities cannot be over-emphasized and such may well be operative from the earliest phases of plant development since seedling mortality, which is very high, appears to be influenced not only by the physical conditions but by the proportions in which the seedlings of different species are present.

Statistical studies have confirmed what general observation had suggested that individual plants are not normally dispersed in a random manner. This was for instance clearly brought out in regard to grassland communities

by G. E. Blackman, in 1935, but it yet remains to be ascertained to what extent such lack of uniformity in dispersion reflects the lack of uniformity in the habitat conditions. For example, the marked tendency towards aggregation of the individuals of the herbaceous species of *Salicornia* is clearly to be expected from the crozier-like hairs upon the testa which anchor the seeds to suitable surfaces, such as the wefts of salt-marsh algae, and to one another, when they are dispersed by the rising and falling tides. So, too, the classical example of the hygroscopic arms of the dissected spore-coats of *Equisetum* which ensure some measure of aggregation of the unisexual gametophytes. These and other similar morphological determinants may clearly be important for survival but unrelated to any permanent feature of the habitats concerned. We still do not know why it is that the annual vegetation of a desert, superficially uniform, may present a Joseph's coat with large areas each dominated by a different species of *Helipterum*. Are such phenomena visual expressions of vagaries of dispersal, or evidences of survival from selection accompanying real though obscure habitat conditions? Attention has more than once been drawn to the phenomenon of certain species that occur with great abundance in an area and produce copious seed only to disappear for a long period subsequently or, if not completely absent, they are rare. A striking example that has been observed both in this country and on the Continent is afforded by the Yellow-wort (*Blackstonia perfoliata*), which is very pertinent to our present context because its root system is of comparatively small extent. The output of its small, almost dust-like, seeds which exhibit a high percentage germination is large[43]. So it is not unreasonable to assume that these are in fact broadcast over the entire area. Hence, one may ask, is it that such species require some nutrient condition, perhaps a trace element in short supply and that this becomes depleted? The discontinuity of the densest population of *Blackstonia* would not warrant suggesting that its roots completely exploit the entire surface soil but it may well be that, from a vast population of seedlings, the mature plants we see are in fact survivors where the requisite nutritional conditions obtain and that the discontinuity of occurrence does indeed reflect the heterogeneity in this respect of a habitat otherwise apparently uniform.

The role of vegetation in the processes of pedogenesis has been studied under conditions where the distribution of the phases of plant development in space corresponds to their sequence in time and thus provide an unequivocal chronological succession over a prolonged period with respect alike to soils and organisms. For sand dunes it has been shown that the soil development is dependent upon a succession of species that incorporate organic material beneath the surface as well as providing deposition upon it and augment water retention and stability so that less and less specialized types can effect colonization ultimately ousting the pioneer specialists. The

original inhospitable soil conditions with an open community of perennial and annual species, characterized by features that enable them to endure the rigorous conditions, is succeeded by conditions favourable to an increasing number of species, far more diverse in their biological equipment, that ultimately constitute a closed community and this in turn may finally give place to scrub and woodland occupying soil that is now favourable to a great diversity of plants but where in fact the number of species has again diminished owing to the dominance of trees and shrubs[44].

The initial edaphic specialization has thus, in the course of perhaps a century, given place to a biotic specialization that in its own way may be almost equally severe. The studies of R. L. Crocker and his associates on the recessional moraines deal with a comparable sequence from an open community of pioneers that in the course of some 120 years has developed to spruce forest and, as in the dune succession, there is an increasing organic content and transition from an initially alkaline soil to one of appreciable acidity with an augmenting gradient in the soil profile[8, 9].

The recognition of the major role in water retention by the soil played by the organic material gives added significance to its vertical distribution and it thus came to be realized that, in the naturally stratified soil the surface layer might be of sufficient thickness and its organic content so high that it constituted a sponge which could starve the lower layers of water except perhaps in the heaviest rainfall. Thus is indicated one of the ways in which during the course of years a tall deeply rooted layer of dominant species continually adding its quota to the superficial organic accumulations can gradually contribute to its own destruction and an acidophile shallow-rooted community replaces the erstwhile dominants.

Each species has its own complex of conditions in which it can best develop. If we grow any one in conditions that vary with respect to one factor, such for instance as soil reaction, we find there is a range over which the plants exhibit maximum growth on either side of which increasing acidity or increasing alkalinity is accompanied by diminishing vigour. In the absence of competition the range of toleration is often wide but in the presence of other species this may become very restricted. This fact emphasizes the fundamental principle of the interaction of habitat factors. For whether it be soil reaction or any other there is usually no absolute optimum but a relativity that is the more complex because any single one may operate in so many different ways. Soil acidity, for example, may be beneficial as enabling certain nutrient ions to be readily available but it may also be directly harmful by reason of toxicity of the hydrogen ions themselves, or indirectly through excess of ions of alumina or manganese in the soil solution, or again it may adversely affect beneficial soil organisms such as the nitrogen fixing bacteria and encourage harmful ones such as *Plasmodiophora brassicae*.

Above all, adverse or beneficial factors cannot be considered in isolation since plants grow where they must and not where they will so that what, in the laboratory experiment, may seem harmful appears in the field as a benefit because the species concerned is more tolerant of this condition than its normal associates. For instance *Viscaria alpina* can apparently tolerate a copper content in the soil toxic to most species. Again what favours vegetative growth is often detrimental to seed production and which of these is the more important may vary from time to time in one and the same plant community. Experiments have repeatedly shown that the optimum conditions with respect to various factors alter with the stage of development of the individual and also its susceptibility.

"The field for the problem and the laboratory for the solution" is only very partially true for ecological studies, for laboratory findings must be transmuted into the far more complex context of so many other variables that experience alone can guide as to what may be applicable and to what degree. But field studies, both observational and experimental, should serve as the means for testing hypotheses based upon what the plant physiologist has ascertained. Ecology is essentially applied plant physiology with the competition factor as an important modifying influence in a physical environment that represents the interaction of climatic, edaphic, and biotic factors that are themselves abstractions from a sequence of continual change.

The emphasis on physiognomy that has formed the basis for some systems of classification of plant communities can be regarded as an attempt to utilize the plants themselves as integrators of the physical conditions and the concept of the so-called indicator species is but another aspect of the same theme.

When extreme conditions are under consideration the correlation of physiognomy with habitat conditions is sometimes surprisingly high as is well exhibited, for example, on some of the sandy arid areas in South-West Australia, where communities are encountered consisting of species of the most diverse genera and families yet resembling one another so closely in their general physiognomy as to be difficult to distinguish except when in flower or fruit. In less differentiated conditions, however, as for instance in the temperate woodland, the same stratum, where there is relative uniformity of environment, often presents a great range of morphological diversity that suggests either that physiognomy is an unsatisfactory guide or that our knowledge must be greatly increased by experiments, in the field of environmental morphogenesis, before we are in a position to assess what morphological characteristics are significant and what are irrelevant.

The stratification and seasonal development of aerial shoots, to which attention was drawn by Kerner Von Marilau nearly a century ago, and of the subterranean organs, which the late Dr. Woodhead was one of the first to

investigate, both affect the competitive efficiency of the species whilst the periodicity of the important phases of the life history and their modifications by the environment are no less significant though too little investigated.

These latter, for economic reasons, are better known with respect to horticultural plants. The gardener is familiar with the fact that most plants are best moved in the dormant state, yet most species of *Helleborus* thrive best if transplanted when in full flower, a difference probably related to the phases of root development. Or again, careful investigations of bulbous species have shown how temperature fluctuations can affect differently diverse cultivars of the same species apparently by reason of their individual rhythms in the production of flower initials. What is true of cultivated plants is probably equally true of wild species and emphasizes for us that the understanding of the communal life of plants is dependent upon a knowledge of the idiosyncrasies of its chief constituents.

The structure and chemical characteristics of the soil as they affected plant life gained no small impetus from the work of Lawes and Gilbert, initiated in the early forties of last century, but the classical work of E. J. Russell on *Soil Conditions and Plant Growth*, which first appeared in 1912 and which passed through eight editions and has been translated into various languages, probably did more than any other single publication to bring before the minds of botanists the complexity as well as the importance of edaphic conditions upon vegetation. The soils that the agriculturist had studied were, however, to a very considerable degree physically homogenized by the processes of cultivation and chemically altered by their manurial treatment. It was not until ecologists began to pay attention to the organization that is exhibited by natural soils that the degree of applicability of the findings of the agriculturists could begin to be assessed. One of the earliest recognitions of the structure of natural soils and its relation to the vegetation which they bear was the study by Gesser and Siegrist of the profiles in the soils of the Aare communities in Switzerland[12A]. In this country the present writer called attention to the striking vertical gradients with respect to organic content, water content, soil reaction, and other features exhibited by woodland and sand-dune soils which provide a gradient of conditions for the root system[39A, 44]. These vertical changes not only contribute to the establishment and maintenance of the complementary communities of species but, as soils derived from a calcareous substratum strikingly show, can provide one and the same root system with a diversity of conditions favourable for the easy acquisition of the whole range of nutrient requirement from an acid surface layer from which the ions of iron and manganese may be readily obtained to an alkaline subsoil from which molybdenum is readily available.

The systems of soil classification developed particularly in relation to

highly differentiated climatic conditions, as for example by K. Glinka[15A], soon led to the recognition of climatic soil types but also the appreciation that under less extreme conditions, such as may obtain in western Europe and especially in Britain, the climatic conditions can cease to be the main factor in soil genesis and the nature of the substrate from which the soil is derived becomes of great significance.

In Britain the criss-cross, of changing climatic characteristics from East to West and North to South, superimposed upon the rapidly changing geological strata from the more recent towards the South and East to the older in the West and North, has produced in the British Isles a peculiarly intricate mosaic of soil conditions that has been still further complicated by the glaciations and the post-glacial loess that now appears to have been even more widespread than had hitherto been envisaged as shown by the investigations of Perrin, Coombe and others[46]. These various soils may enhance or ameliorate the effect of present-day local climate and this has enabled a greater diversity of immigrant species to persist in British plant communities than might otherwise be able to survive[41].

For a long time the significance of soil aeration was ignored and Clements in 1921 did a service to this aspect of ecology by bringing together much of the relevant literature[7]. See also [37]. Recent work would seem to emphasize its importance not merely by reason of its influence on the extent of the root development but also because the actual intake of the nutrients appears to be directly related to efficient aeration of the adsorbing cells that can provide the energy for intake against an adverse gradient.

From the data furnished by Hopkins and his associates[21] it would appear that the intake, of plant nutrients generally, decreases with the reduction of the oxygen content of the atmosphere that surrounds the root-system. The effect upon the intake of the trace elements appears to be less than for the major nutrients whilst sodium intake would seem actually to augment with diminished oxygen supply, a feature that may be of considerable import for vegetation growing on soils liable to flooding by sea-water. Both the oxygen content of the soil-atmosphere and its carbon-dioxide content are important and depend upon the activity of soil organisms and the freedom of diffusion with the air above, which latter is facilitated by volumetric changes due to temperature fluctuations. So it is that under turf or woodland litter high carbon-dioxide concentrations may obtain, in illustration of which we may note that Russell and Appleyard recorded over 3 per cent under grassland and Harley and Brierley under beech-leaf litter from three to eleven times the amount in the atmosphere above[16].

A high organic content is often associated with a large microbial population so that the production of carbon dioxide is copious and the surface litter tends to retard diffusion as well as insulating the surface soil from rapid

temperature fluctuations. In assessing the climatic and edaphic factors as they affect plant life we have in the past been perhaps too apt to regard climate and soil conditions as separate abstractions so that a true soil ecology has been distorted by the partialities that are only valid in isolation.

The investigations of plant physiologists during recent decades have contributed to our appreciation of the direct influence of environment upon vegetation, notably in relation to two types of factors, the climatic and the edaphic. It is now over thirty years since Garner and Allard[12] published the results of their classical experiments demonstrating the influence of the relative duration of daylight and darkness upon growth and reproduction. Since that time the vast volume of literature on the photoperiodic response has revealed that, for a large number of species of flowering plants, flower formation is dependent either on the stimulus of a short period of darkness and a long day or the stimulus of a longer period of darkness and a shorter day. Variations in the relative duration of day and night could moreover retard or inhibit reproduction by seed and also influence the degree and character of vegetative growth[13]. For annual species whose growth rhythm is adjusted to such stimuli the latitudinal changes in photoperiodism may clearly operate as a limiting factor to their distribution, but for spreading perennials the substitution of vegetative multiplication for the production of fruit may well extend their geographical range. *Mercurialis perennis*, for example, so abundant in our basic woodlands, achieves success by means of its rhizomatous aggression although the reproductive capacity from seed towards its northern limits is negligible[43]. The specialization, which response to such stimuli implies, may therefore be advantageous, or the reverse, when the species concerned extends beyond the climatic conditions of its original home. It is significant therefore to note that some species have not developed any response relation to photoperiodic stimulation, as a time keeper of their growth rhythms, and that these include some of our commonest weeds such as the Chickweed (*Stellaria media*), the Shepherd's Purse (*Capsella* spp.), and *Poa annua* which flower and fruit at all seasons when temperature conditions permit and are well-nigh cosmopolitan in their distribution. For these and other such species the lack of photoperiodic response is manifestly a factor in their success and determines in part the role they play in vegetation. It is also to be noted that photoperiodic response can be markedly influenced by temperature and humidity[14] whilst within one and the same species long-day and short-day strains can be evolved.

Probably the chief contribution of physiology to an understanding of the habitat's direct influence in recent years was the discovery of what have been termed the micronutrients or trace elements. That extremely small quantities of certain elements, mostly only requisite in parts per million, were

nevertheless essential for plant life is due to their role in forming catalytic agents of various metabolic activities. Such micronutrients now regarded as generally necessary for the higher plants are boron[49], copper[29], zinc[6, 18, 19], manganese[31], and molybdenum[36]. But in addition to these, various other elements would appear to be at least beneficial, if not actually essential, to certain plants, as for example sodium and iodine, whilst though there is some experimental evidence for stimulation of growth by minute traces of, for example, titanium and arsenic, it seems unlikely that these play any significant part in determining the composition of plant communities or the degree of dominance of species. It should, however, always be borne in mind that owing to the "compound interest law" minute initial advantages may lead to significant final effects.

The quantitative estimation of amounts of such diminitude as that in which the trace elements occur, with an accuracy of within 10 per cent or less, is one of the triumphs of modern spectroscopic technology and these determinations have shown that deficiencies may often occur either through their inadequacy in the soil, through their absence, or through being rendered non-available. The last condition is exemplified in respect to manganese, zinc, and boron in markedly alkaline soils whilst copper deficiencies or manganese deficiencies can be brought about by microbiological activity[26]. The observation that certain characteristic appearances are associated with deficiencies of each of the various nutrients[48], both macro- and micro- alike, made practicable the survey of such occurrences over a far wider area than would have been possible if analyses alone could have sufficed. The outcome has been the recognition that the availability of most of the essential elements for the nutrition of the higher plants is very variable. In natural soils rain-water charged with CO_2 readily brings the calcium bicarbonate into solution and by base exchange with potassium and magnesium these also are readily leached from the soil so that deficiencies of all three are by no means uncommon. Calcium is never wholly absent from soils that can support higher plants since it is an essential constituent of their cell walls but the great range of concentration, from the so-called non-calcareous soils, devoid of free carbonates, to the highly calcareous soils of downs and dunes, is accompanied by a corresponding change in the character of the vegetation which may involve the replacement of a calcifuge by a calcicole species occupying a similar niche or the change from acid moorland to calcareous grassland. A recent review of the role of magnesium as a plant nutrient[23] shows that many natural soils in Europe may contain very small amounts, sometimes less than 0·01 per cent and magnesium deficiency is, in fact, frequent.

The large areas in South Australia that have been rendered fertile, by amending deficiencies of molybdenum, zinc, and copper, is sufficient evidence for the ecological significance of the distribution and availability

of trace elements. Though this is admittedly an extreme example the areas where deficiencies of one type or another have been recognized are continually being added to.

It is of considerable import that evidence has been furnished that some species are much more susceptible to such deficiencies than others whilst some plants can accumulate trace elements in a marked degree so that, when these are essential nutrients, such capacity must be an important asset in competition. On seleniferous soils grass herbage may be quite innocuous to stock whilst species of *Astragalus* if present can accumulate selenium to such an extent as to render the herbage lethal[47]. So, too, clovers will accumulate molybdenum and the Sun Spurge, *Euphorbia helioscopia*, is known to be able to accumulate boron, facts which suggest that competition for the micronutrients may, because they are frequently marginal in concentration, be more severe than for the macronutrients which are more commonly considered from this standpoint. Of these latter, deficiency of nitrogen is common in acid soils and those containing little organic material, whilst phosphate deficiency also characterizes acid soils in areas of high rainfall but especially when these are rich in organic matter since phosphorous in organic combination is even less readily available to the plant than from inorganic compounds such as iron-phosphate. Potassium deficiency is common on chalk, sandy soils, and peat.

Although much is known as to the respective demands that crop plants make upon the various nutrients and of their susceptibility to toxic concentrations of manganese or aluminium, our knowledge of wild species in these respects and of their powers of accumulation of nutrient ions is as yet fragmentary although these might well furnish the clue to many apparent idiosyncrasies of presence and absence in communities.

That the precise form in which an element is present may be far more significant than its amount is manifest from the efficiency of chelated compounds of iron and manganese for relieving deficiencies of these elements where other compounds are wholly ineffectual.

For the ecologist, as for the agricultural chemist, the problem is not the accurate determination of the total amounts of the various nutrients present but the estimation of the proportion of each which is in a form that the plant can assimilate. A recent investigation of New Zealand soils by D. E. Hogg, with respect to potassium, is illuminating in this connection[20]. Utilizing a number of standard methods of assessment he found that determinations of the exchangeable potassium corresponded closely to the response made by plants when potassium was supplied but only in the regions of high rainfall. In the areas of low rainfall assessment based upon nitric acid extraction showed a closer relationship with crop response.

It is manifest that the varying availability of the macro- and micro-nutrients

may have a direct effect upon the distribution of species and communities but the possibilities of indirect effects must not be ignored. We have already referred to the differential absorption of such potentially lethal elements as selenium and molybdenum which can be economically serious in relation to agriculture, but under natural conditions such differences might materially influence the biotic pressure exerted by the grazing animal. So obvious is it that a plant community is a social aggregate of its constituent species that one is apt to forget its implication, that all these must have similar environmental preferences or tolerances, except in so far as the presence of one or more species ameliorate, or exacerbate, the conditions for others. The obvious manifestation of this is the creation of shelter by taller species but there may be many other influences more subtle, as for instance the capacity of some species to tolerate and accumulate ions of alumina and manganese which may conceivably render conditions acceptable to other plants more susceptible to their toxic action.

It may be urged with some justice that many of the features we have mentioned as affecting distribution are mostly as yet only known to operate locally and determine the success of individual species rather than communities. That individual species can bring about vegetation changes of a widespread character is, however, witnessed by the disastrous extension of *Opuntia inermis* in Queensland or the spectacular spread of Rosebay-Willow-herb in Britain. It would appear to be the initial establishment and the build up of the population of a species to the requisite "infection pressure" that presents the major obstacles to marked extension and it is not least in this context that one should perhaps take particular cognizance of such discriminating causes.

So far we have made no reference to one class of biotic influences, namely the effects of animal life upon the nature of the plant community. No doubt in some degree it is true that the vigour of growth of vegetation and its rate of reproduction is adjusted to the hazards of the predators upon it, but it has been shown that Herbert Spencer's facile generalization is invalid[48] and even were it true the imposed burden for survival is a serious handicap in competition. Recently C. B. Huffaker has expressed the view that "changes in plant populations and insect populations are often reciprocally related phenomena"[22]. The profound effect of a high rabbit population in Australia and in Britain and its drastic diminution by myxomatosis has recently brought into prominence the differential influence that an animal population can impose. Only in recent years have population studies shown what high numbers vegetable feeders such as field-voles can attain and whilst the importance of animal life, both large and small, is doubtless profound, yet the assessment of its differential effects on plant communities still remains largely the subject-matter for future research.

Competition between species and its severity in a plant community is dependent upon the requirements of the constituents both as to what demands each makes upon the habitat and the degree of intensity of these demands with respect to time. All flowering plants require water and mineral nutrients and most require light but the claims made upon these may vary greatly with the species concerned. Competition ensues only when the supply is inadequate to meet the full requirements of all, a condition which may be attained with respect to light in open communities and with respect to water in aquatic ones.

Competition for light we have already briefly referred to. It is largely dependent upon potential height and leaf area on the one hand and on the other upon the specific compensation point. Competition for water and nutrients is clearly dependent upon the differing capacity of a species to obtain these and to develop a root system, in the presence of others, adequate to its demands with sufficient rapidity and this can only be accomplished if, *inter alia*, the requisite photosynthetic products are available to effect this growth. In assessing the adequacy of supplies of essentials it is necessary to distinguish, as in the human counterpart, between mere subsistence and what is requisite for vigorous growth.

It has been asserted that there is no competition between the herbaceous layer of a forest and the dominant trees but, as we have pointed out, the former may deprive the deeper-rooted trees of their water supply although in general it is between the species of the same stratum that competition is most severe.

Competition is perhaps most acute in the early stages of growth when mortality is highest. Between individuals of the same species an equilibrium may be established so that over a wide range of population density the total productivity is very similar as has been shown in numerous crop spacing experiments. Between different species the reactions vary greatly. Some, which are closely allied and make similar demands upon the habitat (e.g. *Cerastium semidecandrum* and *C. tetrandrum*) may attain a measure of equilibrium but with open communities priority of establishment is significant and hence the mode and times of germination and the processes of dispersal play their part. In perennials the mode of growth and rate of potential spread can play significant roles.

Plant succession can be thought of as in large part a competitive drift in which at each phase until the climax the constituent species render the habitat more favourable to their successors than to themselves. From this aspect the few species that appear to be able to establish an almost static condition, gain a special significance. The maritime communities dominated by *Halimione portulacoides* and *Spartina townsendii* may be cited as possible examples though their seeming stability may be but an illusion due to the slowness of their change.

The importance of the competition aspect of succession is that it emphasizes the slow rate at which competitive influences may operate, masking the almost imperceptible decline or augmentation of individual species despite the vagaries of seasonal fluctuations. One of the desiderata is for more actual data as to the time scale involved. We know, for instance, that weeds of arable land that reverts may survive for perhaps half a century, that some pioneer dune species may persist nearly a century, but the rate of a decline under various degrees of competitive pressure for the characteristic perennial species of communities could materially assist in estimating the relative importance of reproduction, vegetative spread, and life span as factors in aggressive capacity.

From this brief survey it is apparent that future progress demands a far more detailed analysis of the habitat factors alike in space and time and parallel with this a more meticulous assessment of the constituent organisms (cf.[80]) amongst which the importance of sub-specific taxa may far transcend the specific aggregates in ecological significance, alike with respect to their biological behaviour and their physiological attributes.

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GRUNDFRAGEN UND AUFGABEN DER PFLANZENSOZIOLOGIE*

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Es ist mir eine Ehre zum Festband des 200-jährigen Jubiläums der Royal Botanic Gardens einen Beitrag geben zu dürfen, hat doch das Weltzentrum der Pflanzensystematik, Kew, sehr wesentlich dazu beigetragen, das Grundmaterial des Pflanzensoziologen, die Sippenkunde zu schmieden. Auch ergeben sich zwischen Sippen- und Gesellschaftssystematik deutliche Parallelen, wennschon es die Vegetationskunde nicht mit entwicklungsgeschichtlich verbundenen systematischen Einheiten, sondern mit solchen der Zweckmässigkeit zu tun hat.

Die Pflanzensoziologie, wie wir sie heute verstehen, bildet einen, allerdings sehr bedeutsamen Bestandteil der Biosoziologie (Biozoenologie), die als Basiswissenschaft die Ergebnisse zahlreicher Wissensgebiete unter einem *ganz bestimmten Gesichtspunkt, dem des Zusammenlebens der Organismen, betrachtet* und zu fruchttragender neuer Erkenntnis führt.

Da sich die biosoziologische Forschung bis anhin vornehmlich mit den relativ stabilen, standörtlich gebundenen, wurzelnden und festhaftenden Pflanzengesellschaften befasst hat, während die unsteten Tiergesellschaften eher stiefmütterlich behandelt worden sind, ist es verständlich, dass Erstere ungleich besser bekannt sind als die Gesellschaften der Zoologen, die ihr begriffliches Werkzeug zum guten Teil dem Arsenal der Pflanzensoziologie entlehnen und sich auch zur Umgrenzung ihrer Gesellschaften vielfach auf die von den Pflanzensoziologen erarbeiteten Vegetationstypen stützen. Es ist dies übrigens zu begrüssen, denn nur so lässt sich hoffen, dem erstrebenswerten Ziel, der Erkenntnis der Pflanzen und Tiere umfassenden Organismengesellschaften (Biozoenosen) näher zu kommen. Ein Zoologe[26] (p. 66), der die Collembolenfauna alpiner Pflanzengesellschaften untersucht hat, findet dabei "un parallelisme frappant qui parle en faveur de la méthode biocénotique partant des groupements végétaux autotrophes."

PFLANZENSOZIOLOGISCHE EINHEITEN

Im Luftbild spiegelt sich die Vegetationsdecke der Erde als ein schwer entzifferbares Mosaik aus Wäldern, Wiesen, Mooren, Gebüschen, usw. Dieses Mosaik zu zergliedern, die Einzelglieder unter bestimmten Gesichtspunkten zu Typen zu vereinigen und sie in ihrer Struktur, ihren Lebensverhältnissen, ihrer Verbreitung, ihrem Werden und Vergehen und ihrem

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Verhalten zur Gesamtbiozoenose darzustellen, ist die Aufgabe der Pflanzensoziologie.

Dieses Ziel biosoziologischer Forschung, die Lebensgemeinschaften in ihrer gegenseitigen Bedingtheit und ungeheuren Vielfalt zu erfassen und zu erklären liegt allerdings noch in weiter Ferne. Wir müssen uns vorderhand begnügen, einzelne stofflich und gedanklich abgerundete Teilprobleme einer Lösung entgegenzuführen, sollten aber über dem Erreichten des Fragmentarischen der Resultate stets bewusst bleiben.

Im Vordergrund vegetationskundlicher Betrachtung stehen Fassung und Abgrenzung der Vegetationseinheiten, die in der Natur unter ähnlichen Aussenbedingungen regelmässig wiederkehren.

Diese unter sich mehr oder weniger übereinstimmenden Vegetationsausschnitte, Kristallisationspunkte des Zusammenlebens der Pflanzen, bilden das Grundgerüst der Vegetationssystematik. Wir bezeichnen sie am besten mit dem neutralen Ausdruck Vegetationstypen. Im Mosaik des Pflanzenteppichs treten sie oft schon visuell als deutlich umgrenzte Einheiten hervor. Sie wechseln ab mit Pflanzengruppierungen, die als Mischungen, Verarmungen, oder auch als einmalige Zufallserscheinungen aufzufassen sind.

Die Fassung und Abgrenzung der Vegetationstypen kann nach zwei grundsätzlich verschiedenen Gesichtspunkten vorgenommen werden.

In Gebieten, wo die atomistischen Bausteine der Pflanzengesellschaften, die Arten resp. Sippen, nicht oder ganz ungenügend bekannt sind, muss man sich mit der Unterscheidung *physiognomisch* abgrenzbarer Pflanzenbestände begnügen. Gleichartige Vegetationsbilder, unter dem Begriff der Formation vereinigt, gestatten einen ersten, wenn auch ziemlich oberflächlichen Einblick in die Vegetationsgruppierung. Sie können zur vorläufigen Beschreibung der Pflanzendecke neu erschlossener Länder mit reicher Flora nützliche Verwendung finden.

Die frühesten derartigen Vegetationsbeschreibungen beruhen auf physiognomisch unterschiedenen Formationen und Formationsgruppen. Zu Formationsklassen vereinigt, auf Standorts- oder Klimaverhältnisse, oder auch auf beides zugleich abgestimmt, vermitteln sie grossräumige Vegetationsübersichten, wie sie um die Jahrhundertwende durch Warming[83], Schimper[70], Drude[17], Diels[16], Brockmann-Rübel[10], u.a. gegeben worden sind. Die kartographische Darstellung dieser Vegetationstypen gibt ein gutes Bild ihrer Verteilung auf der Erdoberfläche, ein tieferes Eindringen in die Oekologie dieser umfassenden Vegetationseinheiten ist allerdings schon wegen ihrer standörtlichen Unausgeglichenheit ausgeschlossen.

Schon 1863 hatte Kerner[42] (p. 11) vorgeschlagen zur Schilderung der Pflanzenformationen die sog. Grundformen zu benutzen. Sie sind 1907 durch Raunkiaer zu einem eigentlichen Lebensformensystem ausgebaut

worden, worin die Pflanzen nach der Überdauerungsart ihrer Erneuerungssprosse während der ungünstigen Vegetationszeit angeordnet sind.

Die Berücksichtigung der Lebensformen ermöglicht eine feinere physiognomisch-ökologische Charakterisierung der Pflanzenbestände, dagegen vermögen Lebensformengruppierungen, wie alle auf den Arteninhalt verzichtenden physiognomisch-ökologischen Einteilungen, den Anforderungen einer allgemein gültigen Gesellschaftssystematik nicht zu genügen.

Das einzige objektiv fassbare Ausgangsmaterial hiefür sind, darüber ist man sich heute einig, die Arten (Taxa) der Sippensystematik.

Die auf der floristischen Artenverbindung beruhenden pflanzensoziologischen Einheiten haben den enormen Vorteil, dass aus der floristischen Zusammensetzung gewissermassen automatisch weitere wichtige Eigenschaften wie Aussehen, Entwicklungsgrad, Lebens- und Konkurrenzverhältnisse, Verbreitungsareal usw. der Gesellschaft hervorgehen. Der statistisch-mathematischen Behandlung floristisch gefasster Vegetationseinheiten steht kein Hindernis entgegen.

. Die Frage nach der Natürlichkeit einer solchen Einteilung erscheint müssig. Im Sinne von Kant ist ein System ein nach Prinzipien geordnetes Ganzes. „Ob die Natur an sich ein System bildet oder nicht können wir nicht entscheiden. Diese Entscheidung ist auch für die Wissenschaft von keiner Bedeutung" (Kant zit. in Bloch[4], p. 55).

ABGRENZUNG DER FLORISTISCHEN VEGETATIONSTYPEN

Die Herausarbeitung der Vegetationstypen beruht auf der Synthese unter sich floristisch mehr oder weniger gleichartiger Teilabschnitte des Pflanzenteppichs. Die Abgrenzung dieser Abschnitte (Einzelsiedlungen) ist, der oft unscharfen Grenzen wegen, manchmal nicht leicht. Sie kann auf verschiedene Weise geschehen, doch ist in jedem Fall möglichste Gleichartigkeit der Untersuchungsflächen anzustreben.

Ein objektives Verfahren, das darin besteht, irgendwelche beliebige Vegetationsausschnitte gleicher Grösse floristisch zu untersuchen und die Ergebnisse statistisch auszuwerten, ist äusserst zeitraubend, hat mehr theoretischen Wert und sei vorläufig zurückgestellt (s. p. 159).

Die Abgrenzung der Einzelsiedlungen kann sodann erfolgen nach übereinstimmenden Standortsverhältnissen, nach den vorherrschenden Arten, oder aber nach der regelmässig sich wiederholenden Verkettung bestimmter Artengruppierungen im Gelände.

1. Die grossen Vorläufer der Pflanzensoziologie, ein Sendtner, Kerner, Drude, Delpino, Clements, u.a. haben sich zur Abgrenzung ihrer sehr weitgefassten Gesellschaften vielfach der Standortsverhältnisse bedient.

Eine nähere Umschreibung der standörtlichen Gleichartigkeit stösst

freilich auf grösste Schwierigkeiten, sodass dieses Vorgehen heute höchstens in Verbindung mit andern Kriterien zur Anwendung gelangt.

2. Leichter ist die Fassung der Einzelbestände nach dem Vorherrschen einer oder weniger, durch ihre Dimensionen (Bäume, Sträucher) oder ihre Bodenbedeckung massgebender Arten. Es werden beispielsweise unterschieden ein *Pinus silvestris*-Wald, eine *Nardus*-Weide, ein *Calluna*- oder *Juniperus*- Bestand usf. Streng durchgeführt läuft man bei diesem Vorgehen Gefahr, ökologisch und floristisch durchaus heterogene Pflanzenbestände unter einen Typus zusammenzuschweissen. Auch lässt sich das Verfahren dort, wo deutlich vorherrschende Arten fehlen, nicht durchführen, es ist daher nicht allgemein anwendbar. In besonderen Fällen, wie in artenarmen Gebieten mit einförmiger Vegetation, kann es jedoch gute Dienste leisten. Auf die Dominanz gegründete Vegetationstypen werden mit dem vom VI. Botanikerkongress vorgeschlagenen Terminus als *Soziationen* bezeichnet.

3. Die zur Typisierung am häufigsten gebrauchte, allgemein anwendbare Methode, stützt sich auf das regelmässige Zusammentreten bestimmter Artenverbindungen unter ähnlichen Standortsverhältnissen.

Die drei Abgrenzungsmöglichkeiten lassen sich übrigens bis zu einem gewissen Grad kombinieren und es kann sogar der Fall eintreten, dass alle drei Vorgehen, besonders aber das erste und dritte, zum selben Resultat führen. Dass jedoch der von Du Rietz betonte „geschulte soziologische Blick" die Abgrenzung der Typen erleichtert, ist nicht zu bezweifeln.

Assoziation. Die sich aus der Zusammenfassung gleichartiger Einzelsiedlungen ergebenden abstrakten Vegetationstypen, die Grundeinheiten des floristischen Systems der Pflanzengesellschaften tragen die Bezeichnung *Assoziation.*

Sanktioniert wurde der Terminus am internationalen Botanikerkongress in Brüssel 1910. Die von Flahault und Schröter[23] vorgeschlagene, einstimmig angenommene Definition lautet:

„Eine Assoziation ist eine Pflanzengesellschaft von bestimmter floristischer Zusammensetzung, einheitlichen Standortsbedingungen und einheitlicher Physiognomie. Sie ist die grundlegende Einheit der Synökologie."

Mit der Annahme dieser Definition ist ein wichtiger Schritt zur Verselbständigung der Pflanzensoziologie als Wissenschaft vollzogen worden. Er hat sich nach zwei Seiten hin fruchtbar ausgewirkt.

Die Bedeutung der floristisch gefassten Vegetationseinheit wird anerkannt und kommt der exakten Vegetationsbeschreibung zugute, und indem die Assoziation zur Grundeinheit gestempelt wird, ist bereits die Möglichkeit einer Klassifizierung der Vegetationseinheiten vorweggenommen.

Die Brüsseler Definition, wenn auch späterhin modifiziert, hat sich, wie der gleichzeitig von Jaccard vorgeschlagene Terminus *Pflanzensoziologie*

allgemach einzubürgern vermocht.* Es erscheint daher gerechtfertigt den Beschluss von 1910, dem die grössten Geobotaniker ihrer Zeit zu Gevatter gestanden sind, *als die Geburtsstunde der modernen Pflanzensoziologie zu betrachten.*

Die Gliederung der grossräumigen physiognomisch-ökologischen Vegetationskomplexe, Vereinsklassen (Warming), Formationen usw. ist deduktiv. Sie müssen von oben herab in immer kleinere Einheiten zerlegt werden.

Indem man die Assoziation in den Mittelpunkt der Untersuchung rückt, wird, wie in der modernen biologischen Systematik überhaupt, die von den niederen zu höheren Einheiten fortschreitende induktive Einteilung angebahnt.

Wie können die Assoziationen erkannt und umschrieben werden?

Es empfiehlt sich, vorerst einen Überblick über die Pflanzengruppierungen eines grösseren einheitlichen Territoriums zu gewinnen. Dabei wird man feststellen, dass bestimmte Artenverbindungen unter ähnlichen Aussenbedingungen regelmässig in ähnlicher Zusammensetzung wiederkehren.

Man beginnt am besten mit der Abgrenzung und floristischen Aufnahme dieser einprägsamen Typen. Es werden Flächen bestimmter Grösse ausgewählt und auf alle vorhandenen Arten nebst ihren Mengenverhältnissen, ihrem Gedeihen (Vitalität, Fertilität), ihrer Geselligkeit (Soziabilität), ihrer Schichtenzugehörigkeit und unter Umständen weiterer struktureller Merkmale untersucht. Diese „Aufnahmen" sind, dem verfolgten Ziel angemessen, mehr oder weniger eingehend zu gestalten. In Waldgesellschaften können z.B. mit der Messung des Baumabstandes und des Baumalters auch die abhängigen Epiphytengesellschaften aufgenommen werden.

Die Grösse der Untersuchungsfläche, die beliebige Form haben kann, richtet sich ganz nach der vorliegenden Gesellschaft. Reicht bei manchen Gesellschaften zur Fassung der vollständigen Artenverbindung eine Fläche von 1–4 Quadratmetern aus, so beanspruchen Aufnahmen im Urwald und in Steppengebieten hundert und mehr Quadratmeter.

Anderseits vermindert sich die Aufnahmefläche bei gewissen Flechten- und Moosgesellschaften auf wenige Quadratdezimeter[3].

Die übereinstimmenden Einzelaufnahmen, betreffen sie nun scharf abgegrenzte Kleinquadrate, oder grössere homogene Flächen, sind das Tatsachenmaterial, worauf das pflanzensoziologische Lehrgebäude ruht, ihre Aufnahme verlangt grösste Sorgfalt.

Erstes Erfordernis jeder einwandfreien vegetationskundlichen Aufnahme ist die vollständige Artenliste, wenigstens hinsichtlich der Gefässpflanzen, wichtigeren Moose und Flechten.

Hernach sind die quantitativen Merkmale, Mengenverhältnisse usw. der Arten zu ermitteln.

* Nach Alechin[1] hat Krylow schon 1898 den Ausdruck Pflanzensoziologie verwendet.

Diese Merkmale unterliegen jedoch, besonders in ariden Gebieten, sowohl nach ihrer jahreszeitlichen Entwicklung, als von einem Jahr zum andern, starken Schwankungen. In Therophytengesellschaften sind diese quantitativen Merkmale vielfach nur approximativ feststellbar; schon im südlichen Europa gibt es Trockenjahre wo darin fast nichts zur Keimung gelangt.

Alle floristisch mehr oder weniger übereinstimmenden Siedlungen werden, unter Aussonderung stärker abweichender Aufnahmen, die gesondert zu betrachten sind, tabellarisch zusammengestellt. Ist die Übereinstimmung der Einzelaufnahmen gut, so hat man es mit deutlich ausgeprägten Typen zu tun, ist sie gering, so kann es sich um Durchdringungen und Vegetationsgemische handeln. Je besser die Übereinstimmung, je geringer die Amplitüde der Einzelaufnahmen, umso besser abgegrenzt, umso schärfer gefasst und, falls die Aufnahmen auf ein grösseres Gebiet Bezug haben, umso allgemeiner gültig der Vegetationstypus, umso wahrscheinlicher liegt eine Assoziation vor.

Eine Entscheidung hierüber gestattet der Vergleich aller auf das Untersuchungsgebiet bezüglicher Assoziationstabellen. Durch diesen Vergleich werden die floristische Selbständigkeit der unterschiedenen Einheiten und auch die sich aus dem gesamten Artenbestand ergebenden ökologischen, dynamogenetischen und chorologischen Verwandtschaftsbeziehungen aufgedeckt, da ja jeder Pflanze ein gewisser ökologischer, genetischer und chorologischer Zeigerwert innewohnt.

Des weiteren ergibt sich aus dem Tabellenvergleich das mehr oder weniger stete Auftreten wie auch die mehr oder weniger enge Lokalisierung der Arten auf bestimmte Gesellschaften.

Den *quantitativen* Merkmalen gesellen sich mithin bei der Tabellen-Auswertung zwei wichtige *qualitative* Gesellschaftsmerkmale hinzu: die auf die Stetigkeit des Artvorkommens gegründete *Konstanz*, ein Begriff, von Brockmann-Jerosch[9] geprägt, von den skandinavischen Forschern[18] seiner soziologischen Bedeutung entsprechend in erster Linie zur Charakterisierung der Gesellschaften herbeigezogen und die *Gesellschaftstreue*, worunter das Gebundensein der Arten an bestimmte Gesellschaften verstanden ist.

Gesellschaftstreue.—Jeder Feldbotaniker weiss, dass manche Sippen normalerweise nur an bestimmten Standorten oder in bestimmter Vergesellschaftung vorkommen, die sie charakterisieren helfen. Das Gebundensein dieser Arten an Standort und Gesellschaft bietet eine vorzügliche Handhabe, die Gesellschaften gegeneinander abzugrenzen. Nicht zu Unrecht sind diese Charakterarten mit den Leitfossilien der Geologen verglichen worden.

Welche Ursachen der Gesellschaftstreue zugrunde liegen, bleibt in jedem Einzelfall zu untersuchen. Zumeist handelt es sich um engbegrenzte

ökologische Anpassung der Arten an bestimmte Standortsverhältnisse, weshalb ihre Ökologie auch die Ökologie der Gesellschaft, der sie angehören, zu beleuchten vermag.

Es darf aber nicht, wie gelegentlich behauptet worden ist, geschlossen werden, die Assoziationen seien auf die Treue begründet. Dies ist keineswegs der Fall. Die Assoziation ist eine auf der Gesamtheit der floristisch nahe übereinstimmenden, mehr oder weniger homogenen Einzelaufnahmen beruhende Abstraktion und nicht bloss floristisch, sondern auch ökologisch, dynamogenetisch, und chorologisch charakterisiert. Dagegen erlangt die Gesellschaftstreue für die Unterscheidung der floristisch gefassten Assoziationen ungleich grösseres Gewicht und allgemeinere Bedeutung als alle bloss quantitativen Merkmale, vor allem dann, wenn sich die Treue mit hoher Konstanz verbindet.

Die Einführung des Treuebegriffs eröffnet ferner die Möglichkeit, die Vielzahl der unterschiedenen Vegetationseinheiten unter einen Hauptgesichtspunkt objektiv anzuordnen und damit eine logisch einwandfreie Gesellschaftssystematik zu begründen.

Am Ausbau dieser Gesellschaftssystematik wird heute allerwärts, auch von den Kryptogamenspezialisten, eifrig gearbeitet.

Da aber die Systematisierung der Gesellschaften ein grosses Beobachtungsmaterial (Tabellen) voraussetzt und Schritt für Schritt empirisch erarbeitet werden muss, sind mit fortschreitender Ausweitung unserer Kenntnisse auch etwa Änderungen in der systematischen Einschätzung und Stellung der Einheiten, sowie Namensänderungen verbunden. Die Schmiegsamkeit der Methode erlaubt indessen, sie dem System einzufügen ohne dass an dessen Grundprinzipien gerüttelt wird.

Umwertungen der Treueverhältnisse, die sich gelegentlich der weiteren pflanzensoziologischen Durcharbeitung grosser Gebiete aufdrängen, kann bis zu einem gewissen Grad vorgebeugt werden, indem man, wie Schwickerath[71] vorschlägt die Assoziationen weit fasst und die lokalen Abänderungen als Subassoziationen, Varianten, oder Rassen ansieht, oder aber, und dies scheint der gangbarste Weg, dass die Assoziationen und mit ihnen der Gültigkeitsbereich der Charakterarten auf klimatisch und physiographisch gut abgegrenzte Gebiete bezogen werden. Die Charakterarten haben sodann territorialen Wert.

Heute ist die Assoziationsystematik noch nicht soweit gediehen, eine Generalübersicht der Gesellschaften zu gestatten, doch existieren regionale Übersichten über grosse Gebiete von Europa (Holland, Nordwest- und Süddeutschland, Südfrankreich, Jugoslawien, Polen, Ungarn, Tchechoslowakei, Teile von Spanien) wie auch Zusammenstellungen einiger höherer Gesellschaftseinheiten (Ordnungen, Klassen) und es kann bereits an eine Übersicht der westeuropäischen Pflanzengesellschaften gedacht werden.

Die bisherigen Zusammenstellungen harren aber insofern der Vervollständigung, als darin Übergangsbestände, Mischungen, Verarmungen nicht oder nur unvollständig zur Darstellung kommen.

Wie in der Sippensystematik und in andern biologischen Bereichen hat man eben zuerst die deutlich geschiedenen Typen erkannt und beschrieben. Wenn B. Huber[37] (p. 7) betont, dass es weise Selbstbeschränkung war indem sich die Physiologie erst einmal an den einfachsten Objekten schulte und methodische Sicherheit gewann, so darf dieser Satz wohl auch auf die Vegetationskunde übertragen werden.

Beim Ausbau der pflanzensoziologischen Systematik ergab sich bald die Notwendigkeit, den Begriff der Gesellschaftstreue schärfer zu fassen.

Das absolute Gebundensein einer Sippe an bestimmte Assoziationen ist schon deshalb nicht oft zu erwarten, weil die Artareale das Areal der entsprechenden Assoziationen meist überschreiten. Soziologisch und ökologisch enger gebunden sind territorial begrenzte Charaktersippen: Unterarten, Rassen, Varietäten.

Weiter verbreitete Arten können in mehreren räumlich getrennten Assoziationen als Charakterarten auftreten; um aber unter verändertem Klima bestehen zu können, wechseln sie nicht selten ihren Wuchsort und gehen beispielsweise vom trockenen Südhang des kühlfeuchten Gebietes auf den Schattenhang des benachbarten Trockengebietes über oder umgekehrt; es sind Arten mit breiter ökologischer Amplitüde. *Bromus erectus*, nach Tüxen eine Charakterart des *Mesobromion* Nordwestdeutschlands und Besiedler warmer Trockenhänge, zieht sich im xerischen Mittelwallis mit Vorliebe in das *Brometo-Pulsatilletum* schattiger Nordhänge zurück. *Sieglingia decumbens* des mitteleuropäischen Magerrasens hält sich im mediterranen Languedoc an das bodennasse *Dorycnieto-Schoenetum* usw.

Für diese und ähnliche Erscheinungen haben die russischen Steppenforscher die Begriffe zonal und extrazonal geprägt[1] (p. 365).

Selbstverständlich beziehen sich die Treueverhältnisse der Arten zunächst auf das untersuchte Gebiet, was aber nicht ausschliesst, dass ihnen oft ein viel weiterer Gültigkeitsbereich zukommt. Die von W. Koch[44] für das kleine Linthgebiet in der Schweiz erkannten Charakterarten einiger Wasser- und Sumpfgesellschaften haben sich später als viel allgemeiner gültig erwiesen. Das Gleiche gilt für die Charakterarten der von Br.-Bl., H. Pallmann und R. Bach[7] floristisch und ökologisch, insbesondere bodenkundlich untersuchten Waldgesellschaften des Schweizerischen Nationalparks in Graubünden.

Wird die Treue auf eine bestimmte Assoziation bezogen, so kann man unterscheiden zwischen lokaler, d.h. auf ein bestimmtes engeres, und territorialer, auf ein ausgedehnteres Gebiet bezüglicher Treue; eine strenge Grenze lässt sich freilich nicht ziehen.

Zur Bestimmung des Treuegrades der Arten dienen in erster Linie die Assoziationstabellen. Szafer und Pawlowski[74] geben ein Schema zu ihrer objektiven Bestimmung. Pfeiffer[64] schlägt vor, hiezu den prozentualen Anteil der in Prozenten ermittelten Stetigkeitswerte aller Assoziationen in denen die betreffende Art typisch vorkommt zu benützen.

Die Methode kann weiter objektiviert werden durch Einrichtung einer soziologischen Artenkartei, die Stetigkeit, Abundanz und eventuell Vitalität der Arten im Bereich aller Assoziationen und auch ihr gelegentliches Vorkommen unter Ausnahmebedingungen ausserhalb der tabellarisierten Assoziationen verzeichnet.

Wenn Goodall[28] (p. 454) bei der Besprechung des Treubegriffs annimmt; „It seems that the conclusions (über die Treue) are based on general visual observations rather than on the areas studied in detail" so mag dies in Einzelfällen zutreffen, besonders wenn nur schwaches Tabellenmaterial vorliegt. Selbstverständlich gibt es auch nach pflanzensoziologischen Methoden ausgeführte ungenügende und überflüssige Arbeiten, aber wie Giacomini[24], betont: „Tutto ciō dipende come in ogni altro orientamento dall' intelligenza ed accuratezza di chi lo applica."

Je weiter die Aufnahmearbeit der Gesellschaften fortschreitet, je besser durchgearbeitet die Tabellen sind, umso weniger Schwierigkeiten bereitet die Erkennung der Charakterarten, wie auch jene der sog. Trenn- oder Differentialarten, d.h. der Sippen, die, ohne für eine Gesellschaft charakteristisch zu sein, dazu beitragen, zwei oder mehrere Gesellschaften gegeneinander abzugrenzen.

Beim Ausbau der pflanzensoziologischen Systematik hat sich ergeben, dass die Brüsseler Definition der Assoziation von 1910, um allgemein anwendbar zu sein, einer Erweiterung bedarf. Es sollen ihrer hierarchischen Grössenordnung nach möglichst vergleichbare Typen geschaffen werden. Sodann muss die Definition den Kryptogamengesellschaften Rechnung tragen und so formuliert sein, dass einer allzuweit gehenden Aufsplitterung der Grundeinheit vorgebeugt wird, schon um ein chaotisches Anwachsen der Assoziationen zu verhindern. Dem Vorschlag den Assoziationsbegriff lediglich auf das Vorhandensein einer „bestimmten Artenkombination" zu gründen kann daher schon aus diesem Grund selbst dann nicht stattgegeben werden, wenn zur Abgrenzung allen übrigen gesellschaftsbedingenden Faktoren ein Mitspracherecht eingeräumt wird.

Am nächsten kommt man obigen Anforderungen durch die Verankerung des Treuebegriffs in der Assoziationsdefinition.

Die Assoziation wäre demnach zu definieren als „eine Pflanzengesellschaft von bestimmter Artenkombination und bestimmten Standortsansprüchen, die durch das Vorhandensein von Charakterarten (treuen, festen oder holden) eine gewisse floristische und ökologische Selbständigkeit anzeigt."

In der äusserst artenarmen einförmigen Vegetation Nordeuropas sind die ausgedehnten, ins Auge fallenden Vegetationstypen nicht Assoziationen, sondern auf die Dominanz gegründete Soziationen oder, wenn man will, Subassoziationen oder Varianten. Sie können jedoch, wie Nordhagen[58, 59] dartut, nichtsdestoweniger unter Verwendung der Treue zu Assoziationen und höheren Einheiten vereinigt werden.

Ähnlich verhält es sich mit sehr primitiven Einheiten epiphytischer Flechtengesellschaften (Soziationen, usw.), die nach Barkman[3] erst bei einem Verband oder einer Ordnung eingereiht werden können.

Das Hauptgewicht der Assoziationsdefinition liegt wohlverstanden auf der *charakteristischen Artenverbindung*. Die Charakterarten tragen dazu bei, begrifflich und ihrer Grössenordnung nach gleichwertigere abstrakte Einheiten zu schaffen, sind aber nicht unbedingtes Erfordernis eines *jeden* konkreten Einzelbestandes. Einzelbestände die ihrer gesamten Artenverbindung nach unzweifelhaft einer bestimmten Gesellschaft zugehören, können unter Umständen keine einzige ihrer Charakterarten enthalten.

Die Charakterarten als Indikatoren der floristischen und ökologischen Selbständigkeit der unterschiedenen Vegetationseinheiten zeugen, falls im Einzelbestand mehr oder weniger vollständig vorhanden, für dessen „typische" Ausbildung. Daher enthalten junge, unausgeglichene Bestände oft keine oder wenige Charakterarten. Dieselben erscheinen in der Regel erst, wenn der Biotop eine gewisse Reife erlangt hat.

Vegetationsausschnitte ohne Charakterarten (bei unter sich gleichbleibender floristischer Zusammensetzung) sind entweder ökologisch oder verbreitungsgeschichtlich bedingte Verarmungen, Initial- oder (meist menschlich bedingte) kurzdauernde Übergangsstadien, oder dann Mischungen von zwei (oder seltener) mehreren Assoziationen.

Die Gesellschaftstreue, anfänglich subjektiv eingeschätzt, eine Hypothese, ist mit der Ausweitung unserer Erkenntnisse zur Tatsache geworden, die heute kaum noch angefochten wird. Dass sie auch für die Kryptogamenvereine, wie für die Organismengesellschaften überhaupt zutrifft, geht aus einer Fülle von Spezialarbeiten auf den verschiedensten Gebieten hervor.

Mit der Soziologie der Planktongesellschaften beschäftigen sich Heimans[33], van Oye[61] und vor allem Margalef[51, 52], die Soziologie der kryptogamischen Epiphyten hat kürzlich durch Barkman[3], jene der Pilze durch Höfler[35, 36] und seine Schule wesentliche Vertiefung in unserem Sinne erfahren.

Dass der Treuebegriff auch zur Fassung der submarinen Biozoenosen (Pflanzen- und Tiergemeinschaften) von Wert ist, geht aus einer soeben vor der Sorbonne von Roger Molinier verteidigten Thesis über die Unterseevegetation an der Mittelmeerküste am Cap Corse hervor.

Die Wichtigkeit und weltweite Anwendungsmöglichkeit des Treuebegriffs

für die Abgrenzung der Organismengesellschaften hat ihn auch zum leitenden *Ordnungsprinzip*, man kann sagen, vorausbestimmt:

„En dehors de sa supériorité philosophique indéniable la fidélité présente cet avantage pratique que sa détermination ouvre en quelque sorte automatiquement, la voie aux rapprochements systématiques" Pavillard[63] (p. 94)

Die Gesellschaftstreue erlaubt floristisch und daher auch ökologisch Zusammengehöriges zu immer umfassenderen Einheiten (Verbänden, Ordnungen, Klassen, Klassengruppen) logisch zu verknüpfen, was von keiner bisherigen Systematisierungsmethode in gleichen Masse gesagt werden kann. Gegenüber jedem mehrdimensionalen oder netzartigen Klassifizierungsversuch, hat sie ferner den Vorteil der Klarheit, Geschlossenheit und allgemeinen Anwendbarkeit. Aus dem bisherigen Erfolg dieser Systematik darf auf ihre Berechtigung geschlossen werden.

Dass, wie bei jeder Systematisierung vielgestaltiger Dinge, gewisse Beziehungen des komplexen Zusammenlebens unberücksichtigt bleiben, andere zerrissen werden müssen, lässt sich nicht umgehen.

HÖHERE VEGETATIONSEINHEITEN

Die nach Grössenordnung abgestuften floristischen Gesellschaftseinheiten (Assoziationen, Verbände, usw.) lassen sich nach verschiedenen Gesichtspunkten anordnen: nach ihrer Komplexität, nach den dominierenden Lebensformen, nach der soziologischen Progression (Organisationshöhe), vom strukturell Einfachsten bis zum Vollkommensten u.a.

Als bei weitem fruchtbarste Anordnung hat sich indessen die Klassifizierung nach der floristischen Verwandtschaft erwiesen, die vielfache Beziehungen aufdeckt und weitausgreifende Vergleiche ermöglicht. Sie schliesst die Assoziationen in erster Linie nach ihrer Arten-Übereinstimmung auf Grund von Verbandscharakterarten zu Verbänden, die Verbände zu Ordnungen usw. zusammen. Die über der Assoziation stehenden Einheiten sind meist durch eine stattliche Anzahl ihr eigener Charakterarten gekennzeichnet.

Schon Gisin hat darauf hingewiesen, dass die solcherweise nach der charakteristischen Artenkombination unterschiedenen Lebensgemeinschaften keineswegs nur statistischen Wert haben; „Sie sind gleichzeitig ökologisch, weil die Statistik durch die Korrelationen ökologische Verwandtschaften oder Verschiedenheiten aufdeckt"[27] (p. 154).

Wie die Assoziation, so ist auch der Verband und sind desgleichen alle höheren Einheiten sowohl floristisch, als ökologisch, chorologisch und dynamogenetisch, d.h. nach der Entstehungsart charakterisiert.

Die Unterscheidung und Abgrenzung der hohen Gesellschaftseinheiten ist heute noch im Fluss, doch dürften für unsern Kontinent viele Ordnungen und die meisten Klassen bereits festgelegt sein.

Als eine neue, der Klasse übergeordnete umfassendste Gesellschaftseinheit erscheint die *Klassengruppe*. Hierunter verstehen wir in Anlehnung an einen brieflichen, durch R. Tüxen unterstützten Hinweis von Schmithüsen auf die Notwendigkeit einer höchsten Einheit, Vegetationsklassen örtlich weit getrennter aber klimatisch ähnlicher Lebensbezirke, deren florengeschichtlicher Zusammenhang sowohl durch identische, als insbesondere auch durch zahlreiche vikarierende Arten gleicher Gattungen erhärtet ist. Die Gesellschaften stimmen hinsichtlich der meisten Gattungen überein, die meisten oder fast alle Arten sind jedoch verschieden. Es handelt sich um analog entwickelte Paralleleinheiten ehemals enger verbundener Erdbezirke, die sich klimatisch und ökologisch entsprechen. Die klassenverbindende Treue verschiebt sich aber teilweise von den Arten auf die Gattungen.

Als besonders drastisches Beispiel einer Klassengruppe seien die europäische *Vaccinio-Piceetea*-Klasse und die ihr vollkommen entsprechenden Koniferenwaldungen und Vacciniumheiden des nördlichen Nordamerika und Japan einander gegenübergestellt.

Der von Cooper, Prat u.a. beschriebene *Abies balsamea*-Wald am Lake Superior und im südlichen Canada hat die meisten Gattungen und sogar nicht wenige Arten mit den mitteleuropäischen *Vaccinio-Piceetea*-Waldungen gemein und dürfte einer nordamerikanischen Parallelklasse der *Vaccinio-Piceetea* (*Vaccinio-Piceetea boreoamericana*) entsprechen.

Ähnlich verhält es sich mit den von Tatewaki und Takahashi[77] (p. 86) aus den Bergen von Hokkaido beschriebenen Wäldern von *Picea jezoensis*, *P. glehni*, *Abies sachalinensis*, die sicherlich eine eigene japanische Klasse (*Vaccinio-Piceetea japonica*) darstellen. Die Moos- und Flechtenschicht dieser Waldungen stimmt sogar in der Artenzusammensetzung weitgehend mit jener der europäischen *Vaccinio-Piceetea*-Wälder überein. Unter den Phanerogamen der *Picea jezoensis- P. glehni- Abies sachalinensis*-Soziation finden wir *Oxalis acetosella*, *Mayanthemum bifolium*, *Pyrola secunda* vertreten, ferner Ersatzarten der Gattungen *Abies*, *Picea*, *Polypodium*, *Carex*, *Lycopodium*, *Cornus*, *Solidago*, aber bloss 4 spezifisch ostasiatische Gattungen mit je einer Art. 71 Prozent der Gattungen (Kryptogamen nicht einmal eingerechnet) stimmen mit jenen der europäischen *Vaccinio-Piceetea*-Klasse überein.

Nicht weniger überraschend und auf die tertiäre nordatlantische Landbrücke hinweisend ist die Art- und Gattungsverwandtschaft zwischen der *Empetrum-Vaccinium*-Heide der mitteleuropäischen Hochgebirge und jener der Kurilen. Die sieben von Tatewaki[77A] beschriebenen *Empetrum*-Soziationen zeigen einen ausgeprägten Parallelismus mit Gesellschaften des *Rhodoreto-Vaccinion* der subalpinen Stufe der Alpen.

Ähnliche, durch Gattungsbeziehungen verkettete Klassengruppen sind auch in andern grossen Vegetationskreisen, wie dem saharo-sindischen,

dem mediterranen, nachzuweisen; die Möglichkeit sie herauszuarbeiten ist heute gegeben.

In der Klassengruppe sind in jeder Hinsicht analoge grossräumige Gesellschaften zusammengefasst, die sich in ihren Wohngebieten gegenseitig vertreten und ersetzen.

Zur Fassung dieser Klassengruppen leistet der generische Gemeinschaftskoeffizient gute Dienste. Durch ihn gelangen auch weit zurückreichende florengeschichtliche Beziehungen, sowie ökologische und selbstverständlich physiognomische Übereinstimmungen zum Ausdruck.

Das Ringen um eine pflanzensoziologische Systematik entspringt zwar in erster Linie dem menschlichen Ordnungsbedürfnis, die Systematisierung der Gesellschaften fördert aber auch wichtige Kausalitätsfragen und eröffnet Ausblicke auf einen von vornherein kaum übersehbaren Forschungskomplex, der tief in die angewandten Wissenschaften, Land- und Forstwirtschaft, Kulturtechnik, Gewässerkunde usw. eingreift.

Der Ökologe ist am Ausbau der pflanzensoziologischen Systematik insofern interessiert, als sie eine stabile Vergleichsbasis vorbereitet, die erlaubt, ökologische Untersuchungsergebnisse von verschiedenen Punkten und aus verschiedenen Gebieten auf einen Nenner zu bringen und direkt miteinander zu vergleichen. Auf bestimmte Gesellschaftseinheiten bezogen, gewinnen die ökologischen Messungen an Vergleichswert und tragen zum besseren Verständnis des Gesellschaftshaushaltes bei.

Erfreulicherweise beteiligen sich heute auch Kryptogamenforscher am Ausbau der pflanzensoziologischen Systematik und Untersuchungsmethoden. Bei dem wachsenden Interesse, das die Zoologen den generellen biosoziologischen Problemen entgegenbringen (Phillips[65], Prenant[66], Thieneman[78], Westhoff-Moerzer[84], Gisin[26, 27], Margalef[51, 52]; Rabeler[67], Remane[68], Giacomini u. Sacchi[25], u.a.), ist eine fortschreitende Verallgemeinerung wichtiger Grundbegriffe und Termini zu erhoffen.

Nach welchen Richtungen sind weitere Fortschritte auf dem Gebiet pflanzensoziologischer Forschung möglich und zu erwarten?

1. *Statistik*

Im Vordergrund stehen gegenwärtig Diskussionen über die Anwendung statistischer Methoden bei den Siedlungsaufnahmen und bei der rechnerischen Auswertung der Gesellschaftstabellen. Beide Bestrebungen sind streng auseinander zu halten.

Die mathematische Behandlung der Aufnahmen verlangt ohne irgendwelche Voreingenommenheit völlig objektiv abgegrenzte, gleichgrosse Untersuchungsflächen. Diese objektive statistische Ausgangstechnik hat Goodall im australischen Mallee-Shrub angewandt.

Es wurden 256 regelmässig über eine Fläche von 640 m² verteilte Kleinquadrate von je 5 m² auf das Vorhandensein von 14 häufigen Arten untersucht. Aus der vergleichend-statistischen Behandlung dieser Quadrate folgert der Autor[28] (p. 62), dass die Vegetation ein Kontinuum darstelle, die Unterscheidung von Assoziationen infolgedessen rein künstlich sei.

Berücksichtigt man, dass Goodall fünf Tage benötigte um seine Kleinquadrate statistisch auszuwerten, so wird man Ellenberg[20] (p. 16) beipflichten müssen, der annimmt, dass blosse vergleichende Beobachtungen wahrscheinlich viel rascher zum gleichen Resultat geführt hätten.

Dürfen diese Resultate aus dem *Eucalyptus*-Busch verallgemeinert werden? Ist die Methode (Auswahl von 14 Arten) einwandfrei und wie lässt sich damit in strukturell komplizierter Vegetation arbeiten? Dies alles sind offene Fragen.

Die Auffassung der Vegetation als Kontinuum kann nicht befriedigen. Abgesehen von der Aufteilung der Biosphaere in Wasser, Luft und Boden mit den entsprechenden, deutlich getrennten Lebensbezirken treten uns scharfe Assoziationgrenzen überall dort entgegen, wo die Aussenfaktoren (vor allem die edaphischen) einem raschen, durchgreifenden Wechsel unterliegen. Wir haben 1926[6] (p. 257) darauf aufmerksam gemacht, dass allmähliche kleine ökologische (edaphische) Änderungen auch eine allmähliche Änderung des Artenbestandes bedingen. Ähnliche regelmässige Mischungen und Durchdringungen sind besonders im Grenzgebiet zweier Klimaxgesellschaften nicht selten, bleiben aber auf ein relative schmales Übergangsgebiet beschränkt.

Ein anscheinend regelloses Gemisch aus verschiedenen Gesellschaften ist nur dort zu erwarten, wo der Standort oft wiederholten biotischen Eingriffen von wechselnder Intensität unterliegt, oder wo die edaphischen Faktoren auf kleinstem Raum mosaikartig wechseln.

In Gegensatz zu Goodall anerkennt Guinochet[31] die Existenz der Assoziationen, doch setzt auch er sich für die statistische Technik bei der Vegetationsaufnahme ein. Er verlangt, dass die Aufnahmenflächen nicht subjektiv ausgewählt werden, doch sollen sie floristisch homogen sein, eine Forderung die das Kriterium für die Flächenauswahl einfach auf die *Homogenität* verlagert.

Was haben wir unter *Homogenität* der Vegetation zu verstehen? Hierüber gehen seit Nordhagen[58], Kylin[46], Romell[69] die Meinugen zu weit auseinander, als dass eine Einigung zu erhoffen wäre. Der Begriff lässt übrigens an Klarheit sehr zu wünschen übrig (s. 64).

Guinochet bringt die Homogenität mit dem Minimiareal in Verbindung und bezeichnet als homogen einen Vegetationsausschnitt, der dem Minimiareal entspricht. Damit gerät man jedoch in einen circulus viciosus, sind

doch, um das Minimiareal zu bestimmen, *floristisch homogene* Aufnahmen erforderlich.

Die Ausgeglichenheit (Homogenität) ist anscheinend mathematisch überhaupt nicht fassbar; sie richtet sich nach der zu untersuchenden Vegetation und wird von der subjektiven Auffassung des Forschers beeinflusst. Auch regelmässige Mischungen zweier oder mehrerer Gesellschaften können homogen aussehen. Wenn Kalliola[41] (p. 40) bemerkt, „Wie hoch die qualitative und quantitative Homogenität sein muss, lässt sich nicht genau bestimmen" so muss man ihm wohl beipflichten. Numata[60] (p. 209) schreibt: „The fitness of the law of geometrical progression of the population density to a plant community is a reflex of a communal homogeneity. But the law was *denied* at several vegetation which we had investigated."

Ein Mathematiker[2] gelangt zum Schluss: „On n'a encore jamais pu caractériser une surface homogène."

Es empfiehlt sich somit bei der Abgrenzung der Untersuchungsflächen zwar auf möglichst grosse floristische und physiognomische Einheitlichkeit in den Hauptschichten und in den Standortsverhältnissen zu achten; man darf aber eine scharfe Präzisierung dieser Homogenität nicht erwarten.

Ist für die Auswahl und Abgrenzung der Einzelsiedlungen (Assoziationsindividuen) im Gelände von der Statistik wenig zu erhoffen, so verhält es sich anders bei der statistischen Auswertung der Assoziationen und Assoziationstabellen.

Als Erster hat wohl Jaccard[38] (p. 86) darauf aufmerksam gemacht. Er schreibt. „La lutte qui s'établit entre tous les candidats à l'occupation d'une station détérmine donc une véritable sélection, l'une sélective, l'autre éliminatoire. Mais ce qu'il importe de noter, c'est que cette sélection s'effectue non au hasard, mais suivant certaines règles, suivant certaines proportions numériques qui trouvent leur expression dans le *Coéfficient de communauté des espèces.*"

Durch den Gemeinschaftskoeffizienten Jaccards lässt sich die floristische Übereinstimmung der Aufnahmen einer Assoziation, wie auch die der Assoziationen untereinander statistisch ausdrücken, doch ist nicht zu vergessen, dass es nicht allein genügt zu zählen; es müssen, wie schon Pavillard[62] betont, die Arten auch nach ihrer soziologischen Wertigkeit abgewogen werden.

Eine Weiterentwicklung der Ideen Jaccards, unter Zuhilfenahme der von Cekanowsky für anthropologisch-systematische Studien verwendeten graphischen Methode versuchte Kulczynski[45] anlässlich der Beschreibung der Pflanzenassoziationen der Pieninen. Er gelangte zur Aufstellung sogenannter Verwandtschaftskoeffizienten. Die angewandte Methode ist jedoch sehr zeitraubend und stösst auf derartige Schwierigkeiten, dass sie wenig Anklang

gefunden hat. Motyka[56] und Matuskiewicz[53] haben sich ihrer bedient. Sehr ähnlich ist auch Sörensen[72] vorgegangen.

Motyka betont[56] (p. 154) die Resultate nähern sich jenen der Zürich-Montpellier-Schule, wenn sie auch nur selten völlig damit übereinstimmten, auch könnten gewisse Aufnahmen unter zwei und sogar drei Assoziationen untergebracht werden. Die statistische Bearbeitung von 100 Aufnahmen durch Matuskiewicz endlich hat ergeben „dass die objektive, wenn auch umständliche statistische Methode von Cekanowsky-Kulczynski zu gleichen Resultaten führt wie die direkte Analyse auf Grund des Charakterartensystems, welche zugleich viel einfacher und zugänglicher ist"[53] (p. 215).

Am Ende seiner Forscherlaufbahn, kommt Jaccard selbst[40] (p. 135) zum Schluss: „j'éprouve pour ma part une légitime sceptique vis à vis des lois mathematiques donnant une interprétation générale des faits complexes de la biologie."

Besteht also vorderhand keine Ursache bei der Assoziationsbildung vor dem Kult der mathematischen Statistik (Leibundgut) zu kapitulieren, so mag immerhin unter Umständen eine statistische Kontrolle angezeigt sein. Durch diese Kritik wird natürlich der Wert des Gemeinschafskoeffizienten an und für sich nicht berührt (s. p. 20).

Einen wesentlichen Fortschritt bei der statistischen Auswertung der Vegetationstabellen bedeutet die von Goodall[29] zu pflanzensoziologischen Zwecken eingeführte Lochkartenmethode (fiches perforées), die gestattet, in kürzester Frist und auf einfachste Weise eine grosse Zahl von Aufnahmen zu vergleichen, die Gemeinschaftskoeffizienten zu ermitteln und auch weitere zeitraubende Berechnungen und Vergleiche, wie die Herausarbeitung von Charakter-und Trennarten und beliebige Korrelationen ohne Zeitverlust durchzuführen.

2. *Synökologie*

Der Unterscheidung der Pflanzengesellschaften und ihrer floristischen Beschreibung parallel läuft das Studium der Kausalität. Es hat aus begreiflichen Gründen mit den Fortschritten der pflanzensoziologischen Systematik nicht Schritt zu halten vermocht, wiewohl die ökologische Vertiefung, die ja erst zum richtigen Verständnis des Zusammenlebens führt, ein vordringliches Postulat darstellt. Die Klärung der ökologisch bedingten Gesetzmässigkeiten im Vegetationsgeschehen durch Messung der Aussenfaktoren ist nach wie vor eine der wichtigsten Aufgaben der Vegetationsforschung.

Auch Untersuchungen an Einzelpflanzen, im Rahmen bestimmter Gesellschaften, können synökologisch ausgewertet werden, handelt es sich doch beim Zusammenleben der Pflanzen um eine Art Kommensalismus.

Von der autökologischen unterscheidet sich die synökologische Betrachtungsweise durch die Einschaltung der Artenkonkurrenz. Dem äusserst

wichtigen Konkurrenzfaktor ist allerdings schwer beizukommen, am ehesten wohl durch das Experiment in der Natur und auf dem Versuchsfeld, mit künstlichen Artenmischungen.

Glücklicherweise führt uns aber die Natur selbst eine Reihe glänzender Freiexperimente vor, in der gürtelartigen Anordnung von Pflanzenbeständen, wobei der Wechsel der Bestandesgürtel parallel geht mit einer Änderung von Standortsfaktoren[73] (p. 17).

Synökologisch aufschlussreich sind auch Feststellungen von Artenkorrelationen innerhalb der Gesellschaften im Wettbewerb um Raum und Nahrung. Zu ihrer Erfassung kann der Gemeinschaftskoeffizient Verwendung finden.

Die Schwierigkeit synökologischer Untersuchungen wird erhöht durch die enge Wechselwirkung der zahlreichen Einzelfaktoren, die eine Isolierung und getrennte Untersuchung aussichtslos erscheinen lassen, da die Lebensäusserungen der einzelnen Gesellschaftsglieder jeweilen vom gesamten Faktorenkomplex beeinflusst werden und die Faktoren sich gegenseitig beinflussen.

Zudem ist es in der Regel mit örtlich und zeitlich beschränkten Beobachtungen und Messungen nicht getan und erweisen sich vielfach zeitraubende Dauеruntersuchungen als notwendig.

Man muss sich daher vorderhand mit der Lösung bestimmter Teilprobleme bescheiden und dabei soweit möglich auch auf Untersuchungsresultate bei Einzelpflanzen zurückgreifen, wenn sie innerhalb bestimmter Assoziationen gewonnen worden sind.

Messungen von Lebensäusserungen wie Assimilation, Transpiration usw. haben umso eher Vergleichswert, je enger umschrieben die systematische Stellung der Gesellschaften, worin die Untersuchungen ausgeführt worden sind, ist.

Eine Vertiefung ökologischer Probleme erfordert kostspielige Apparaturen, die ständiger Vervollkommnung unterliegen und daher rasch veralten. In den U.S.A. hat sich ein „Commitee for Microenvironment" der „Ecological Society of America" gebildet, das Auskunft erteilt über Instrumente zur Standortsmessung und die Möglichkeit ihrer Beschaffung, eine Einrichtung die auch anderwärts Nachahmung verdient.

3. *Gesellschaftsdynamik* (Entwicklung)

Vor nahezu einem Jahrhundert schon hat A. Kerner darauf hingewiesen, dass die Pflanzengesellschaften keine stabilen Grössen darstellen. „Welcher Reiz" schreibt er[42] (p. 12) „liegt nicht im Studium des Entwicklungsganges einer jeden Formation und in dem Verfolgen ihres Entstehens, ihres Werdens und Verschwindens."

Die diesem Gedankengang innewohnende Idee ruhte lange Jahrzehnte

um erst um die Jahrhundertwende jenseits des Ozeans zum Durchbruch zu gelangen. Dem mitreissenden Schwung der Lehren eines F. Clements war es vorbehalten, das Studium der Vegetationssukzession, wenn auch hypothesenbelastet, zu weltweiter Anerkennung zu bringen[13a]. Seither spielt im englischen Sprachbereich die dynamische Vegetationsbetrachtung, das Sukzessionsstudium, eine führende Rolle.

Den Vegetationsänderungen liegen Veränderungen der Standortsbedingungen zugrunde, die sowohl durch äussere (exogene) Ursachen (Bodenentwicklung, Bodenabtragung, Zufuhr von Material, Klimaänderungen, biotische Einflüsse), als auch durch die Tätigkeit der Organismen, Pflanzen und Tiere selbst (endogen) bedingt sein können. Den herrschenden Arten werden ihre Lebensmöglichkeiten entzogen; andere, dem veränderten Biotop besser entsprechende fassen Fuss und breiten sich aus. Bei den Pflanzengesellschaften führt der normale Entwicklungsgang von strukturell einfachen, labilen, zu komplizierten Gebilden mit längerer Lebensdauer.

Eine Hauptrolle bei der Besiedlung von Neuland spielt der Transportfaktor, doch wird der Zufallseinfluss erheblich herabgemindert durch die Auslesewirkung des Standorts, seine „accessibilité"[34], welche das Unpassende ausschliesst.

Die natürliche Vegetationsentwicklung verläuft der Bodenbildung parallel und ist durch das Klima vorgezeichnet.

Dieser in Zusammenarbeit mit den Pedologen empirisch aufgestellte Satz findet durch die Theorie seine Bestätigung[50] (p. 410).

Der Entwicklungsgang endet bei der sog. Klimax- oder Schlussgesellschaft, die falls nicht zu eng umgrenzt, für ein weites, klimatisch einheitliches Gebiet Gültigkeit besitzt.

Innerhalb einer in erster Linie klimabedingten progressiven Sukzessionsserie können sich indessen kürzere zyklische, meist menschlich bedingte Sukzessionsvorgänge abspielen.

Ihren konkreten Ausdruck erlangen die Sukzessionen im Artenwechsel. Sie können natürlich unabhängig von jeder pflanzensoziologischen Systematik verfolgt werden, gewinnen indessen an Vergleichswert, wenn sie sich in das Gesellschaftsschema einfügen.

Mit Tansley[75] bezeichnen wir als Klimax den relativ stabilen Endzustand einer Sukzessionsserie. Eine wegweisende Besprechung der z.T. sehr divergierenden theoretischen Anschauungen über den Klimaxbegriff geben neulich Churchill und Hanson[13]. Sie unterscheiden zwischen Monoklimax, Polyklimax und Populationenklimax (population pattern Climax).

Clements, ein Vorkämpfer der Monoklimaxlehre, fasst die Gesellschaften sehr weit und gelangt zum Schluss, dass die Vegetationsentwicklung unter gleichbleibendem Klima einem und demselben Endzustand zusteuert.

Diese Auffassung hat zahlreiche Anhänger gefunden und dürfte für grosse Gebiete auch zutreffen, falls die klimatische Schlussgesellschaft nicht zu eng gefasst ist und man das Vorhandensein lokaler Ausnahmen (z.B. durch extreme Lage oder stark abweichende Bodenverhältnisse bedingt) zugibt, denn auch in Gebieten mit einheitlich gleichgerichteter Bodenentwicklung gibt es Standorte, welche die Ausbildung der Klimaxgesellschaft nicht zulassen.

Der Vegetationsklimax wird oft von einer oder einigen wenigen konkurrenzkräftigen, gesellschaftsbildenden Arten mit breiter ökologischer Amplitüde beherrscht.

Beispiele von Klimaxgesellschaften sind das *Quercetum ilicis galloprovinciale* Südfrankreichs, das *Querceto-Carpinetum* Mitteleuropas, das *Rhodoreto-Vaccinietum* und das *Curvuletum* der Zentralalpen.

Die Monoklimaxlehre darf aber nicht unbesehen übernommen und keinesfalls verallgemeinert werden. Sie lässt sich auf klimatisch extreme Gebiete, wo die Bodenbildung in den Anfangsstadien stecken bleibt und die Pflanzendecke durch das tote Substrat massgeblich beeinflusst wird, nicht anwenden. Dies trifft zu an den Grenzen des Pflanzenlebens im hohen Norden und in den Gipfelgebieten der Hochgebirge. Hier steht die Kürze der Vegetationszeit der Ausbildung einer geschlossenen Vegetationsdecke entgegen. Unter ariden Klima stellen sich auf verschiedenen Böden verschiedene, edaphisch bedingte Schlussgesellschaften ein, wobei es ausgeschlossen erscheint, dass die eine je in die andere überzugehen imstande ist. Ein Monoklimax vermag sich weder in der Arktis[13] oder in den Hochgebirgen, noch in extrem ariden Gebieten auszubilden.

Bei sehr enger Fassung der Gesellschaften zerfällt die Schlussvegetation in einen Komplex kleiner und kleinster Klimaxeinheiten, einen Mikroklimaxkomplex, Klimaxschwarm[80], der dem „population pattern Climax" Whittakers entsprechen mag.

Durch die unter dem Einfluss von Firbas, Godwin, Welten, Lemée, u.a. in den letzten Jahrzehnten stark ausgebauten und lebhaft geförderten pollenanalytischen Studien sind auch die grossen Züge der klimabedingten säkularen Sukzessionen, wie sie sich seit dem Palaeolithikum abgespielt haben mögen, aufgehellt worden.

Die heutige Vegetationsentwicklung objektiv zu erfassen dient das Sukzessionsexperiment[79, 49, 43]; der effektive Sukzessionsverlauf wird auf Dauerflächen verfolgt, deren Vegetationsdecke, von Zeit zu Zeit aufgenommen, die floristischen Veränderungen anzeigt. Als Beispiel hiefür seien drei Aspekte eines Dauerquadrats aus der alpinen Stufe des Schweizerischen Nationalparks wiedergegeben, welche die zehnjährigen äusserst geringen, endogen bedingten, Änderungen eines *Polytrichetum sexangularis*-Schneebodens illustrieren.

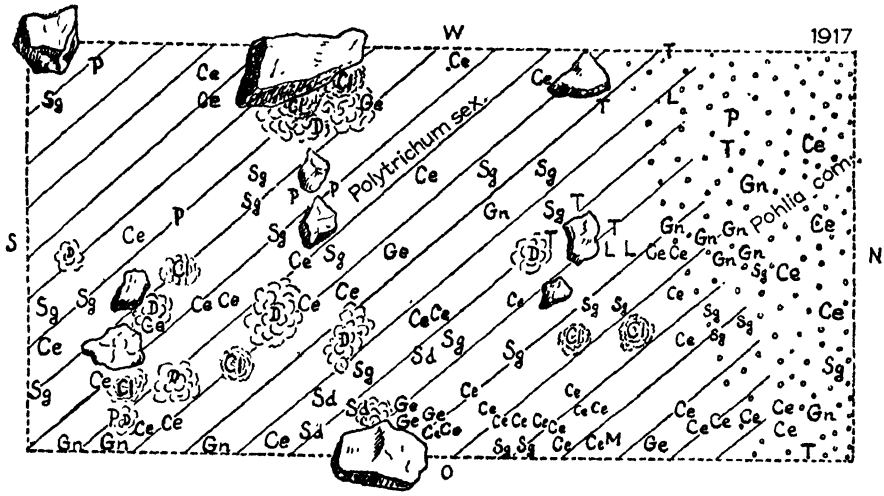


Fig. 1. Schneeboden am Macunsee (Engadin) 2650 m. Aufnahme Juli 1917

Sg = Sagina saginoides; Ce = Cerastium cerastioides; Gn = Gnaphalium supinum; Ge = Gentiana imbricata; P = Poa alpina; Pl = Poa laxa; M = Ligusticum mutellina; L = Chrysanthemum alpinum; T = Taraxacum alpinum; Sd = Sedum alpestre; V = Veronica alpina; Si = Sibbaldia procumbens.

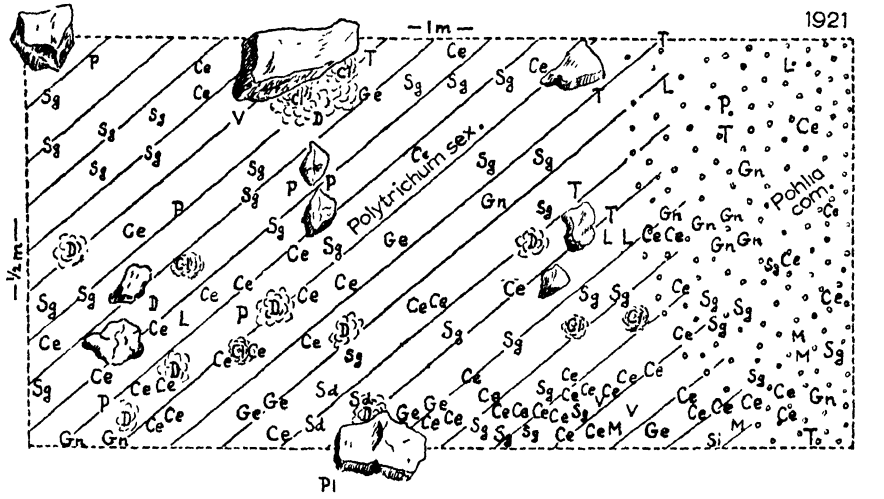


Fig. 2. Schneeboden-Dauerquadrat Macunsee 1921

In schroffem Gegensatz zu dieser Konstanz steht die, hauptsächlich auf exogene Faktoren (Wind, Anschwemmung) zurückzuführende Vegetationsentwicklung an den Lagunen bei Montpellier, die erstaunlich rasch fortschreitende Veränderungen zeigt.

Die Figuren 4 und 5 geben ein Bild der sich von 1915 bis 1958 am Lagunenrand bei Palavas vollzogenen und von Zeit zu Zeit kontrollierten Vegetationsänderungen.

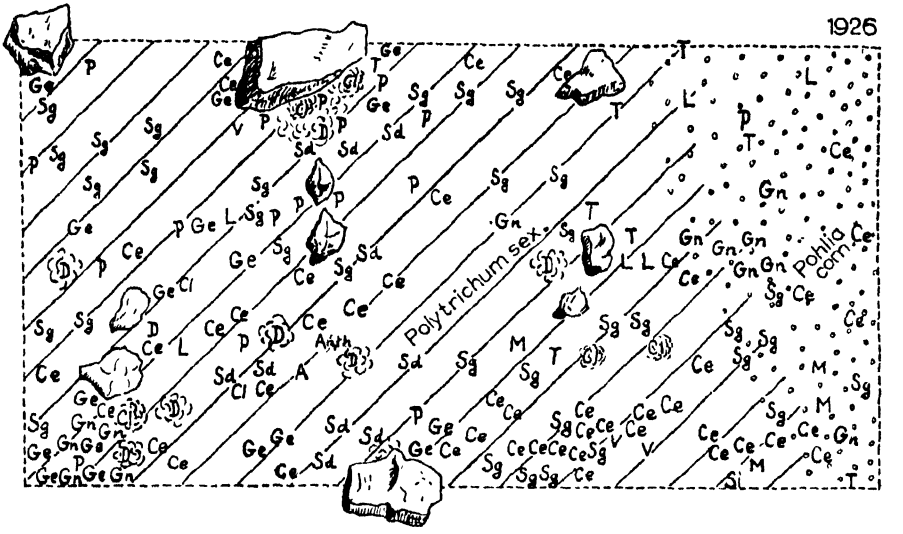


Fig. 3. Schneeboden-Dauerquadrat, am Macunsee 2650 m, 1926

Sg = Sagina saginoides; Ce = Cerastium cerastioides; Gn = Gnaphalium supinum; Ge = Gentiana imbricata; P = Poa alpina; Pl = Poa laxa; M = Ligusticum mutellina; L = Chrysanthemum alpinum; T = Taraxacum alpinum; Sd = Sedum alpestre; V = Veronica alpina; Si = Sibbaldia procumbens.

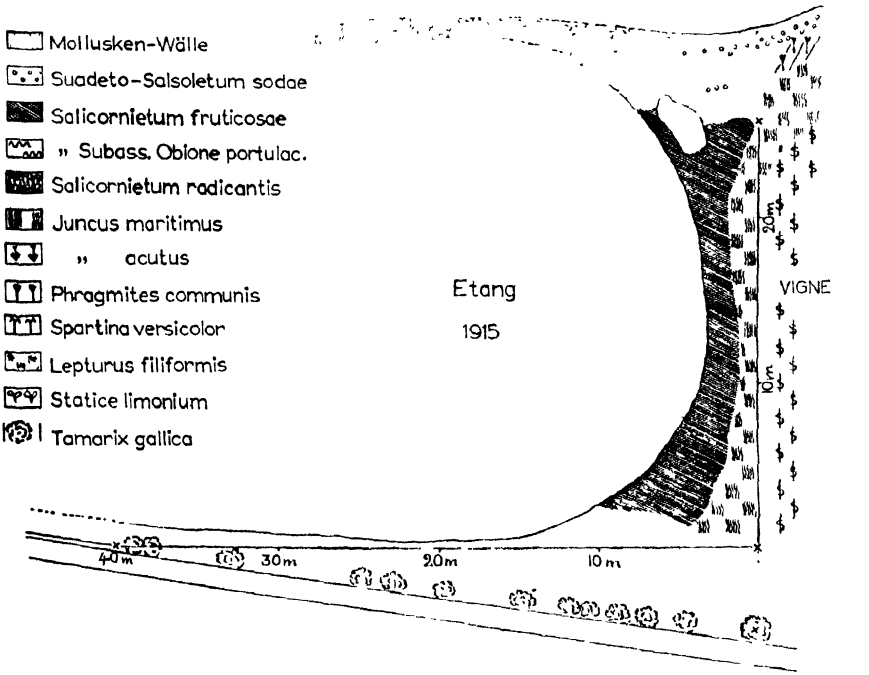


Fig. 4. Daueruntersuchungsfläche am Etang von Palavas, Aufnahme 1915

Aus den Ergebnissen derartiger Daueruntersuchungen werden sich allgemeine Gesetzmässigkeiten der Vegetationssukzession herauskristallisieren und die Hypothesen ersetzen helfen.

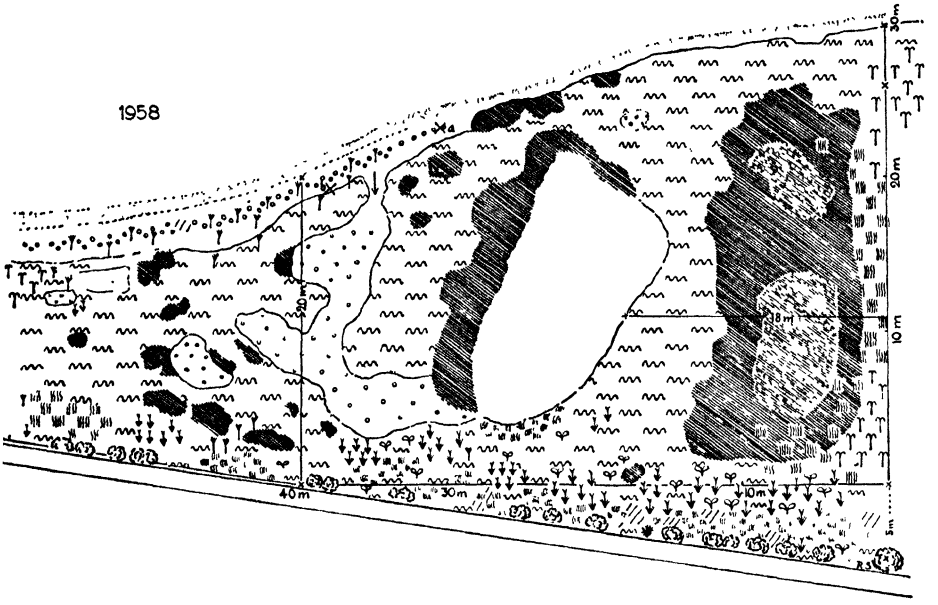


Fig. 5. Dieselbe Fläche am Etang von Palavas, Aufnahme 1958

4. *Synchorologie*

Über die Gesellschaftsverbreitung ist man noch recht wenig unterrichtet. Grosse Teile der Erde sind pflanzensoziologisch so gut wie unbekannt. Aber auch in vegetationskundlich besser durchgearbeiteten Gebieten bleibt das Areal der beschriebenen Gesellschaften noch genauer zu umgrenzen, eine Aufgabe zu deren Lösung auch der geobotanisch weniger Geschulte beitragen kann. Mit der Vergrösserung der Gesellschaftsareale ergeben sich, durch das örtlich lokalisierte Auftreten einzelner Sippen charakterisierte geographische Abänderungen, vikariierende Rassen, die florengeschichtlich bedingt sind[71] (p. 103).

Zur synchorologischen Umschreibung leisten Arealkarten der vegetationskundlich wichtigeren Sippen gute Dienste.

Das Zusammenfallen einer grösseren Anzahl von Artarealen gestattet, nach dem Vorgang von Meusel[55] Arealtypenspektren zu konstruieren, die entweder auf florengeschichtliche Elemente, oder auf beliebig umgrenzte Gebiete Bezug haben.

Auf der pflanzensoziologischen Karte wird die Farbe in der Regel flächenhaft aufgetragen.

Eine besondere Art der Farbengebung verwendet E. Campbell bei der

Darstellung der Pflanzengesellschaften des schweizerischen Nationalparks, indem er die Farben längs der Höhenkurven strichweise aufträgt. Expositionsunterschiede in der Verteilung der Gesellschaften, Mischungen und Durchdringungen treten dabei viel schärfer hervor, als bei flächenhafter Farbengebung und die Darstellung der Mischungen wirkt naturnäher.

Zentren gleichgerichteter pflanzensoziologischer Kartierung bestehen heute schon in Frankreich (Emberger, Molinier), Deutschland (Tüxen, Oberdorfer), Belgien (Noirfalise), Holland (Westhoff), Jugoslawien (Horvat), Polen (Szafer, Pawlowski) um nur die wichtigsten zu nennen.

Eine internationale Einigung über die Zeichengebung und eine Angleichung der Farbtöne für die höheren Vegetationseinheiten, wenigstens innerhalb ein und desselben Vegetationskreises, ist zu erstreben.

5. *Angewandte Pflanzensoziologie*

Die engen Beziehungen zwischen Land- und Forstwirtschaft und den natürlichen Lebensgemeinschaften in Feld und Wald haben schon frühzeitig pflanzensoziologische Gedankengänge in die Praxis Eingang finden lassen. Heute bildet die Vegetationskunde einen nicht mehr wegzudenkenden Bestandteil der land- und forstwirtschaftlichen Grundlagenforschung und wird an zahlreichen Hochschulen als Spezialfach gelehrt.

Forstlich und landwirtschaftlich gerichtete Arbeiten schiessen wie Pilze aus dem Boden und es ist nur zu wünschen, dass über der analytisch-statistischen, die kausal erklärende Betrachtung nicht zu kurz kommt.

Durch Physiologie, Bioklimatologie, Zoologie, Geographie, Bodenkunde befruchtet, wirkt die Pflanzensoziologie ihrerseits anregend auf diese Nachbardisziplinen. Auch Kulturtechnik, Landschaftsplanung, Landschaftspflege ziehen mehr und mehr Gewinn aus der Vegetationsforschung.

Bei den vielfachen Berührungspunkten und Abhängigkeitsbeziehungen, welche die Vegetationskunde mit den Nachbarwissenschaften verknüpfen, erscheint heute die Arbeit "par équipes,, notwendiger denn je. Der weitere Fortschritt der biosoziologischen Forschung ist weniger von der statistischen Seite her, als vom verständnisvollen Zusammenarbeiten der Forscher verschiedenster Richtungen zu erhoffen.

Immer schwerer legt sich in den Kulturländern die Hand des Menschen auf die letzten verbleibenden Reste ungestörter Vegetation und wie Thienemann[78] zu Recht bemerkt, steigt mit der kulturellen Erschliessung auch die Gefahr einseitiger Massnahmen, die das Gleichgewicht der Lebensgemeinschaften stören. Dringend ertönt der Ruf nach Schutz der Naturgüter. Um aber den Schutzmassnahmen den gewünschten Erfolg zu sichern, erweist sich die Kenntnis der grossen pflanzensoziologischen Zusammenhänge als unerlässlich. Die Pflanzensoziologie ist mit dazu berufen das Verantwortungsbewusstsein der kommenden Generationen der Natur gegenüber

zu schärfen, die unabwendbaren Eingriffe in das erste Naturheiligtum der Erde, seine Pflanzendecke, dosieren und in die richtigen Bahnen lenken zu helfen.

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PLANT GEOGRAPHY

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PLANT geography or phytogeography deals with the ranges of plants on or near the surface of the earth and its waters. The biosphere is vertically narrow, but, with some exceptions, co-extensive with the layer of meeting of atmosphere with lithosphere. Roots and soil organisms penetrate some feet into the soil and subsoil, the tallest trees grow upwards a few hundred feet, while light disseminules and some bacteria may float at higher levels but beyond a few thousand feet at most probably never again function. Even in seas and oceans, holophytic plants are limited to the depth of penetration of sunlight (that is, to the photic region which is said to extend to a depth of 40 m), and at lower depths only saprophytic or parasitic fungi and bacteria can exist. There are, however, few extensive areas of the earth's surface entirely devoid of plants. The extreme polar regions, and particularly the Antarctic, have few vascular plants, and there are a few high mountains whose peaks rise above the altitudinal limits of seed plants, but some cryptogams such as mosses and lichens extend beyond the latitudinal and altitudinal limits of seed plants and pteridophytes. Deserts are relatively barren but most have spatially or temporarily scattered plants except in locally restricted areas.

Plants can be classified in many different ways for different purposes. In systematic botany, they are classified on the basis of "characters," structural and functional, into taxonomic groups (taxa) called families, genera, species, etc. In plant ecology, they are classified, generally as taxonomic species, into plant communities, often designated formations, associations, societies, etc. In economic botany, they are grouped according to their use for mankind into rubber plants, grain crops, "vegetables," timber trees, and so on. For plant geography, they are classified into phytochoria, that is into plant regions, provinces, domains, etc., on the basis of the geographical ranges of the taxa, consideration being also given, in defining the phytochoria and determining their boundaries, to the ranges of relevant plant communities. It is most important to remember that the taxa of the systematic botanist are the units most often used in other classifications. Above all, the "species" has been the fundamentally practical unit, in spite of all the uncertainty in the application of the "species concept." This is true even for such classifications as those into ecotypes, etc., or into demes. It is here emphasized that taxonomy is basic to plant geography, though phytogeographical findings can often help in improving plant taxonomy.

There is no sharp line of division between plant ecology and plant

geography. Ecology is concerned with the relationship between plants and their surroundings and with the grouping of plants into kinds of vegetation. On the whole, plant ecology is intensive while plant geography is extensive in outlook, but both are concerned with plants and, in attempting to correlate observed structure and behaviour with "causes," both refer to the same sum total of environmental factors though the emphasis varies. The term "geobotany" includes both plant ecology and plant geography. As far as possible it is desirable to refer to ecological "distribution" when describing the habitat conditions and limitations and to phytogeographical "range" when defining the geographical boundaries of taxa, plant communities, etc. It is, however, to be noted that by long usage "distribution" is frequently synonymous with "range." Phytochoria should be defined by their ranges though many other data are included in their descriptions.

The aims of plant geography may be briefly defined as: 1. to find out and to record the occurrences of plants, especially as species, in localities fixed geographically; 2. to determine the units into which the earth can be divided on the basis of similarity of ranges of taxa and to describe these units; 3. to name and classify these units as phytochoria; 4. to determine, as far as possible, the causes which have resulted in the ranges and in the make-up of the phytochoria.

We have noted that plant geography is based on taxonomy and is very closely associated with ecology. From some points of view it can be considered a branch of geography. When "causes" of ranges are under discussion it becomes obvious that it is the most synthetic branch of botany. Not only does the phytogeographer have then to take into account the morphological and physiological particulars of the plants themselves as individuals, as taxa, or as plant communities but he has to obtain data from geology, from archaeology, from history, from meteorology, from pedology, from zoology, and from his botanical colleagues who have specialized in the study of this or that aspect of plant life.

Plant geography as a subject in its own right is relatively modern. It is true that records of plant ranges, as then known, are given by many early authors but they are usually incidental to other studies. Theophrastus, in his *Enquiry into Plants* heads Book IV with "Of the trees and plants special to particular districts and positions" (see English translation by Sir Arthur Hort, I, pp. 287–413, 1916) and gives interesting information for many plants of the eastern Mediterranean Region. There is little in the works of the herbalists, or of pre-Linnean authors generally, that can be called plant geography in any proper sense, though there are many references to places whence plants came and some local studies of range and distribution. Tournefort, in his *Relation d'un voyage du Levant*, 1717 (English translation 1718), described, somewhat vaguely, altitudinal zonation on Mt. Ararat

in Armenia. Linnaeus (1707–1778) recognized and described plant communities, mainly for Scandinavia. Albrecht von Haller of Bern (1708–1777) for Switzerland and Jean-Louis-Giraud Soulavie (1752–1813) for southern France published accounts that include phytogeographical material for the areas with which they were concerned. Carl Ludwig Willdenow (1765–1812), in his *Lehrbuch der Botanik* (1792) has a chapter on the history of plants of which he says "Unter Geschichte der Pflanzen verstehen wir die Einflus des Klimas auf die Vegetation, die Veränderungen, welche die Gewächse wahrscheinlich erlitten haben, wie die Natur für die Erhaltung derselben sorgt, die Wanderungen der Gewächse und endlich ihre Verbreitung über den Erdball." There is much in Willdenow's chapter relevant to plant geography, but more that is better considered as concerning plant ecology.

It is generally held that Alexander von Humboldt (1769–1859) was the "father" of plant geography. He published with A. Bonpland an *Essai sur la Géographie des Plantes accompagné d'un tableau physique des régions equinoxiales*, Paris, 1805. In 1817 there appeared his Book *De distributione geographica plantarum secundum coeli temperiem et altitudinem montium Prolegomena*. This is written in Latin and deals with the range and distribution of plants in relation to climate, with the major zones of torrid, temperate, and frigid. Both latitudinal and altitudinal zonation are considered and his coloured diagrams of the latter are famous.

Auguste Pyramus de Candolle (1778–1841), published in 1809, in the *Dictionnaire raisonné et universel d'Agriculture*, an account of "Geographie agricole et botanique," and in 1820, in the *Dictionnaire des sciences naturelles* XVIII his "Essai élémentaire de géographie botanique" of 64 pages. In these works he deals especially with the relationship between land utilization, botany, and the external factors of the environment.

Joachim Friedrich Schouw (1789–1852), a Dane, published a general textbook of plant geography in Danish in 1822 and in German (*Grundzügen einer allgemeinen Pflanzengeographie*). In the first part of his book he deals with the ecological factors, warmth, moisture, light, etc., and in the second part with the occurrence, range, and distribution of single species, genera, families, and the whole plant kingdom. He first used the ending -etum for plant communities, such as Ericetum, Coryletum, Fagetum, and Quercetum. In the third part he gives a summary of the flora of the earth on the basis of zonations in longitude, latitude, and altitude.

An interesting work that is often overlooked is that of F. J. F. Meyen, *Grundriss der Pflanzengeographie*, Berlin, 1836, of which an English translation by M. Johnston was published in 1846 by the Ray Society under the title *Outlines of the Geography of Plants*. This mainly follows the lines laid down by Humboldt and Schouw but is still well worth reading. It has an extensive "Supplement" dealing with the history of cultivated plants.

Alphonse de Candolle, in 1855, published two volumes on plant geography. J. D. Hooker (in *Hooker's J. Bot.* 1856, 8, 54–64, 82–8, 112–21, 151–7, 181–91, 214–19, 248–56) has a long essay-review on this work. Its historical importance is that it appeared shortly before the announcement of the theory of natural selection by Darwin and Wallace (1858) and the publication of Darwin's *Origin of Species* (1859). It is a clear account of the facts of geographical ranges and of ecological relationships as then known and understood but is based on the idea that the majority of species were created such as they now exist. J. D. Hooker was at this time in an "on-the-fence" position regarding the general theory of evolution and his comments on and criticisms of A. de Candolle are extremely illuminating to anyone who tries to understand the mental difficulties of those who were first meeting with the new evolutionary ideas that were so quickly to become biologically orthodox.

Many other names of botanists who contributed to the knowledge of phytogeography in the first half of the 19th century could be mentioned. One has to remember that from the time of Linnaeus to the time of Darwin there was a tremendous amount of geographical exploration that often included botanical research. It is true that this was very largely systematic and economic but without taxonomy there can be no development of plant geography. Collections poured in from all over the world and were described in "floras" and monographs. Gardens, botanic and horticultural, were enriched and systems of classification were gradually improved. The work of botanists, whether in taxonomy or in phytogeography, was then essentially descriptive and classificatory. In plant geography, however, there had been some advances on this somewhat static position in that correlations were found between ranges and environmental factors. The theory of evolution was, however, not generally accepted till after the publication of Darwin's *Origin of Species* in 1859. The influence of evolutionary theory in explaining the facts of plant geography very speedily became apparent in the writings of botanists. It is also worth noting that Darwin considered biogeography as of very great importance in supporting his theory of evolution by natural selection. He devotes two chapters to "Geographical Distribution" in the *Origin of Species* (chapters XI and XII in ed. 1, chapters XIII and XIII in ed. 6).

The development of plant geography was very great during the second half of the 19th century. The flora and vegetation of many countries were explored and described and many of the problems that arise in attempting to explain their origin were often clearly stated. Only a few outstanding names can be mentioned and that of J. D. Hooker is foremost because of his work "in the field" and his extensive publications in this subject. Hooker (Assistant Director of the Royal Botanic Gardens, Kew, 1855 to 1865,

Director 1865–1885), as Assistant Surgeon and Botanist, accompanied James Clark Ross in the *Erebus* and *Terror* expedition to "Antarctica" (1839–1843) and collected and studied the flora in Madeira, Cape Verde Islands, St. Helena, Kerguelen Island, Tasmania, The Falklands, Hermite Island, New Zealand, and the Cape. His journey to the eastern Himalaya and botanizing in Sikkim and Assam occupied the whole of 1848 and much of 1849. In 1860, he visited Syria and Palestine, in 1871 Morocco, and in 1877 North America on botanical expeditions. A full account of the phytogeographical researches of Sir Joseph Dalton Hooker was published in 1953 (Turrill[209]).

Partly contemporaneous with J. D. Hooker were the great German botanists—A. Grisebach[75], A. Engler[61, 62, 63], and O. Drude[54] with their text-books and other comprehensive works on plant geography. The important series of monographs by various authors edited by Engler and Drude under the general title *Die Vegetation der Erde* covered many countries of the world. Karsten und Schenck edited the volumes of *Vegetationsbilder* Jena, 1904 to 1944, 1, 26.

Since 1900 a number of general books on plant geography have been published. The following are given in the bibliography and have been consulted in preparing the accounts of modern methods and results that follow: H. Solms-Laubach[132], Graebner[73], Hayek[86], Campbell[29], Wulff[230, 231, 232], Cain[27], Good[71], Croizat[47], and Dansereau[44].

Special mention must be made of the improvements in plant geography resulting from the rise of ecology and the more recent advances in physiological ecology. The great work of A. F. W. Schimper, *Pflanzengeographie auf physiologischer Grundlage*, Jena 1898, with its English translation *Plant-Geography upon a physiological basis*, by W. R. Fisher, revised and edited by P. Groom and I. B. Balfour, Oxford 1903, had a tremendous influence in stimulating interest and research in the subject. Some of Schimper's conclusions, as those on xeromorphism, have been strongly criticized and have to be modified as a result of more evidence though it is interesting to note that more recently still it has been shown that some of the criticisms were too extreme. A third edition of Schimper's *Pflanzengeographie*, by F. C. von Faber, was published at Jena in 1935 in two volumes. A text-book by E. Warming was originally published in Danish, in 1895, under the title *Plantesamfund*, with German editions in 1896 and 1902. What is described as "practically a new work" by E. Warming assisted by M. Vahl, based on *Plantesamfund*, appeared in 1909 as *Oecology of Plants, an introduction to the study of plant-communities*, Oxford. There were later German editions of which the fourth by E. Warming and P. Graebner has the title *Lehrbuch der ökologischen Pflanzengeographie*, Berlin 1930–1933. While Warming's first book quoted above is ecological rather than

phytogeographical, the last edition is wider in its outlook. E. Rübel's scheme for the delimitation and nomenclature of plant communities is also of phytogeographical importance. The full account was published as *Pflanzengesellschaften der Erde*, Bern-Berlin, 1930. Like the works of Schimper and Warming, it has an ecological basis.

It is worth recording that the text-books on plant geography and closely related plant ecology mentioned above contain numerous bibliographical references. The boundary between ecology and phytogeography is frequently passed in many of the papers published in ecological journals such as the *Journal of Ecology* (1913 onwards), *Ecology* (1920 onwards), *Oikos* (1949 onwards), and *Vegetationsbilder* (1904–1944). The publication *Pflanzenareale* (1926–1940), with range maps and explanatory text, is more definitely phytogeographical but has apparently ceased publication.

The use of palaeobotanical evidence in plant geography can be gauged from Wulff's 1932–1944 publications already noted and from Seward's book *Plant-Life through the Ages*, Cambridge, 1931. There are also the very important works of Reid and Chandler[151] and Chaney[33, 34, 35], and the publications referred to in Cain[27].

Recently there has been the introduction of cytogenetical data into the realm of plant geography. There is no doubt that researches on the cytology and breeding phenomena of plant species will become of increasing importance in tracing the history of their ranges. At present the known facts are meagre relative to the number of species in even poor floras, while cytogenetic investigation of the rich floras of the tropics has been little more than commenced. The number of research papers on cytogenetics with implications for plant geography is rapidly increasing but wide generalizations based on these are still largely tentative and no general text-books devoted to cytogenetical phytogeography have yet appeared. Cain, in his 1944 book mentioned above, has a part dealing with the significance of polyploidy in plant geography, but already much can be added to this.

MODERN METHODS

1. *Collection of Data*

Most often data are best collected under the headings of taxonomic species and a loose-leaf card filing system is desirable. The following particulars have to be obtained, as far as possible, for every species:

A. geographical, including localities and altitudinal limits.
B. ecological, including habitats, habit, life form, flowering period, pollination mechanism, dispersal mechanism, etc.
C. cytogenetical, including chromosome number and breeding data.
D. special, including economic uses and vernacular names.

A. Geographical data have to be obtained from field studies, from herbarium specimens, and from published literature. Taxonomic soundness is essential, hence the value of preserved material for constant checking, correction of taxonomic errors, and bringing the taxonomy up-to-date with the improved views of specialists. Localities should be given exactly by place names, by the name of the district, and by latitude and longitude. The names given should include at least one that can be found in a good atlas or gazetteer since local names, as of small villages, are often difficult to trace and are frequently changed. Altitudes should be given in metres.

B. Ecological facts are often classified into climatic, edaphic, and biotic. For the first, plant geographers have to rely mainly on the long range records of meteorologists and climate as a phytogeographical factor is discussed below. Soil and biotic factors are much more local than most climatic ones and broad classifications can be used for scoring in the field. The nature of the underlying rock, such as limestone, sandstone, granite, or serpentine, the general nature of the soil, such as sand, clay, terra rossa, or laterite, and the broad nature of the plant community such as forest, brushwood, meadow, sand-dune, bog, or marsh can be given without trouble and such data help greatly to precise the habitat. Autecological information of value to the plant geographer is concerned with the method of pollination (by wind, insects, selfing mechanisms, etc.), the means of dispersal of disseminules (by ocean currents, wind, birds and other animals, etc.), and the periods of vegetative development, flowering, and fruiting. The study of life forms has yielded instructive results. Raunkiaer's scheme (see his collected papers translated into English by H. Gilbert-Carter and published by the Clarendon Press, Oxford, 1934, under the title *The Life Forms of Plants and Statistical Plant Geography*) has not yet been supplanted and is easily modifiable for special purposes. It is, however, often advisable both to use Raunkiaer's life form classification and to devise others for the investigation of restricted floras or special problems. Records of simple habit (tree, shrub, herb, and heights), of leaf size, of armature, and so on can yield interesting results in a final synthesis.

C. Cytogenetical data for wild plants of known origin are still too few for the phytogeographer to use them as more than supplementary to facts obtained by other methods. Much cytology has been based on garden plants of unknown history and on few samples, and sometimes taxonomic determinations cannot be checked because voucher specimens have not been kept. Nevertheless, there can be no doubt that chromosome counts, classification into breeding systems, and determination of cytogenetical barriers to interbreeding will become of greatly increased use to the plant geographer in the near future. There are already published hypotheses relating ranges to polyploidy and, in several genera, chromosome number

and behaviour and the results of experimental breeding have thrown light both on the history and range of taxa and of the plant communities of which they are constituents.

D. The plant geographer cannot ignore man and his activities. While we are here concerned mainly with the natural flora and vegetation of the earth and, therefore, regard the geography of crop plants as outside our scope, there are plants generally referred to as "weeds and ruderals," which may throw important light on some of our problems and they should be scored as fully as "natives." In addition, a wild plant or a weed of today may become the ancestor of a cultispecies tomorrow, and the reverse may also occur. It is thus worth while recording the economic uses to which any species has been put by natives of any area and to have the vernacular name or names also on the filing card.

2. *Synthesis and Classification of Data*

The information which it has been suggested must be accumulated by the plant geographer is best collated together on filing cards. Sooner or later a "closing date" has to be fixed for a given piece of research and then the data have to be collated, correlated, and synthesized. It is probable that a punched card system would often prove useful at least as a supplement to a set of cards kept in systematic order. For publication of results and for the task of tracing causes of ranges, there has to be summarizing in tables and in maps. The primary essential is that, for any given piece of research and, indeed, for as wide a field as possible outside this, tables and maps shall be easily and accurately comparable. Figures, symbols, scales, etc., must retain the same value throughout. Numbers of species, under genera and families, the numbers in different habitats, at different altitudes, showing different habits and life forms, flowering at different seasons, and so on give the fundamental facts for the determination of phytochoria and partly for explaining their constitution. Figures can be used both without treatment and after calculation as, for example, on a percentage basis. It may be argued that the figures obtained are not exact, that there is the probability of fairly considerable errors from a variety of causes and especially because of incompleteness of knowledge and that the magnitude of the possible errors cannot usually be expressed by any statistical device. Nevertheless, it is a general experience that figures are preferable to vague relative terms such as small, large, tall, short, few, numerous, and so on. The figures are usually summated in classes with stated class ranges and, if these be formed with care based on considerable experience, errors are considerably reduced.

The graphic representation of ranges by plotting them on maps has much to recommend it. There are many ways of preparing such maps and also considerable difficulties are encountered from the initial stages up to

publication. The Royal Geographical Society published a series of papers as a pamphlet on the matter, under the title "The Cartographical Presentation of Biological Distributions," in 1954. Such matters as projections, scales, and symbols have to be decided before the maps can be prepared and must partly depend on the purposes in view. Since the maps are not ends in themselves their use in finding correlations with past and present environmental factors must be borne in mind. Hence the need for uniformity in treatment. It is extremely difficult to compare maps of different projections or scales or those using different symbols. Maps in colour can be impressive and easily interpreted but they are costly to reproduce. When possible, maps with a superimposed grid system based on lines of latitude and longitude have considerable advantages. Such are now being used for detailed study of the ranges of plants of the British and Dutch floras. In areas whose flora is less well known, and especially when of large size, geographical divisions based on physical features or even on political boundaries may be preferable to a grid system. While different kinds of maps may have to be used for different purposes it is unscientific to use, say, a certain projection or scale to over-emphasize some preconceived hypothesis. Maps are most valuable but, since they are abstracted representations of the earth's surface or of a part thereof, they need interpretation. The earth is a sphere and, even as a reduced representation, every map in two dimensions is distorted more or less. On a world wide vista the plant geographer should always use a globe.

When the data suggested above have been obtained and grouped in tables or visually expressed on maps for every species of an area the possibilities of classifying ranges have to be considered. There is no doubt that different phytogeographical groupings or classes can be determined so as to have a considerable use in the working out of the causes that have led to the extent and limits of ranges. These phytogeographical groupings are conveniently termed phytochoria (see Turrill[211]). Their diagnosis, description, limits, and nomenclature are, at present, less precise or uniformly accepted than one would desire. It is probably best to describe and name a standard which experience leads one to conclude is typical and to expect that, with some exceptions, the boundaries of the whole phytochorion thus standardized will be a belt and not a line. That is, one phytochorion will often merge more or less gradually into another or into others. A phytochorion is composed of a number of species, often a large number, every one with its own range and though the ranges show some similarities they will not be the same, some are wider some variously restricted, many overlap, and some are relatively included one within another and some completely excluded. The phytogeographer in determining phytochoria uses various criteria and generalizes and has to admit there are exceptions to his generalizations. He

must never ignore such exceptions but they do not necessarily disprove the value of the generalizations.

There are three broad criteria used in determination of phytochoria: 1. the degree of community of taxa and of their ranges; 2. the degree of community of ecological groupings and their ranges; 3. the degree of correlation of ranges of taxa and of plant communities with environmental factors. The first is the most important and the last has to be used with great caution. Due weight has to be given to dominant or especially characteristic species, to endemics, to absentees, and to cultivated crops.

It is convenient, if not essential, to arrange phytochoria in a hierarchical system. Unfortunately there is no such system yet established by "international rules" and the scheme used here is provisional. The largest division is termed a *realm* and is a grouping of regions that show marked resemblances especially at the taxonomic level of families and family or tribal ranges and which have a high degree of similarity in their floristic history. The most fundamental phytogeographical division is that of the *region* determined especially by resemblances at the taxonomic level of genera and of plant communities at the level of formations or below. The *province* or *domain* is a portion of a region based essentially on statistically distinct assemblages of species and their ranges and less on major climax vegetational communities. Further subdivisions can be made almost indefinitely according to the scale of the work and the facts available. It is usually sufficient to distinguish such subdivisions either by figure or letter symbols or by local vernacular names.

3. *Interpretation of data*

The ranges of taxa and of phytochoria depend upon the characters of the plants themselves (inherent factors) and on the environment (external factors). Plants vary greatly in their reactions to their surroundings and there are two ways of looking at this interrelationship. One can attempt to summarize their degree of tolerance or one can determine the factors that limit their spread beyond their present ranges.

The inherent factors of importance in plant geography are numerous and varied and their detailed study is the subject-matter of autecology and here one need do little more than enumerate them. The mechanisms and and efficacy of dispersal primarily determine ranges. By seeds, spores, or vegetative propagules plants have reached the localities where they grow and the nature of the disseminules is genetically fixed though external factors (wind, water, birds, etc.) are often involved in the actual dispersal, and always so over long distances. Successful spread next involves establishment or ecesis. Seeds may reach a locality away from their parent or parents but unless they germinate and the seedlings establish themselves there can be no extension of range or even the maintenance of a general geographical

range. There are many barriers or limiting factors to both dispersal and establishment and if these be traced some explanation of range may be found. Final incorporation of a species in a phytochorion only occurs when it can tolerate the environmental conditions within the area of the phytochorion. That is, the genetic constitution must be such that the plant reacts favourably to the climatic, edaphic, and biotic factors of its new habitat. With slight modifications of wording these limitations to range changes apply whether immigrants or taxa evolved *in situ* are under consideration. In determining the effects of inherent factors on the ranges of plants, the phytogeographer has largely to draw on ecological and cytogenetical data.

The external factors, summated as "environment" can be analysed in many ways. A division into climatic, edaphic, and biotic is often convenient as a first stage. The climatic factors include temperature, light, precipitation, air humidity, and wind; the edaphic factors are all those connected with the substratum on or in which the plant is growing; and the biotic factors are those involving animals and plants other than the organism being considered. The biotic factors are often overlooked, perhaps because they are the most complex and we know least about them. It must be remembered that analysis into climatic, edaphic, and biotic factors is an artificial device of the phytogeographer, in the sense that all the external factors interact in their influence on the plant increasing or limiting the action one of another. A plant reacts to its environment as a whole, but not infrequently one factor can be determined as the, or the main, limiting factor for range. It appears that on a wide scale "climate" is the most important factor controlling plant ranges. The phytogeographer has to use the data supplied by meteorologists when he correlates ranges with climatic factors and he must remember that very often certain of the figures supplied in meteorological tables have been worked up as, for example, being "reduced to sea level." Temperature and precipitation are of first importance and averages, maxima, and minima (such as frost days) have all to be taken into account and their seasonal distribution may be of considerable significance. Monthly data are usually sufficient for the phytogeographer. Data on air humidity are often more difficult to obtain than those for temperature and precipitation. Meteorological stations have most often not been located to suit the needs of botanists and frequently one has to do the best one can with very incomplete facts. Light and winds vary more locally than temperature and precipitation, as on sea coasts, in high mountains, and within vegetation (micro-climates). Exceptions to this generalization concerning light are the limits of its penetration into ocean and lake depths and the "length of day" as between the tropics and higher latitudes.

Climate acts directly on plant life and indirectly by partly to mainly controlling soil formation and biotic factors. The question of the reciprocal

action of vegetation on climate has been much discussed. It is certain that vegetation produces micro-climates since conditions of temperature, light, and moisture are different inside a forest or brushwood or even within tall grassland from what they are in the open. It is possible that tall forest may, to a very slight extent, increase precipitation. Brooks[21] concluded that true precipitation over forests is found to average only one or two per cent above that in the open. More important is the great transpiration from the tree canopy, the protection this gives against evaporation from the ground surface, and the conservation of water in the humus layer of forests. This hold-up of water by the spongy nature of the fallen foliage and other debris prevents or reduces rapid run-off and consequent soil erosion.

The vast majority of vascular plants are rooted in the soil. The importance of the parent rock of soil in giving a certain kind of soil varies greatly. Thanks to the pioneer work especially of Russian pedologists it is now clear that soil formation depends on climatic and biotic as well as on geological factors. Over large areas of the earth's surface the climate and the vegetation are dominant in controlling the nature of the surface soil. In other areas, especially where the soils are "young," as in the British Isles since the Glacial Epoch, the nature of the parent rock still mainly determines whether the soil be a clay, sand, or loam, whether it be acid or alkaline in reaction, and so on. That plant ranges are largely determined by soil conditions is certain but the control is nearly always much more local than is that of climate. There are many examples, even within the European flora, of interaction of climatic and edaphic factors, for example in that species limited to limestone soils in the northern parts of their ranges are indifferent to the kind of soil towards the southern parts of their ranges.

Biotic factors are those involving animals or plants in their action on plants. They are, like soil factors, secondary in general importance to climatic factors because they themselves partly depend upon climate and because they are most often more local and less continuous. Animals of one kind or another may be involved in pollination or in seed dispersal, they may be pests, they may restrict or modify vegetation by browsing or grazing (in the broad sense) or by trampling, they add to the humus content of the soil, and in other ways also plants are concerned with animals as part of their environment. Man as a biotic factor needs consideration separate from that of other animals because his influence is world wide, is so diverse, frequently changes, is both destructive and constructive, and is often unpredictable or difficult to ascertain. Again and again the phytogeographer has to meet the problem of whether a given range is "natural" or is due, more or less, to man's interference. That plants form part of the environment of plants is realized by field ecologists and, one might add, by gardeners. It appears to be a factor less appreciated by some phytogeographers. The composition

and maintenance of many phytochoria, especially those of lower grade, largely depends on competition among the plants themselves. It is extremely difficult for immigrants to become established in a closed plant community. Even on a large scale one may see from range maps of taxa how extensive closed vegetation may be a barrier to range spread of many spcies. Thus, the tropical rain forest of the Congo Basin and part of West Africa has curtailed the ranges of species some of which, so to speak, curve round it. A large area of forest may be as effective a barrier to spread of ranges as a desert, a mountain range, or a sea, though it may not be so permanent on a geological time scale.

The climatic, edaphic, and biotic factors act on the existing plant life but they have acted also over immense periods of geological time. Moreover, the plants have themselves evolved from pre-existing kinds. In other words, there are the historic aspects of both internal and external factors to be considered. One is, indeed, tempted to say that phytochoria are the accidents of geological history. The processes of organic evolution have provided and still provide the taxonomic units of which phytochoria are composed. This is true whether immigration or *in situ* development be involved. Mutation, hybridization, natural selection, and other factors cannot be dealt with in detail as processes here but certain special aspects of evolution in relation to plant geography are dealt with later. It is with their results that we are mainly concerned. For changes in the environmental factors the botanist has to consult the geologists, palaeontologists, and palaeometeorologists, and he rarely finds complete agreement in answers to many, to him, fundamental questions. We do not know when, where, or from what the flowering plants (angiosperms) arose. Very few lineages have been traced in plant fossils. The determinations of many fossil specimens of scraps of leaves, etc., are open to suspicion. The gaps in our direct knowledge of plant evolution, especially for flowering plants are enormous. Great help can sometimes be obtained from the recorded geology of an area, especially of transgression and regression of sea relative to land surface, foundering or raising of land masses, and alteration of land surfaces. The possibilities of continental drift and of changes in the earth's axis (wandering of the poles) are matters of great importance in phytogeography and are given consideration later.

That climatic changes have occurred in the past cannot be disputed nor can their importance in tracing the history and development of phytochoria. The sequence of climatic changes in Europe and North America has been investigated in some detail. We know that in the early Tertiary (Eocene) the climate was tropical to subtropical, that there was a general lowering of temperature from middle to later Tertiary times, and that this culminated in the on-coming of the Glacial Epoch. The more minor variations in climate in interglacial and postglacial times have been traced in various ways, as by

the study of rocks and rock deposits, of fossil soils, of animal fossils, of the remains of roots, stems, leaves, fruits, and seeds, and by pollen grains in peat. Data obtained by similar methods are slowly accumulating for other parts of the world but are at present very incomplete.

There are two major methods of synthesizing the data of ranges of species. Each has its uses and they are not antagonistic. The ranges of species can be built up into ranges of genera and these into ranges of families, or taxonomy, above the species level, can be relegated to second place and species having more or less similar ranges can be classified into phytochoria. The former method is perhaps as much a branch of taxonomy as of plant geography while the latter links on to ecology. Here the division of the world's flora into phytochoria is to be considered, for two main reasons: ranges of taxonomic units of flowering plants in themselves have been given prominence in the works of Irmscher[103], Good[71], and Croizat[47], and these are easily accessible, while an outline account of the major phytochoria, with emphasis on recent researches, would appear to be more generally useful in this essay. Special problems which emerge from a study of ranges considered on a taxonomic basis, are, however, dealt with later.

The literature quoted has been carefully selected to include at least some of the more important classical books or papers but with preference to recent contributions. Most of these have references, often in the form of extensive lists, to earlier publications and by consulting these the student can easily build up a fairly full bibliography to the plant geography of a given area. Attention is here called to the useful volume by Blake and Atwood[15]. Unfortunately, this has apparently not been followed by a second instalment.

MAJOR PHYTOCHORIA OF THE WORLD'S FLORA

I. *Northern Realm*

1. *Arctic and Subarctic Region.* Some earlier writers, as J. D. Hooker, limited the Arctic Region to lands north of the Arctic Circle, but it is now realized that this is phytogeographically an arbitrary line and it is widely agreed that the northern limit of closed coniferous forest is a much more satisfactory regional boundary. However, to the north of the closed coniferous forest line there are areas that are certainly not extremely Arctic (Iceland for example) and yet it is not possible over the whole area to separate "Arctic" from "Subarctic" with reasonable clearness, hence here we accept a combined Arctic and Subarctic Region. Two general features stand out: first compared with corresponding latitudes in the southern hemisphere (Antarctic) the flora is rich even if often localized, and, secondly, a very large proportion of the species are more or less circumpolar. Hultén[97], it is true, notes that there are very few *completely* circumpolar plants, that is, species found without considerable discontinuities all round the North Pole, but the usual generic,

and to a large degree the specific, similarity of the floras of any two large areas north of the coniferous forest limit makes natural subdivision difficult and rather arbitrary. Land continuity is one explanation of this since the only significant gap is between Scandinavia and Greenland. Ostenfeld[142, 143] has shown that Baffin Bay and Davis Strait are not important as barriers to the dispersal of Arctic plants whose disseminules can travel over winter ice and snow.

Environmental factors of importance in limiting plant life in the Arctic are the severity of the climate, the short growing season, the long days of summer, the frozen subsoil (permafrost), and the low precipitation, the acid soil, and the large areas permanently covered with ice and snow. The most striking feature of the vegetation is the negative one of complete absence of trees. The woody plants are low bushes of willows, birches, junipers, and some *Ericaceae*. There are four main kinds of plant communities: tundra, cold desert, strand, and aquatic. The tundra has a relatively closed or continuous plant cover with a protecting snow cover in winter. It is variously subdivided and is composed in differing proportions of dwarf shrubs (*Betula, Salix, Sedum, Arctostaphylos, Rhododendron, Vaccinium*), sedges, grasses, and other herbs, and, in poorer forms, largely of mosses and lichens. The cold desert may be rocky or of scree or gravel and the vegetation is extremely open though the flora may be varied with species of *Silene, Saxifraga, Draba, Epilobium, Astragalus, Pyrola, Cerastium, Stellaria, Papaver, Eriophorum, Carex, Festuca, Poa*, etc. Lagoons and salt-marshes near the coast, and dunes and rocky shores have special strand-plants such as species of *Juncus, Arenaria, Cochlearia, Puccinellia, Elymus*, and other genera.

The Arctic flora is at least fairly old in that it is preglacial in origin and during the Glacial Epoch extended much farther south. The flora of the European Arctic is a floristically compact phytochorion and the apparently poorer flora of the Asiatic Arctic can scarcely be separated from it with our present knowledge. Porsild[152] has divided the American Arctic into 1. the arctic parts of Alaska and Yuokon, 2. the arctic parts of continental Northwest Territories and Ungava, 3. the Arctic Archipelago and 4. Greenland. The works of Polunin[150] and of Porsild[153] on the Canadian Arctic and the long bibliographies they give may be consulted. The flora and vegetation of Greenland have been extensively studied and reference may be made to the numerous papers published in *Meddelelser om Grönland* (Copenhagen). There are important botanical differences between the east and west coasts and it is also concluded by various investigators that early Norse settlers introduced a number of species that have survived. The history of the flora is apparently more complicated than might be thought and plant survival even through the extreme periods of the Glacial Epoch on nunataks is accepted by many botanists. Study of fossil pollen is throwing some light on

problems of such survival (Iversen[104]). A modern flora is that of Böcher, Holmen, and Jakobsen[16].

Iceland is a very good example of a subarctic area and has been relatively well explored botanically. Reference should be made especially to Rosenvinge and Warming[165] and to Ostenfeld and Gröntved[144]. The flora consists of about 511 species of vascular plants, excluding 76 apomicts of *Taraxacum* and *Hieracium*. The tallest plants are birches of 4 to 8 m in height and there are also willow coppices. The various plant communities have been described as those of the coast, fresh water, hot springs, bogs, swamps, rocky flats, gravelly flats, mountain slopes, sandy areas, grassland, and extensive heath-moors. A modern outlook is given by A. and D. Löve's work on the cytology of the Icelandic flora[124] which supplements their earlier paper[123] dealing with chromosome numbers of northern species. The Faeroes also are subarctic and their flora and vegetation are very fully dealt with by Warming[225].

2. *Boreal Region.* This is essentially the conifer belt that stretches across much of northern Eurasia dominated by forests of spruce, pine, and larch. In the European portion most of Scandinavia (except the extreme north, south, and south-west) and northern Russia is included in it and the Russian name "taiga" is frequently applied as a general term to it. The taiga in in Northern Asia is practically continuous with this European conifer belt and the genera concerned are mostly the same though the species may be different. The most important trees are the spruce (*Picea abies*, also known as *P. excelsa*) in the west and the Siberian spruce (*P. obovata*) to the east of the White Sea. In the Kola Peninsula and east of the Urals there are said to be intermediates and it would be interesting to know if there be a cline from one to the other species. The spruce occupies, though not uniformly, half the area of European Russia. Five spruce communities in European Russia have been distinguished (Sukachev[191]) with different structure and different associates.

3. *Central European Region.* This region occupies the largest part of Europe and is bounded to the north by the coniferous forest belt, to the south by the Mediterranean Region, and to the east by the western extension of the Central Asiatic Region. It is ecologically characterized by broad-leaved forests but these have been so heavily exploited that few primitive forest areas remain. Oaks, *Quercus robur*, *Q. petraea*, and, towards the south, *Q. lanuginosa*, and beech, *Fagus silvatica*, are the commonest trees. Others that may be locally important belong to the genera *Fraxinus*, *Tilia*, *Acer*, *Populus*, and *Ulmus*, and, in wetter habitats, *Alnus* and *Salix*. The western parts of the Region have a more equable climate often designated "Oceanic" and it is possible to denote many species as "Atlantic" or "Continental" in their ranges but it is difficult to determine any boundary line or belt for

sub-regional phytochoria on this basis. On sandy and gravelly soils in western Europe there are extensive areas of heathland with species of heath, heather, gorse, and heath grasses. There are also peat bogs and grasslands, the latter mainly secondary origin. Conifers are few except at higher altitudes. The high mountains of the Pyrenees, Alps, and Carpathians show a typical altitudinal zonation of the vegetation and flora. Below, there are deciduous forests, usually mixed oak forests, then a beech zone more or less in a cloud belt, followed by a conifer belt forming the upper forest limit with pines, spruce, larch, and white firs. Above this there is a wide or narrow belt of low shrubs (junipers and dwarf pines) and a high mountain herbaceous belt extending to the limits of permanent ice and snow. The "alpine" meadows and pastures and rocky and stony habitats are the special homes of primulas, saxifrages, gentians, pinks, buttercups, globe-flowers, white dryas, campanulas, dwarf willows, eidelweiss, etc. The altitudinal zonation in the European mountains has been compared with the latitudinal zonation from south to north but there is one interesting major difference, the beech goes above the deciduous oaks into the cloud belt of the mountains but the oaks extend farther north than the beech. In the south-east there are the European steppe areas in Hungary, southern Russia, Dobrudja, and northern Bulgaria, but some of these are secondary and many parts are cultivated.

The literature on the flora and vegetation is very extensive. Apart from general text-books reference may be made to the floras by Hegi[88] and Hermann[90] and to Hultén[98] who maps the ranges of species of the Scandinavian flora. Some interesting suggestions regarding the origin of the temperate flora of Eurasia are made by Takhtajan[199].

4. *Mediterranean Region.* There has been considerable diversity of opinion regarding the boundaries of the Mediterranean Region. Engler[61, 64] accepted a very wide range from the Iberian Peninsula to Armenia and Persia. At the other extreme are those authors who restrict the Region to a narrow, and even discontinuous, belt around the Mediterranean Basin. Most recent work has favoured the narrower view which, with some modifications, is accepted here. The vegetation is characterized by the dominance of evergreen hard-leaved plants and this is correlated with a hot dry summer and mild wet winter. *Pinus halepensis* (s. l.) woods and evergreen oaks (*Quercus ilex* and *Q. coccifera* as trees or shrubs) with macchia (maquis) brushwoods are characteristic. The macchia is a mixture of, often tall, shrubs including *Arbutus* spp., *Myrtus communis*, *Olea europaea*, *Juniperus* spp., *Laurus nobilis*, *Spartium junceum*, and others, with climbing *Smilax*, and is often difficult to penetrate because of its density and spiny or prickly nature. Degenerate forms are the phrygana of Greece, the garrigues of France, and the tomillares of Spain. At higher altitudes are woods of deciduous oaks,

ash, and sweet chestnut and the tree limit was naturally formed of fir woods in many places, but these have now been mostly destroyed.

The literature on the Mediterranean Region has been very fully listed in Rikli's important work[162] and only papers by Schmid[168] and Regel[157, 158] need be noted here.

The Mediterranean flora is a relatively old one in that it contains a large number of Tertiary relicts. The area was not glaciated (except at most very locally) during the Glacial Epoch but the climate was then almost certainly wetter ("Diluvial Period") and the Mediterranean flora and vegetation extended farther south, and perhaps east, than it does now. There is evidence that many Mediterranean elements have extended their ranges northwards in recent times.

Macronesian Sub-region—The North Atlantic islands of Madeira, the Canaries, the Azores, and the Cape Verde Islands, are difficult to place phytogeographically. The flora generically is largely Mediterranean but there is a considerable African element and a smaller American one, with a high proportion of endemic species. The African element is most marked in the Cape Verde Islands but is also evident in the flora of the Canaries. The literature is large but scattered and reference may be made for Madeira to Lowe[126], Vahl[213], Menezes[132], Cockerell[44]; for the Canaries to Pitard et Proust[148], Bannerman[8], Børgesen[18], Lindinger[120], Burchard[25], Ceballos[31], Schmid[169]; for the Azores to Godman[68], Trelease[203], Palhina[145], Tutin[212]; and for the Cape Verde Islands to Chevalier[39, 40].

5. *Central Asiatic Region or Regions.* This is an enormous region and probably will have to be divided at least into subregions though Roi[164] maintained that Drude was right in regarding it as a "unit," including Mongolia, Tibet, Turkestan, and the steppes near the Caspian Sea, except that Tibet has more relation with the Himalaya. A very great amount of work on the phytogeography of this area is now being carried out by Russian botanists. Reference may be made to the periodical *Geobotanica* (1934) 1—(1957) 11. The papers in this are in Russian, sometimes with summaries in West European languages. The results have been in part co-ordinated phytogeographically in the two volumes edited by Lavrenko and Soczava. In the great *Flora S.S.S.R.* the major divisions used for Asiatic Russia are: Caucasus (Ciscaucasia, Dagestan, West Transcaucasia, East Transcaucasia, South Transcaucasia, Talyah), Western Siberia (Yenisei, Lena-Kolyma, Angara-Sayan, Dauria), Far East (Kamchatka, Okhotsk, Zeya-Bureya, Udsk, Ussuri, Sakhalin), and Central Asia (Aralo-Caspia, Balkhash, Dzungaro-Tabagatai, Kyzyl (Kizil) Kum, Kara Kum, Mountain Turkmenia, Amu Darya foothills, Syr Darya foothills, Pamir-Altai, Tien Shan). A full foristic analysis of Asiatic Russia must await the completion of this *Flora.* Roi[164] for the vegetation of Central Asia recorded the following vegetational

climaxes: coniferous forest, deciduous forest, grassland, and scrub. For constitutive elements of the flora he lists plants under the headings: endemic genera and species, Central Asiatic-Mediterranean genera, the subtropical flora, the Euro-Siberian element, and Asia and America. He rightly points out that many phytogeographers have regarded Central Asia as a centre of distribution and notes that it is rich in endemics and relicts which formed a more extended vegetation during the Tertiary period than at present. Younatov[233] describes the zones and belts of vegetation under: vegetation of the high mountains, forests, montane steppes, true steppes, desert steppes, and deserts. It is definitely claimed that the aridity of Central Asia is of very ancient origin and has existed at least since the end of the Cretaceous.

Very interesting research has been, and is being, made into the history of the flora of Asiatic Russia, by palaeobotanical investigations. Here one can only refer to the papers of Kryshtofovich[111, 112] and Iljin[102].

Reference should be made to extreme eastern Asia, politically now under Russia. The flora of Kamtschatka by Hultén[96] and a paper by Popov[151] will serve as guides to the literature.

6. *The Regions of the Nearer East.* The large and botanically most interesting area of what is best termed, to use Hogarth's phrase, the Nearer East, often now misleadingly called the Middle East, comprises eastern North Africa, the Balkan Peninsula, and western Asia from Anatolia, Israel, Syria, and Lebanon eastwards to Pakistan. No general phytogeographical account of the area has yet been published and there is no inclusive flora since that of Boissier's *Flora Orientalis* (1867–1888). The Nearer East is a meeting place of races, religions, climates, and plant regions. Just how many of these last it is best to distinguish is not fully settled. Eig[60] recognized three: Mediterranean, Saharo-Sindian, and Turanian. The Mediterranean Region is delimited in a very narrow sense by Eig and is dealt with above. The Central European Regions extends into the northern and central parts of the Balkan Peninsula and south-western Arabia has close botanical affinities with tropical Africa. We must briefly consider the Saharo-Sindian and the Turanian Regions.

From the Sahara across Egypt, Arabia, and southern Persia to the borders of India and including parts of Jordan, Syria, and Iraq, is the great belt of desert and semi-desert country with a comparatively small flora highly specialized to survive drought. It is the country of the date palm (*Phoenix dactylifera*). In the extreme deserts, plants are absent or extremely scattered. Where there are oases or where there is rainfall at, often irregular, intervals a more varied plant life occurs of deeply rooted xeromorphic species or of ephemerals. Where saline water occurs the goosefoot family (*Chenopodiaceae*) is represented by one or more species of a number of genera (*Anabasis, Arthrocnemum, Atriplex, Haloxylon, Salsola, Suaeda*, etc.). It is to be noted

that there is no great development of succulent plants, such as are found in the semi-deserts of South Africa (*Ficoidaceae*, *Crassulaceae*, *Euphorbiaceae*) or America (*Cactaceae*). It is probable that at least a high proportion of the species of this region have been derived from ancestors whose relatives are now found in neighbouring non-desert regions and especially the Mediterranean Region. Indeed, recent research has shown that quite definite Mediterranean genera and even species occur far inland in the Sahara as in the Haggar Mountains.

The Turanian Region, as recognized by Eig, is less well defined than the Saharo-Sindian. It is assumed to be an extension south-westwards of the flora and vegetation of southern Central Asia, but its characteristics and relationships need much more investigation. The abundance of individuals and species of *Astragalus* (*Leguminosae*), one of the largest genera of flowering plants, is noteworthy. It seems probable that to the Turanian Region (or some segregate or other of it) belong parts of Israel, Jordan, Syria, Iraq, Persia, Afghanistan, and Pakistan, and much of the interior of Anatolia.

From the rather diffuse literature one may select the following for mention: Täckholm and Drar[196], Täckholm[195], Eig[60], Holmboe[93], Zohary[234], Krause[110], and Louis[121].

7. *Eastern Asiatic Region or Regions.* i. *China.*—The enormous area covered by China is botanically diverse. As Handel-Mazzetti[81] pointed out, the number of plant species known to range over almost the whole of China but not occurring elsewhere can be counted on the fingers of one hand. Large parts have still to be investigated as the recent discovery of *Metasequoia* demonstrates. It is satisfactory to know that trained Chinese botanists are now engaged in this task and it may well be that in a few decades sufficient information will be available for an agreed phytogeographical division of the whole country and of the relationships of the divisions to those of surrounding areas. Here only three schemes can be mentioned. Handel-Mazzetti[81] made eight essentially different "floral areas": 1. The North Chinese-Korean mixed forest district; 2. The desert district of the southern Gobi; 3. The North Chinese loess-steppe district; 4. The North Chinese-Central Japanese laurel district; 5. Tropical China; 6. The highland and the high mountains of Yunnan and West Setschwan; 7. The East Tibetan grassland; 8. The Upper Burma-West Yunnan monsoon district. Hui-Lin Li[118] recognized fourteen "regions" for the whole of China: 1. The Southern China Maritime; 2. The Tonkin Gulf; 3. The Mid-Mekong; 4. The Sino-Himalayan; 5. The Southwestern China Plateau; 6. The Upper Yangtze; 7. The Middle Lake; 8. The Eastern China Maritime; 9. The Northern China Plain; 10. The Northern China Loess-Highland; 11. The Northeastern Chinese and Korean; 12. The Mongolian Desert-Grassland; 13. The Sinkiang Basin; 14. The Tibetan Plateau.

Teng[200, 201] has the following regions as based on the distribution of climax forest communities correlated with physiography and climate: Syansk-Altai, Tienshan, Kilien-Inshan, Changpai, Khingan, Loess-Highland, Tsingling-Tapa, Minshan, Northern Sikang, Southern Sikang, Southeastern Sikang, Central Yunnan, Yangtze, Southeastern Maritime, Luichow-Hainan, Salween-Mekong, Taiwan, and Tsangpo Gorge. These "regions" are grouped under or based on seven major plant communities or "formations": subboreal forest, subalpine forest, montane forest, deciduous forest, subtropical forest, tropical forest, and monsoon forest. It is probable that Teng's "regions" are, at least in part, better referred to as domains or provinces. He has a valuable bibliography at the end of his paper.

The flora and vegetation of Tibet remains little known except for that of some of the peripheral parts. For these the books and papers of Kingdon Ward[220–224] and a paper by Teng may be consulted. Manchuria will also be included in any general phytogeographical survey of Eastern Asia and researches on this area include those of Shaw[175], Takahasi[197], and Sochava[181].

ii. *Japan*—The long stretch of the islands of Japan was divided by Takeda[198] into three main regions: northern, middle, and southern. The northern region has forests of deciduous oaks, birches, cherries, elm, maples, poplars, and the peculiar *Ceridiphyllum japonicum*, with *Salix* spp. in more or less damp places and conifers such as *Abies*, *Juniperus*, *Larix*, *Picea*, and *Thujopsis*. There is an abundant undergrowth of bamboos and many woody climbers are present. In the middle region the coasts are lined with graceful trees of *Pinus thunbergii* and the forests are rich in species of other species of pine, *Cryptomeria*, *Prunus*, *Pyrus*, and numerous other genera. Tall bamboos (especially species of *Phyllostachys*) add a special feature to the vegetation. The mountain ranges show marked altitudinal zonation of the plant life which has been well studied for Mt. Fuji, the highest volcano in Japan (*c.* 12,450 ft). The southern region is subtropical and is the region of figs (*Ficus* spp.), with which are found broad-leaved evergreen trees such as species of *Quercus*, *Hibiscus*, *Myrica*, and *Lauraceae*. On their branches are epiphytic orchids, ferns, and lycopods. In the dense moist forests are many subtropical to tropical ferns (*Angiopteris*, *Cyathea*, *Dicksonia*, *Gleichenia*, *Osmunda*, *Pteris*), with woody climbers such as *Bauhinia japonica*. In the Loochoo Islands (Ryukyu) the vegetation is even more tropical and *Cycas revoluta* flourishes along with many interesting orchids and ferns.

Another phytogeographical scheme is that of Hayata[85] who lists special and characteristic species for his subdivisions.

8. *North American Regions.* The great North American continent has been intensively studied phytogeographically and is botanically the best known of the continents outside Europe. There is, however, no complete flora of the

whole continent and the major divisions of the flora and vegetation suggested by different authors vary considerably. Harshberger[82] dealt with the whole area and his major subdivisions are into seven principal "zones" (probably better considered "regions" or groups of such) subdivided into "regions" (possibly better termed provinces or domains): I. Arctic and Sub-Arctic Zones (1. Arctic regions of Labrador, northern Mackenzie, and the Arctic shore; 2. Sub-Arctic forest region of North Canada and Alaska). II. North American Temperate Zone, Atlantic Section (1. St. Lawrence-Great Lake region; 2. Atlantic-Gulf Coastal region; 3. Piedmont-Appalachian-Ozark Plateau-Mountain region). III. North American Temperate Zone, Xerophytic Section of the Interior (1. Prairie region; 2. Rocky Mountain Region; 3. Great Basin Region). IV. North American Temperate Zone, Pacific Section (1. Sitka region; 2. Columbian region; 3. Californian region). V. Mexican Subtropic Zone and Mountain Regions (1. Sonoran Desert region; 2. Western Sierra Madre region; 3. Chihuahuan desert region; 4. Eastern Sierra Madre region; 5. United Cordilleran region). VI. North American Tropic Zone, Section of Mexico and Central America (1. Jaliscan region; 2. Gulf region; 3. Guatemalan region; 4. Costa Rica region). VII. North American Tropic Zone, West Indian Section (1. Antillean region; 2. Bahaman region; 3. Bermudan region). Harshberger's work has been severely criticized by other North American botanists but here it must suffice to refer to the more recent biogeographical scheme of Dice[50]. He terms his major divisions "provinces" which he names as follows: Eskimoan (essentially the Arctic and Subarctic Region north of the conifer forests), Hudsonian (essentially the equivalent of the "taiga" or conifer region of Eur-Asia), Canadian, Carolinian, Austroriparian, Illinoian, Texan, Saskatchewan, Kansan, Comanchian, Aleutian, Sitkan, Oregonian, Montanian, Coloradan, Navahonian, Palusian, Artemisian, Californian, Sanlucan, Sonoran, Mohavian, Sinaloan, Apachian, Durangan, Chihuahuan, Tamaulipan, Potosian, and Veracruzian. Both Harshberger and Dice give long bibliographies.

There are numerous "floras" and "manuals" published for states, provinces, or other divisions of North America. The comprehensive *North American Flora* (New York Bot. Gard. 1905) is far from complete while Britten and Brown's work (see Gleason,[67]) includes only the northern United States and Canada. A useful account of the Canadian flora is that by Adams[1] and the comprehensive bibliography by Adams and Senn[2] is most valuable for reference.

Recent researches into the history of the North American flora by the study of deposits of fossil plants are yielding valuable data. Cain[27], pp. 29–122, and Chaney[32] should, in particular, be consulted.

In very broad terms, the flora and vegetation of North America may be

briefly outlined. To the north there is the Arctic and Subarctic area already considered. Immediately to the south is the wide belt of the region of conifers. Farther south are the eastern and western forest regions separated by the prairies and semi-deserts. In the extreme south the plant-life becomes subtropical.

Of particular phytogeographical interests are the extra-American relationships of the eastern and western floras. Asa Gray and Hooker (see Turrill,[209]) discussed these very fully and, in particular, the occurrence of "Japanese" genera in the eastern flora. The explanation offered was that in Miocene times there was a general community of flora between Europe, North America, and Asia. The gradual on-coming of the Glacial Epoch and its culmination drove the flora southwards in so far as it was not exterminated. On the retreat of the ice at the end of the Glacial Epoch the temperate flora again extended northwards, leaving Arctic and Subarctic plants as relicts on the mountains of both eastern and western America. The high lands of the west retained glacial conditions for a much longer period than did the eastern part of the continent and the old temperate flora failed in large part to return there. Relicts, such as *Sequoia*, were left but much of the existing Californian flora came from Mexico.

II. *Palaeotropic Realm*

1. *Indian Regions.* The great area of the Indian subcontinent has a wide range of climate and a corresponding diversity in vegetation and flora. The masterly "sketch" by J. D. Hooker[95], has still a great deal that recommends it as a basis for further study of the flora. He has nine provinces as follows: 1. Eastern Himalayan, 2. Western Himalayan, 3. Indus-Plain, 4. Gangetic Plain, 5. Malabar, 6. Deccan, 7. Ceylon, 8. Burmese, 9. Malayan Peninsula. A modification of Hooker's scheme was made by Chatterjee[36] who, including Burma but excluding Ceylon and the Malay Peninsula, has ten main divisions: 1. Deccan, 2. Malabar, 3. Indus Plain, 4. Gangetic Plain, 5. Assam, 6. Eastern Himalaya, 7. Central Himalaya, 8. Western Himalaya, 9. Upper Burma, 10. Lower Burma.

There is an enormous literature on the botany of India and surrounding countries. References to much of this, in part with summaries, are given in Turrill[209] and need not be repeated here. Very briefly we may note a few of the more important of the general phytogeographical features. Northwest India (now mostly included in Pakistan) comes partly within the "Oriental" Region of some earlier authors, partly within an extension of the Central Asiatic Region, and largely within the North African-Indian Desert Region. The Himalaya are clearly divisible into a Western and an Eastern Province or Subregion with a transitional district in Nepal. The Eastern portion is very closely linked botanically with the mountains of North Burma and

south-western China. The flora and vegetation of Peninsular India and Ceylon are tropical and often rich and lush with monsoon rainfall and with altitude largely determining the kinds of plant communities. The flora of Ceylon differs from that of Malabar especially in having many more Malayan elements, especially of *Dipterocarpaceae*. The affinities of the northern Burmese flora are with that of Assam and the Eastern Himalaya, differing from that of central and southern Burma in the absence of teak (*Tecona grandis*), the paucity of species of *Dipterocarpaceae*, and the presence of sal (*Shorea robusta*) and of *Pinus insularis* (*P. khasya*). Western and southern Burma have a vegetation of dense evergreen forests where dipterocarps, oaks, and bamboos are conspicuous features and ferns, climbing palms, and orchids abound. The Malay Peninsula is considered with Malaysia below.

2. *Malaysian Region.* The Malay Archipelago and the Malay Peninsula have one of the richest floras in the world. A great deal of work has been done on it by British, Dutch, American, and German botanists in particular. A start has been made on the publication of a great *Flora Malesiana* (editor C. G. G. J. van Steenis), to cover the Peninsula, the Archipelago, and New Guinea. If this be completed as planned it will include the ecology and phytogeography of the area as well as the taxonomy proper. There is much information on the plant geography in the parts already published and the historical and bibliographical section are very valuable. It is proposed that the phytogeography be fully dealt with in volume 3. The volumes are not being published in numerical order.

The boundaries assigned to the Region as a whole pass through the isthmus of Kra, between the Philippines and Formosa, through the Torres Straits, and include the Louisiades and the Bismarck Archipelago. In the northwest quite a number of typical Malaysian genera of forest plants fail to occur any farther in the Indochinese Peninsula, e.g. *Rafflesia*, *Rhizanthes*, *Dryobalanops*, *Agathis*, *Eusideroxylon*, *Koompassia*, etc. The Philippines possess an almost entirely Malaysian flora, in contrast to Formosa's Japano-Chinese floral character. The flora of New Guinea was formerly assumed to be essentially Australian in basic composition on account of a relatively few, but striking, plants of obvious Australian affinities. Later studies have demonstrated a much more important Malaysian element.

Various subdivisions of the region have been proposed, but the following are accepted by van Steenis[186]; two major lines are 1. to the east of the Philippines and the west of Celebes, and 2. to the north of Java and south of Borneo and Celebes, and these with less important lines as boundaries give the subregions: Malay Peninsula, Sumatra, Borneo, Philippines, Celebes, Moluccas, Java to Timor, New Guinea, Bismarck Archipelago and associated islands.

The bibliography given, and continuing to be given in the *Flora Malesiana*,

is as complete as possible and must be consulted by all students working on this area. For plant communities attention may be called to Richards[160] and the references he gives.

3. *Tropical African Regions.* Africa south of the Sahara is, in the main, a geologically old land area. There is evidence of climatic fluctuations but, since the appearance and rise to dominance of the angiosperms, it is doubtful if these have been so extreme as in other parts of the world. The flora is rich and the vegetation ranges from tropical rain forest to desert. Floristically, there is very considerable activity in research. *The Flora of Tropical Africa,* prepared at Kew, is now out-of-date except for some of the latest published parts but floras of more restricted areas have been published or are in course of preparation. Thus there is the *Flora of West Tropical Africa* by Hutchinson and Dalziel (1927–1936) with a new edition by Keay partly published[107], the *Flora of Tropical East Africa* edited by Turrill and Milne-Redhead, partly published (1952–), and the *Flora Zambesiaca,* edited by Brenan, Exell, and Wild, being prepared. These are all published, or to be published, by the Crown Agents for Overseas Governments and Administrations (formerly the Crown Agents for the Colonies), London. It is interesting to note that the early botanical exploration of tropical Africa was peripheral, that is collections were made independently at many different points on or near the coast with varying penetrations inland. These collections were worked out very largely as separate units with the consequence that synonyms were used for many species and a uniform taxonomy and consequent tracing of correct ranges is only becoming possible now that most parts of the continent have been or are being made accessible to botanists. A great deal of comparative investigation still remains to be done and general schemes are therefore tentative.

Good[71] recognizes the following regions: Sudanese Park Steppe, North-east African Highland and Steppe, West African Rain-forest, East African Steppe, and the Flora of the Tropical African Mountains. A portion of the North African-Indian Desert Region also comes south of the Tropic of Cancer.

There have been published numerous ecological and phytogeographical accounts of different parts of tropical Africa and several attempts to construct a classification for the vegetation of the whole area. The following is an outline of a scheme proposed at an international meeting of plant ecologists at Tangambi, Belgian Congo, in 1956 (see Boughey[19]).

I. Closed Forest formations.

A. Climatic forest formations.

(a) Forests at low and medium altitudes. (1) Moist forest; (2) Dry deciduous forest; (3) Thicket.

(b) Forests at high altitudes. (1) Moist montane forest; (2) Dry montane forest; (3) Bamboo forest.

B. Edaphic forest formations.

(a) Mangrove. (b) Swamp forest. (c) Periodic swamp forest. (d) Riparian forest.

II. Mixed forest-grassland formations and grassland formations.

A. Woodland.

B. Savanna. (a) Savanna woodland. (b) Tree savanna. (c) Shrub savanna. (d) Grass savanna.

C. Steppe. (a) Tree and/or shrub steppe. (b) Dwarf shrub steppe. (c) Succulent steppe. (d) Grass and/or herb steppe.

D. Grassland. (a) Aquatic grassland. (b) Herb swamp. (c) High montane grassland.

A selected list of references to recent important accounts of the flora and vegetation of tropical Africa is now given under the major geographical divisions:

West Africa: Lavauden[114], Aubreville[6, 7], Jeannel[105], Trochain[204], Chipp[41], Shaw[175], Keay[107].

East Africa: Barbosa[9], Chesters[38], Pichi-Sermolli[47], Hedberg[87].

Central Africa: Brass and Brenan[20].

Congo: Duvigneaud[57], Robyns[163], "Flore du Congo Belge et du Ruand-Urundi," Bruxelles, 1948– .

4. *Mascarene Region.* Madagascar and its associated island groups are of great phytogeographical interest. Madagascar itself is nearly 1000 miles long and has an average breadth of 250 miles. It is only 260 miles from the nearest point on the East African coast. The botanical taxonomy is still being investigated and the comprehensive *Flore de Madagascar* (edit. H. Humbert[99]) is not yet completed. The estimates for the known indigenous vascular plants are 184 families, 1139 genera, 6765 species. The total known number of species of seed bearing plants is 7370 and of pteridophytes 505. The largest families (with number of known species in brackets) are *Orchidaceae* (685), *Compositae* (440), *Polypodiaceae* (366), *Euphorbiaceae* (334), *Cyperaceae* (316), *Gramineae* (301), *Papilionaceae* (273), *Melastomataceae* (265), *Rubiaceae* (242), *Acanthaceae* (240). There are three endemic families, *Chlaenaceae*, *Rhopalocarpaceae*, and *Didieriaceae*, and a large number of endemic genera, while a majority of the indigenous species are only known in the island. For species, the following are the percentages of endemics in five biological groups: annuals 58, perennial herbs 85, lianes 90, shrubs, 94,

trees 94. Approximately 15 per cent of the known flora is considered as forming a "recent exotic element" introduced by currents, wind, birds, and man. Of the older floristic elements there may be distinguished five groups: a western or African, about 25 per cent of the total flora; a pantropical, about 42 per cent; an oriental, about 7 per cent; an austral, about 3 per cent; and an essentially Madagascar about 6 per cent. Perrier de la Bathie[110] suggests the following history of the flora: 1. A very ancient period, perhaps going back to the Upper Cretaceous, before the Senonian transgression, during which Madagascar was united both to the southern continent and to the tropical zone. From this period is dated the primitive bases of the flora, that is all the archaic taxa as well as those of southern, oriental, or pantropical origin. 2. A period of connection with Africa only, of Tertiary age, probably post-Aquitanian, in the course of which the Mascarene Region was invaded by a great number of African elements and, via Africa, of more pantropical elements. 3. A long period of insularity, dating at least from the Pliocene, during which arrived oriental, pantropical, and African elements by ocean currents, winds, and migratory birds, and, during the last two thousand years, by the activities of man, a host of species now naturalized. There is no evidence of a later, even temporary, connection between Madagascar and Africa.

The natural vegetation has been largely destroyed or greatly modified by man. About three-tenths of the island, however, still has remains of the primitive vegetation, especially in the north-east of the eastern watershed, on some mountain massifs, and on the plains of the south-west. Three domains are recognized by Perrier de la Bathie[110]. The oriental domain covers the eastern slopes to 800 m and has abundant precipitation. There are strips of a littoral forest of 20–30 m mean height, with rich foliage and abundance of endemic species mixed with some introduced by marine currents. Inland from this are remains of the oriental forest with a great richness in species and changing gradually in species as the mountains are approached. The central domain has a lower temperature and a longer dry season with winds and fogs. Its vegetation is generally lower and denser with smaller but persistent and coriaceous foliage. The flora is very rich and covers all the central plateau and mountains to the highest summits (2800 m). The western domain is the warmest and has a long dry season. Its soils are varied and the vegetation changes with the soil. There are remains of forests on siliceous terrains, characterized by the absence of tall trees, with deciduous species mixed with some with persistent or semi-persistent leaves. There is an almost total absence of ferns and epiphytes. On limestone terrains forests only exist on rocky parts where fire has not destroyed them. Many of the trees have a baobab habit and xerophytes are frequent in the undergrowth (see Leandri[116]).

Space will not permit a discussion on the flora and vegetation of other islands within the orbit of Madagascar. For the Seychelles, attention is called to the paper by Summerhayes[192] and for Mauritius to the publications of Vaughan and Wiehe[214].

5. *Pacific Region.* The immense area of the Pacific Ocean with its scattered islands and island groups offers a great many problems to the phytogeographer. This is partly due to the size and diversity of the area and partly to the incompleteness of botanical exploration. While the plant life of some islands, those of the Hawaian group for example, has been well studied, that of others, especially the more remote ones, is very incompletely known. The literature is considerable as is shown by Merrill's bibliography (Merrill[136]). Many of the problems involved are also discussed in a very readable form by Merrill[135].

In general the Pacific islands fall into one of two groups: high (or "continental") islands and low (or "oceanic") islands. The high islands have high mountains or hills, have often a rugged topography, are largely volcanic, and have most often a forest vegetation with a flora relatively rich in species. They include Fiji, Samoa, New Caledonia, Hawaii, Tahiti, and the Marquessas, together with some smaller more isolated islands such as Pitcairn and Easter. The low islands, in contrast, are generally associated with atolls or the remnants of atolls and owe their presence to the growth of coral reefs. They are usually raised only a short distance above sea level and their surfaces are more or less flat. The native flora is relatively very poor and much the same from island to island and is largely or entirely limited to species of strand vegetation. There is little doubt that the flora of the low islands has been introduced naturally by disseminules brought by ocean currents and by man. It is the distinct, often highly endemic, floras of the high islands that pose phytogeographical problems.

As an example of the plant life of high islands that of the Fiji group may be briefly considered on the basis of recent researches (Smith[180]). The vegetation is largely controlled by rainfall and soil. The rocks of the larger islands are mostly plutonic but many of those of the smaller islands are upraised limestone. Thus, in the Lau Group the limestone soils support a dense forest of varied elements whereas the volcanic soils have a comparatively poor flora. The south-eastern slopes of the larger islands have a heavy rainfall (often over 200 in. annually) and support a dense rain-forest. The northern and western slopes have a lighter, markedly seasonal, rainfall of usually 70–80 in. annually and the predominant vegetation is grassland with scattered thickets and pockets of forest. In general the rain-forest ascends to the highest summits (1323 m). Variations in temperature are comparatively slight throughout Fiji.

The flora is still inadequately known but 1253 indigenous species of

phanerogams are recorded of which nearly 70 per cent are endemic. Of the indigenous non-endemic species nearly half are pan-tropical or pan-Pacific. Of the endemic species, 784 (over 90 per cent) have their closest taxonomic relationships in the floras of Malaysia or Papuasia, suggesting that most of the floristic elements of Fiji entered the region through a New Guinean-Melanesian route. Some 5 per cent of the endemic species have close relationships with New Caledonian or Australian plants, while a still smaller number indicate the presence of Polynesian, New Zealand, or "Antarctic" elements. Of the 444 genera with indigenous species, 33 per cent occur in both hemispheres while 50 per cent are Indo-Malaysian. There are comparatively small numbers derived from New Caledonian, Australian, and Polynesian floras. Only 13 genera are considered endemic and there is one endemic family, *Degeneriaceae*.

It is impossible in the space available to consider all the islands of the Pacific Basin and their botanical problems. The works already quoted will enable the reader to trace most of the scattered literature. Attention is, however, especially called to the following papers as dealing with matters of wide general interest: Setchell[172], Merrill[133], Guillaumin[76], Williams[228], Merrill[134], Andrews[4], Kanehira[106], and Guillaumin[77]. A useful account of the Pacific islands is given in the book edited by Osborn[141].

III. *Neotropical Realm*

1. *Tropical and Subtropical American Regions.* The great area of Latin America, that is Mexico, Central America, the West Indies, and South America, is well covered botanically by the papers by many authors in the volumes edited by Verdoorn entitled *Plants and Plant Science in Latin America*, 1945, and by the long lists of references given by the writers. No attempt is made here to refer to research before 1944 since most of this can be traced, at least with a little trouble, in Verdoorn's "collection of articles." Richards[160] and his references will enable students to trace much that is ecological for the area.

Latin American plant life has usually been classified mainly on the kinds of plant communities and their distribution. Smith and Johnston (in Verdoorn[215]) have the following major phytogeographic divisions for the whole of America south of the U.S.A.

I. Forests or Wooded Regions: 1. Tropical and subtropical rain-forest; 2. Tropical deciduous forest; 3. South Brazilian forest and savanna zone; 4. Palm forest; 5. Subantarctic beech forest; 6. Thorn forest.

II. Grasslands and Savannas: 1. Savanna regions, a. True savannas, b. Uruguayan savannas, c. Campo; 2. Pampean grassland.

III. Deserts or Semi-desert Regions: 1. Coastal deserts of Pacific South America; 2. Patagonian Fuegian steppe; 3. Desert scrub; 4. Transitional vegetation of central Chile; 5. California chaparral.

IV. Montane Zone: 1. Mexico, Central America, and the larger West Indies; 2. Northern Andes; 3. Southern Andes.

V. Maritime or Littoral Zone.

The temperate parts of South America included in the scheme just given will be considered separately later. A few remarks about the tropical and subtropical areas may be given. The Amazonian rain-forest is the most extensive continuous rain-forest in the world, extending some 2200 miles east to west and 1200 miles north to south under conditions of high even temperature, heavy rainfall, and alluvial soil. In addition to Amazonian Brazil, the rain-forest covers much of the Guianas, southern and eastern Venezuela, and the portions of Colombia, Ecuador, Peru, and Bolivia drained by tributaries of the main river. The Upland Forests on somewhat elevated land are not subjected to inundation, while the Forests of the Varzeas or bottom lands are periodically flooded during the rainy season. The flora consists of an enormous number of species of many families amongst which may be mentioned *Palmae*, *Leguminosae*, *Lauraceae*, *Cunoniaceae*, *Myrtaceae*, *Myrcinaceae*, *Bombacaceae*, and many others with tall trees. Lianes are abundant, especially members of the *Bignoniaceae*, *Leguminosae*, *Sapindaceae*, *Malpighiaceae*, and *Cucurbitaceae*. The epiphytes are abundant and include bromeliads, orchids, ferns, some *Cactaceae*, and species of *Peperomia*. Palm forests are characteristic of the north-central part of the Brazilian plateau and are largely composed of species of *Copernicia*, *Mauritia*, *Euterpe*, and *Orbignya*. Thorn forests with open or dense growth of usually deciduous thorny small trees or arborescent shrubs of such genera as *Prosopis*, *Acacia*, and *Mimosa* are common in Mexico, Central America, and the West Indies. In the savannas the predominant plants are bunch grasses of the genera *Andropogon*, *Cymbopogon*, *Trachypogon*, etc., with *Cyperaceae* and such woody plants as species of *Curatella*, *Bowdichia*, *Byrsonima*, and *Mauritia*. The numbers and kinds of more or less scattered trees and shrubs vary in different areas. There is a coastal desert or semi-desert belt, 50–100 miles wide, extending from northern Peru to the south of Coquimbo, Chile. Most of this has a very open and sparse scrub vegetation with few trees.

Of recent literature on the areas, mostly with bibliographies, the following may be consulted with advantage: Leopold[117], Styermark[190], Beard[12], Dodge[53], Asprey and Robbins[5], Beard[11], Fanshawe[65, 66], Pulle[155], Lindeman[119], Ducke and Black[55], and Schultze-Rhonhof[171].

IV. *Southern Realm*

1. *South African Region.* The flora and vegetation of South Africa are in many respects very peculiar and a great deal of research has been and is being done on them. Much of the work up to 1938 has been brought together with references to original papers, by Adamson[3]. The principal

communities are classified as bush (sclerophyll), forest, savanna, grassland, and semi-desert. Some of the communities and a fair proportion of the flora represent southern extensions of Tropical African vegetation and flora but some communities and many taxa are endemic. Phytogeographically the vegetation is divided into four groups: (a) East Central African, occupying the whole of the eastern portion and including Low Veld, Bush Veld, Temperate Savanna, Grassland, Montane, Warm Temperate and Subtropical Forest, and Karroo Bush; (b) Kalahari in the north-central part and represented by the Bush Savanna; (c) Southern African in the south-western parts, comprising Sclerophyll, Succulent Bush, and probably Temperate Forest; (d) Namib in the north-west, represented by the *Rhigozum* and Desert communities.

Earlier phytogeographical divisions are those of Bolus (1905), Pole Evans[117], and Marloth[127]. Bolus proposed six "regions," as follows: I. The Western Coast Region; II. The South-Western Coast Region; III. The South-Eastern Coast Region; IV. The Karroo Region; V. The Upper Region; VI. The Kalahari Region. Pole-Evans has the Cape Region and the South African Region and in the latter recognizes "four main provinces": 1. The Namaqualand Desert Province; 2. The Karroo Province; 3. The Kalahari Park and Bush Province; 4. The South African Steppe and Forest Province. Marloth notes that two floras of fundamentally different origin occur within the limits of South Africa: A. The Southern extension of the great Old-African Plant-World, which is related to the vegetation of Madagascar and India, and B. The Domain of the Cape Flora. Six principal sub-divisions are made in the former: I. Tree veld, with more or less park-like landscapes; II. The Highveld; III. The subtropical coast belt of Natal; IV. The Karroo and karroid plains; V. Namaqualand; VI. The Namib.

The flora of the Union of South Africa is both rich in species and has many endemic taxa. Mention must be made of a few of the predominant families and genera. The *Proteaceae* are represented especially by *Protea* and *Leucadendron*, the heaths (*Erica* spp.) are more richly represented than anywhere else in the world, the *Restionaceae* occur in many genera and species, grasses abound in great variety, geophytes of monocotyledonous families (*Liliaceae*, *Amaryllidaceae*, *Iridaceae*, and *Orchidaceae*) with bulbs, corms, tubers, or rhizomes, die down to ground level in the hot dry seasons and are present in a great diversity of genera and species many of which are endemic, *Ficoidaceae*, with the *Mesembryanthemum* group now often split into numerous genera, *Crassulaceae* (*Crassula*, *Cotyledon*, *Rochea*, etc.) and *Euphorbiaceae* provide numerous succulents, while *Geraniaceae* (*Pelargonium*), *Leguminosae*, *Labiatae*, *Solanaceae*, *Rubiaceae*, *Compositae*, and many other families are well represented.

Africa, including South Africa, is for the most part an ancient land geologically and the evidence is that its flora has long developed more or less *in situ*. There was in South Africa no Pleistocene Ice Age comparable to that of the Northern Hemisphere. There are some connections between the flora of South Africa and that of Australasia and South America but they are mostly at the family level. While they may indicate a common link via a previous Antarctic continent it is possible that more palaeobotanical evidence may provide other explanations. The records of fossil *Proteaceae* in the Northern Hemisphere, for example, need modern investigation. The main affinities are with the rest of Africa and these in part suggest extensions southwards and in part extensions northwards. The heaths, with their great specific development in South Africa and their smaller deversification in the Mediterranean Region are partly linked in generic range by the occurrence of the genus (*Erica*) on Tropical African mountains. It is sometimes overlooked that other genera show somewhat similar range behaviour and *Dianthus* and *Silene* may be quoted as examples where the larger number of species are in the Mediterranean Region, few occur in Tropical Africa, and what appears to be a secondary area of species development is found in South Africa.

2. *New Zealand Region.* The flora of New Zealand shows resemblances to but also important differences from that of Australia. Over three-quarters of its species of flowering plants are endemic. There is a great range in vegetation from kauri (*Agathis australis*) forests in the north to temperate rain forest in the south and low-growing high mountain plants at high altitudes. Another contrast is between the wet western slopes of the mountains of Otago and the drier areas to the east in the "rain-shadow." The northern Kermadec islands are subtropical, the southern islands (Antipodes, Auckland, Campbell, and Macquarie) are subantarctic. The flora has some peculiar relationships. About 1800 species of vascular plants are known from the Dominion. There is a strong Australian element, especially at the generic level but also numerous "absentees," that is genera which one would expect to find in both Australia and New Zealand if their floras had had a recent common origin. Thus the prominent Australian genera, *Acacia*, *Boronia*, *Callistemon*, *Casuarina*, *Eucalyptus*, *Melaleuca*, *Prostanthera*, and *Xanthorrhoea* are absent from New Zealand which has only two species of *Proteaceae*, a family of many conspicuous species in Australia, particularly Western Australia. There are only about 30 *Leguminosae* in New Zealand compared with some 1200 Australian species. The Malayan element is particularly marked among the ferns. The South American (Fuegian) link with Australasia is exemplified in New Zealand by *Notofagus*, *Hebe* (or *Veronica* section *Hebe*), *Pernettya*, *Drimys*, *Uncinia*, and many other genera. It has been widely held that the floristic relationships between the southern

continents are best explained by former land connections via a now reduced Antarctic continent.

There has been, and is, a very keen interest shown in New Zealand in the flora and vegetation and the literature is considerable. Much of this has been ably summarized by Cockayne[42, 43] and other important works include those by Oliver[138, 139, 140], the summaries in McLuckie and McKee [129], and Cheeseman's *Manual* (1925).

Cockayne[13] makes the following provinces for the region. 1. The Kermadec Province, embracing all the Kermadec group of small islands; 2. The Northern Mainland Province, including North Island north of a line a little south of Tauranga to the River Mokau but extending to the north of the Mamaku Plateau; 3. The Central Mainland Province, with the remainder of North Island, Kapiti Island and South Island up to a line passing from Greymouth to Amuri Bluff; 4. The Southern Mainland Province, including the remainder of South Island and Stewart Island; 5. The Chatham Island Province; 6. The Subantarctic Province of the subantarctic islands.

3. *Australian Region.* Australia is a continent, with some surrounding islands, of nearly three million square miles. Its general botanical picture has been described as a great arid stretch of desert, steppe, and scrub in the centre and north-west, with surrounding concentric belts where increasing rainfall towards the coast supports savannah woodland, Eucalyptus forests, and rain-forests. The most striking floristic features are the forests of *Eucalyptus* (with some 500 species now recognized), members of the *Myrtaceae* (*Leptospermum, Melaleuca, Callistemon*, etc.), the wattles or species of *Acacia* (with over 450 species), the many genera of *Proteaceae* (*Banksia, Grevillea, Dryandra*, and so on), the numerous genera and species of *Leguminosae*, and the heath-like *Epacridaceae*. There are also many orchids and ferns (especially notable being tree-ferns), insectivorous plants (*Drosera, Utricularia*, and the localized *Cephalotus follicularis*). Mention should also be made of the strange "grass trees" or "black boys" of the genus *Xanthorrhoea* (*Liliaceae*). The cycads are represented by species of *Cycas, Macrozamia*, and *Bowenia*. The largest families in terms of species are *Leguminosae* (1300), *Myrtaceae* (1000), *Proteaceae* (600), *Compositae* (600), *Gramineae* (400), *Cyperaceae* (400, *Orchidaceae* (400), *Epacridaceae* (300), *Goodeniaceae* (300), and *Euphorbiaceae* (250). The endemic families are *Tremandraceae* (30 species), *Byblidaceae* (2 species), and *Cephalotaceae* (1 species). Families that are mainly Australian are *Epacridaceae, Goodeniaceae, Pittosporaceae, Stylidiaceae*, and *Stackhousiaceae*. There are many endemic genera, some with 50 to 100 species, and many more that are mainly Australian. The total number of known species of vascular plants exceeds 12,000 classified into over 1600 genera.

The flora of Australia has, on the whole, been long isolated, that is to say

it has very largely developed *in situ* at the generic and specific levels. The old and mainly endemic element is the largest in the flora. This Australasian element is partly, but with notable exceptions, shared with New Zealand and some of it extends into New Guinea. There is an "Austro-Malaysian" element common to Australia, especially Queensland, and Malaysia, indeed one may say that the extra-Australasian floristic connections are with Malaysia via New Guinea, and it is not always easy to determine which way ranges extended from an original centre. The so-called "Antarctic" elements are found in all or several of the southern countries: Australia, New Zealand, southern parts of South America, and South Africa. The South African connections are the weakest of these. The explanation of a former linkage via an extended Antarctic continent has been mentioned above.

Crocker and Wood[46] have summed up a good deal of the modern research on the phytogeography of Australia. The evidence is strongly in favour of a pan-Australian flora in the early Tertiary when the continent was reduced to an almost perfect peneplain. The uniformity was broken by marine transgressions, volcanic activity, and earth movements which reached their maximum in the late Tertiary. Habitat diversity was increased in the Pleistocene by the generally high rainfall causing erosion. A post-Pleistocene period of aridity followed and the severe desiccation destroyed a considerable portion of the pre-arid flora. Remnants survived in numerous refuges and later re-colonized vast areas when climatic conditions slightly improved. It is concluded that broadly the flora of the great arid parts is a blending of the Indo-Melanesian element from the north and north-east with the Australian element from the south-west, south, and south-east, which has occurred subsequent to the Great Australian Arid Period. The plant communities are very young and their distribution within a climatic zone has been determined chiefly by edaphic factors. The richness of western Australia in endemics is explained by its isolation from the south-east in Miocene times and especially by edaphic barriers.

The literature on the Australian flora and vegetation is very considerable and the results of recent research still need bringing together as a unit. Diels[51] dealt with Western Australia south of the tropics. The relationship between soils and vegetation is considered by Prescott[154]. McLuckie and McKee[129] give an outline account of the flora and vegetation. Bentham's *Flora Australiensis*[14] is now very much out-of-date but all the states have more recent floras either published or in course of publication. Wood[229] gives a general account of the vegetation, with the following "formations": desert, savannah, shrub steppe, scrub, savannah woodland, sclerophyll forest, rain forest, and high moor.

4. *Regions of Temperate South America.* These include nearly the whole of Uruguay, and most of Argentina, Chile, and Paraguay. General summaries

of the flora and vegetation of these countries will be found, with bibliographies, in Verdoorn[215]. The important researches of Skottsberg are summarized by Turrill[205, 210] and a general phytogeographical survey on a mainly statistical basis is given by Good[70].

The following figures for angiosperms are given by Good: families 177, genera 1478, species between 12,000 and 12,500. There are 32 families of monocotyledons by far the largest being *Gramineae*, followed, on the basis of number of genera, by *Orchidaceae*, *Liliaceae*, *Amaryllidaceae*, *Bromeliaceae*, and *Cyperaceae*. The dicotyledons are grouped in 145 families, the largest being *Compositae*, followed by *Leguminosae*, *Rubiaceae*, *Solanaceae*, *Asclepiadaceae*, *Boraginaceae*, *Bignoniaceae*, *Caryophyllaceae*, *Cruciferae*, *Euphorbiaceae*, *Labiatae*, *Malpighiaceae*, *Scrophulariaceae*, and *Umbelliferae*. The richness of the flora, in genera at least, decreases from north to south. Probably some 90 per cent of the species and 20 per cent of the genera are endemic, but there are only two endemic families (*Myzodendraceae* and *Aextoxicaceae*) and these are small with a total of 3 genera and about 15 species. The relationships are mainly with northern areas but some with South Africa and Australasia and the latter are of considerable phytogeographical interest.

A very good account of the vegetation of Argentina is given by Hauman and others[34]. Cabrera[26] divides Argentina phytogeographically into two regions with subdivisions into domains and provinces. The major areas he recognizes are: I. Region Neotropical, A. Dominio de la América Subtropical, B. Dominio Chaqueña, C. Dominio Andino; II. Region Austral, A. Dominio Subantártica, B. Dominio Antártica.

Attention is called also to the paper by Beetle[13] on the phytogeography of Patagonia and to that of Kunkel[113] on the woody vegetation of South Chile.

5. *Antarctic Region.* The term Antarctic has been used in various ways in phytogeography. J. D. Hooker's *Flora Antarctica*, for example, includes Lord Auckland's group, Tierra del Fuego, the Falkland Islands, etc., and he uses the phrase "antarctic plants" to include Australian and New Zealand plants as well, that is to say for the flora of a large part of the Southern Hemisphere. Here we restrict the Antarctic Region very definitely to the Antarctic continent and nearby islands. The greater part of the area is covered with permanent ice and snow and is devoid of land plants. Only two native flowering plants are known from the Region, and both of these only from Graham Land and the adjacent islands: *Deschampsia antarctica* (a grass) and *Colobanthus crassifolius* (*Caryophyllaceae*). Their ranges are fully considered by Skottsberg[179] who says that, though they probably belonged to the Preglacial Antarctic flora, it "seems safer to regard them as Postglacial immigrants, the only Vascular Plants that managed to cross the wide Drake Strait and establish themselves successfully in high southern latitudes." A

single specimen of the introduced weed *Poa annua* has been recorded from Whalers' Bay, Deception Island.

The marine algal flora is relatively rich (see Skottsberg,[176]), and on land, from nunataks, a large number of lichens and mosses, with fewer hepatics, have been collected (see Dodge[52], and Herzog[91]). Among the cryptogams there are endemic genera and species. The general phytogeographical relationships are diverse and very wide and still require detailed analysis before valid conclusions can be reached. Earlier work on Antarctic plant life is lucidly discussed by Rudmose Brown[23, 24].

A brief reference may be made here to the probable former importance of an enlarged Antarctic continent, more or less free of ice, and, at least partially, linking the southern continents. The discovery of fossil plants in Antarctica proper shows that in Mesozoic and Cainozoic times conditions were temperate or even subtropical. References are to Hill[92], Skottsberg[177, 178], Du Rietz (1940), Copeland[45], Gordon[72], and Turrill[209]. It appears that many of the phytogeographical problems concerning the southern land mosses are solved by postulating a link between South America, Australasia, and even South Africa via an extended Antarctica.

SPECIAL ASPECTS OF PHYTOGEOGRAPHY

We have briefly outlined the history, scope, and aims of plant geography and have given some selected details of the work on or linked to phytogeography in major phytochoria of the earth. The various realms and regions have been treated somewhat unequally and differently. This was partly done deliberately to illustrate different "vistas," different methods of approach, and different kinds of emphasis. The subject is so vast, has so many "side-lines," and is once again, with new outlooks, so dynamic that arbitrary limits had to be set. This is the excuse for having to leave out much of interest and importance.

There are many subjects within phytogeography that have special problems and some of these have been selected for condensed consideration under a number of headings.

Kinds of Ranges

Ranges of species are of various kinds, though there are intermediates between any classes one makes. Ranges may be exceedingly wide even almost cosmopolitan, as for *Pteridium aquilinum*, or very small as for *Ramonda* (*Jankaea*) *heldreichii*; they may be relatively continuous, as for *Pinus halepensis*, or markedly discontinuous, as for *Convolvulus nitidus*; they may show clinal structure, as in *Ajuga chamaepitys*, or they may not, as in *Arbutus unedo*; they may be divisible into subspecific ranges, as in *Silene vulgaris*, or there may be no marked geographical correlations with intraspecific variation, as in

Fritillaria meleagris; they may be restricted to a given geographical area when the species is said to be endemic to the area, as *Petromarula pinnata* is endemic to Crete, or they may extend beyond a geographical area, as do the vast majority of the species of the British flora.

Two general statements must be made: the different kinds of ranges just enumerated for species occur, with slight modifications of wording, in connection with taxa of higher rank than species and our data for past ranges as based on reliable fossil evidence is, for the angiosperms in particular, relatively meagre. We must also note that "continuity of range" means only that the species (or other taxon) occurs without wide geographical breaks but ignoring ecological breaks. If there be no major problem as to dispersal of disseminules from population to population the range is considered continuous in a wide sense. There is, however, every intermediate between isolation of populations within a species, that is, separation of groups of individuals within a phytochorion so that one cannot interbreed with another because of external barriers, and wide geographical isolation. Some of the problems of discontinuous ranges are well dealt with by Cain[27], and the statistical study of wide and restricted ranges is the basis of much of Willis's work on "age and area" (see below). The importance of clines is discussed by Huxley[100, 102], though mainly from the zoological standpoint. Corresponding to clines in taxonomy and population studies are ecotones in ecology. Clines are defined as character gradients within groups while ecotones are the transitions between adjoining plant communities.

It is very doubtful if polytopism (the origin of a taxon independently at more than one locality) occurs except at a low taxonomic level, assuming, of course, that the taxonomy be sound. We have to accept that most taxonomic entities have had one place of origin. It is sometimes claimed that the centre of a range, or the place of greatest frequency or of maximum variability or of lushness of development indicates the area of origin more or less precisely. Certainly all of these facts have to be taken into account but none of them is conclusive. They must all be considered together and with the independent conclusions of taxonomic affinities as based on modern synthetic taxonomy. There are, however, many facts concerned with range that have evolutionary significance. Variation at the margins of ranges is frequently different from that near the centre. Often this can be correlated with different environmental factors and the action of natural selection is plain, as with *Silene martitima* subsp. *islandica*. The division between species and subspecies is not sharp and there seems circumstantial evidence from the study of ranges (combined with taxonomic data) that subspecies can give rise to fully isolated species.

Endemics are defined as species (or other taxa) limited in present range to a

given geographical area. Some endemics are such because they are of relatively recent origin, presumably within their present range, and have not yet had time to extend over all their area of tolerance. These are neo-endemics and are often microspecies (or microtaxa). At the other extreme there are the palaeo-endemics which originated long ago but have either never been able to extend their ranges or have gradually "lost ground" from competition with other species, often correlated with environmental changes for which their sum total of biotype diversification is unsuited except in their now restricted endemic range. This is the explanation of what is sometimes referred to as species senescence. Taxa do die out, as the fossil record proves, but they do not become "old" in the sense of old age of individuals.

Rare and Relict Species

The term "rare" is relative. It may indicate a species that has a very small range but is common within that range, or a species with a more or less wide general range within which it is represented by few individuals, or, in the extreme, it may be a species with a small range with few individuals within that range. For the broader problems of phytogeography we usually mean a species with a small range or at least with a small approximately continuous range. Rare species may be restricted in their ranges either because they are young and have not had time to spread or because their characters (expressed in one or in more than one biotype) are not suited for any environment outside the narrow range to which access has been obtained or they may be relicts, that is, they have ranges that are smaller than formerly. There seems no valid reason for supposing that new species are being formed in smaller numbers than at any time, say, since the beginning of Tertiary times. Indeed, with the making of new environments by man, with the greatly increased plant dispersal by man, and by the consequently increased chances of hybridization it is probable that new kinds of plants are appearing at an increasing rate, though how many of these may be acceptable taxonomic species is another matter. On the other hand, palaeobotanical research proves that taxa become extinct. Unfortunately, we know little about the causes of extinction of taxa; indeed, we know far too little, in any systematic manner, regarding the death of individuals in nature.

Two general facts have to be used by the plant geographer: that organic evolution has continued throughout plant history and that environments are are continually changing. Comparisons between phylogeny and ontogeny may be misleading. Thus it is probably incorrect to talk about the wear-out or old age of a species as similar to senescence in an individual. The most successful species are those that meet with the fewest limiting factors for completing their life cycles over the widest ranges and are able to disperse over these ranges. The environment, however, may change—as by the

on-coming of a glacial epoch or increased aridity, or the appearance of better equipped biotic competitors—and the species may be so specialized, may have so few biotypes, or may have too little potentiality for producing suitable mutations that it cannot survive or at least maintain its existing range. It may be able to "migrate" or it may be exterminated, or it may indefinitely continue to exist very locally as a rare relict.

Space will not allow the enumeration of actual examples. Such are given by Griggs[74], Stebbins[184, 185], Cain[27], Wildeman[227], and Matvejev[130].

Vicarious Species

The comparison of taxa that have been thoroughly studied often shows that taxonomically related varieties, species, or genera have distinct non-overlapping ranges and these can sometimes be clearly correlated with different environments. The ranges may be more or less contiguous or discontinuous. Vierhapper[216, 217] attempted to distinguish between vicarism and pseudovicarism, the former when the nearly related "Sippen" (or as we should now say "taxa") have originated in the areas or formations from a common ancestor, the latter when one of these conditions does not hold or both do not hold. He introduced the word "vicariads" for the members of a pair of vicarious taxa and notes that they may be separated horizontally (or geographically), altitudinally, ecologically, or seasonally (or temporarily). The pseudovicariads are probably a mixture: either they are not very closely related and it is uncertain that they should be considered derived from a very near common ancestor or it is more or less certain that they represent convergent evolution, and often they belong to different sections of a genus. It is rather doubtful if one can reasonably speak of vicarious families and tribes in a very strict sense and even some of the supposedly vicarious genera may be questioned. It is at, or below, the species level that vicarism can best be studied from the phytogeographical and evolutionary points of view. There are fairly numerous pairs of closely related species of which one is found in eastern North America and the other in Europe. Examples are: *Vallisneria americana* and *V. spiralis*, *Anemone quinquefolia* and *A. nemorosa*, *Maianthemum canadense* and *M. bifolium*, and *Scrophularia marilandica* and *S. nodosa*. Examples of altitudinal vicariads are *Myosotis silvatica* and *M. alpestris*, *Centaurea pseudophrygia* and *C. plumosa*, *Trifolium pratense* and *T. nivale*, *Soldanella major* and *S. hungarica*, etc., and quite a marked proportion of high mountain plants in Crete and Greece could be quoted as examples by comparison with lowland congeners. Ecological vicariads may be correlated with different substratum conditions (degree of acidity, water content, chemical or physical nature), as *Stachys palustris* and *S. silvatica*, *Lotus major* and *L. corniculatus*, *Geum rivale* and *G. urbanum*, *Gentiana clusii* and *G. kochiana*, *Rhododendron hirsutum* and *R.*

ferrugineum. Other limiting factors are temperature and light and there is undoubtedly interaction of factors often involved in determining ranges of vicariads.

Vicariads have usually been paired off as a result of taxonomic and phytogeographical or ecological studies. It is being realized that they can throw much light on evolution when more detailed researches are made on them. Löve[122] says that the fundamental difference between true and false vicariads is that the former penetrated into their areas prior to their successive morphological and genetical differentiation while the latter differentiated before their dispersal to the new territory. He rightly stresses the need for cyto-genetical researches on supposedly vicarious pairs of taxa and shows, mainly on chromosome number and morphology, that some that have been accepted as vicariads are pseudo-vicariads, as *Zostera marina* and *Z. stenophylla*, *Gentianella procera* and *G. detonsa*, and *Glyceria grandis* and *G. maxima*, while *Populus tremula* and *P. tremuloides* and *Scirpus* (*Schoenoplectus*) *lacustris* and *S. acutus* are to be retained as true vicarious pairs.

The comprehensive study of the bladder campions (*Silene maritima* and *S. vulgaris*) by Marsden-Jones and Turrill[128] has shown something of the complexity of the taxonomic, ecological, and evolutionary relationship of pairs of species. The two species, at least in their typical subspecies as found in the British Isles, are ecological vicariads. They have the same chromosome numbers and can cross reciprocally to produce fertile offspring but their ranges are different, though they overlap, and their ecological distribution is, with few exceptions, quite different. As populations, again with few exceptions, they keep distinct. Yet within each, and especially within *S. vulgaris*, considering the whole of their ranges there are vicariads within the subspecies, for example, *S. vulgaris* subsp. *vulgaris*, subsp. *glareosa*, and subsp. *alpina*. Moreover, *S. vulgaris* subsp. *alpina* might well, on definition, be considered pseudovicarious with *S. maritima* subsp. *maritima* and as showing quite marked evolutionary convergence.

Age and Area Hypothesis

An important view was put forward by J. C. Willis in 1915 and dealt with fully in his book *Age and Area*, Cambridge (1922), and in other publications. Without qualifications, this states that the range of a species is determined by the age of the species, in the sense that a large range indicates an old age and conversely a small range a recent origin. Willis, partly to meet criticisms, hedged round his expression of "the rule" so that it became unworkable (see Turrill[206], pp. 465–72). Thus he says (Willis, 1922, p. 63): "The area occupied at any given time, in any given country, by any group of allied species at least ten in number, depends chiefly, so long as conditions remain reasonably constant, upon the ages of the species of that group in

that country, but may be enormously modified by the presence of barriers such as seas, rivers, mountains, changes of climate from one region to the next, or other ecological boundaries, and the like, also by the action of man, and by other causes." It has been found by the present writer and others that it is only by breaking away from the limitations imposed by this "expression" that one can test for any value in the general hypothesis that on the whole a larger range is a criterion of greater age in a given country. The main criticisms of the hypothesis have been that it fails to distinguish new species from "old," that limiting factors do not cancel out in groups compared, and that species formation has a number of "causes" of which sudden large mutation is not so important as Willis believes. On the other hand, there is no doubt that the hypothesis is useful in that it directs attention to the time factor in range formation and that its application does sometimes explain existing ranges. Further, attention will have to be paid by phytogeographers to many of the questions Willis asks, particularly in a later book (Willis, *The Course of Evolution by Differentiation or Divergent Mutation rather than by Selection*, Cambridge, 1940).

Hemispherical ranges.

The tropical belt separates a North Temperate from a South Temperate zone. While the floras of these two zones are very largely different, especially in species, genera, and predominance of tribes or families, they have some taxa in common, those round about the generic level being of particular phytogeographical importance. Both floristic resemblances and differences raise problems connected with what has been called "bipolar distribution" but had better be known as "bihemispherical ranges." It is true that there are mountain ranges, particularly in America and Tropical Africa, with a main north to south direction and which might serve as a highway for migration of a number of temperate taxa across the tropics. One has, however, to remember that while attitude affects temperature and precipitation the factors of photoperiodism remain and their influence on north to south (or the reverse) extension of ranges has been largely ignored and, indeed, we have little knowledge on this subject which is one that requires experimental investigation. A second, and major, difficulty at arriving at any valid conclusion as to the history of present-day bihemispherical ranges is the meagre palaeobotanical evidence available. If the occurrence in Tertiary deposits of the Northern Hemisphere of what are now taxa limited to the Southern Hemisphere be accepted, and the evidence for this is stronger than it was, then the postulated place of origin of such families as the *Proteaceae* need not be restricted to southern latitudes. That evolutionary convergence occurs is frequently demonstrated in detailed taxonomic studies but most often it concerns one or a few characters and not the gamut of

organs. Polytopy, the origin of taxa in more than one place independently, is possible, indeed sometimes probable, at lower taxonomic levels but the chances of its occurring are proportionally less the greater the number of differential common characters involved. It is usually unwise to fall back on polytopism to explain discontinuity of generic ranges unless the taxonomy has been thoroughly revised by modern synthetic methods. Moreover, polytopy may only push the problem back a stage, so to speak, and not solve it. Thus, if one said *Empetrum* arose independently in the northern and southern hemispheres, the question of how the ancestor or ancestors attained discontinuous ranges takes the place of the original problem.

Leaving aside the possibility of occasional polytopy, there have been two main theories regarding bihemispherical ranges: that the taxa concerned arose in the northern hemisphere and extended southwards or that they arose in the southern hemisphere and extended their ranges northwards. At present, the main land masses are in the northern hemisphere and the older view, ably supported by Thiselton-Dyer[202], is that "all the great assemblages of plants which we call floras seem to admit of being traced back at some time in their history to the northern hemisphere." It is, he notes, "easy on this supposition to account for their possession of common characters which, in their widely scattered southern distribution is not readily explained on other grounds." Similar views have been supported by various botanists and also, on the zoological side, by some zoologists. In marked contrast are the views of Camp[28] and Croizat[47], amongst others. Camp, for example, considers the ranges of 103 plant families with restricted territories and shows their concentration in the southern hemisphere. He concludes that most of these families originated in the southern hemisphere and spread northwards, and that this is particularly true of primitive families. Further, he postulates a more continuous land mass in the south contemporaneous with the Palaeozoic of the northern (Holarctic) land mass and that the divergences of the basic, generalized familial groups had been accomplished on this southern land mass certainly by the Mid-Mesozoic. Du Rietz (1940) discussed at length the problems here being considered. It is somewhat difficult to determine his standpoint on the major problem. He more or less rejects long distance dispersal of disseminules and the hypothesis of continental drift but accepts the need for "epeirogenetic transtropical highland bridges older than the mountain-chains of the Alpine Orogen. Such highland bridges may have existed not only in Africa, but also bordering the transtropical Alpine geosynclines (i.e. the Andean and the Malaysian geosynclines), partly passing over present deep sea bottom."

Since we do not know when, where, or from what the angiosperms were evolved, their early differentiation into families must largely remain a matter for speculation. Even more than phylogeny must the centre or

centres of origin be hypothetical. Hypotheses are essential but they must not become dogmas. Two matters are worth bearing in mind. If there has been considerable drifting of continents and large wanderings of the poles the question of northern or southern origin of the families of angiosperms becomes largely meaningless as at present stated. Secondly, assuming that the continental masses and the positions of the poles have not greatly changed since the origin of the angiosperms, apart from the accepted regressions and transgressions of the sea proved by geological researches there would appear to be good reasons for migrations to have occurred in both north and south directions. Certainly one has to postulate the diversified evolution of some taxa in the temperate regions of the Northern Hemisphere and of others in the Southern Hemisphere independently.

Continental Drift and Polar Wanderings

The Pacific, Indian, and Atlantic Oceans are great expanses of water, separating continental land masses, with floras and faunas having some families, genera, and, more rarely, species in common. To account for common biological features it has frequently been postulated that there were land connections across which disseminules were more or less gradually and continuously dispersed. On the geomorphological side there was the possibility of former connecting land having sunk beneath the oceans or of formerly joined land masses having drifted apart. It is first essential to be clear concerning the problem involved. Geological evidence is conclusive that there has been throughout the geological periods regressions and transgressions of the sea relative to dry land. All marine sedimentary rocks now forming part of land masses were laid down beneath seas and, whatever the depth of these, they formed barriers to dispersal of land plants as effective as deep oceans relative only to their extent. Conversely, none can dispute that former land linked many islands to continents, as Great Britain to Europe, or peninsula to peninsula, as Asia Minor to Greece. Even if the Mediterranean Sea be accepted as the relict of a very ancient and more extensive Tethys Sea its outlines have changed enormously through the ages. The problems we have to consider here are both much greater and more controversial. Have the ocean basins, beyond the continental shelf always been very much as they are now or have they previously been land? If the latter, has their formation been due to submergence of land or to drifting of continents? If either submergence or drifting has occurred when did it happen?

Biologists who have demanded continuous land surfaces to account for existing ranges of plants and animals have between them, in imagination, pretty well filled up all the oceans with land. On the contrary, many geologists and geomorphologists have accepted the view of the permanence

of the great ocean basins so strongly put forward by J. D. Dana and summarized in his own words as "The continents have always been the more elevated land of the crust, and the basins always basins." This view has often been stated in geological text-books and was widely accepted though challenged by scientists from time to time, and especially, as far as Gondwanaland was concerned, by Suess and others. Gondwanaland is the name given to a supposed great southern continent, wide enough to include much of South America, South Africa, India, part of Australia, Antarctica, and the intermediate areas now oceanic. It was thought to have persisted through the Palaeozoic era to Upper Cretaceous times. The geological, palaeontological, and biogeographical evidence for some kind of former linkage of existing and now separated lands in the Southern Hemisphere is considerable but objections to the foundering of huge areas of land to provide the oceans or parts of the oceans now separating the Gondwanaland fragments have been raised by geophysicists and others.

More recently there has come to the fore the idea of drifting continents. This is now largely associated with the name of Alfred Wegener, though it appears it was, in one form or another, put forward by other geomorphologists before Wegener. Briefly, it is postulated that in Palaeozoic times there existed one great original continent, Pangaea, surrounded by a primeval Pacific Ocean. Then, during the Mesozoic and Cainozoic eras this one original continent broke up, and by the drifting of its fragments oceans gradually opened up between them. Wegener adopted the old idea that the continents are composed mainly of the lighter silicates, having a mean density near that of granite, and float on a layer of heavier, viscous silicates. He postulated a general drift of the continental blocks away from the poles and towards the west. The details of Wegener's scheme have been modified in various ways by more recent workers but the general principle of continental drift is widely accepted and yet, one must add, often opposed. Many biogeographers are inclined to accept continental drift as solving all their problems, which it certainly does not do, and the main criticisms have come from palaeobotanists and geophysicists, the latter being concerned with the source of the energy needed to shift continents.

The whole subject has been complicated by linking continental drift on to hypotheses concerning "wanderings of the poles" and variations in the inclination of the earth's axis. (Köppen and Wegener traced polar displacements, with tabulated records of latitude and longitude, from the Devonian to the present positions of the poles.) The majority of palaeobotanists, from a study of the records of fossil plants, especially those around the present North Pole, have been emphatically against polar migrations. Most recently there have been important researches on the permanent magnetization of the rocks and deductions therefrom. Evidence has been produced

that the direction of magnetization of rocks (particularly of iron oxide minerals) perpetuates that of the earth's field at the time of their formation. Hence, by examining rocks of known age it is possible to discover any variations that have taken place in the direction of the earth's field and the conclusion has been reached that the geomagnetic field has undergone repeated reversals in geological time. It has been assumed from these accepted displacements of the magnetic pole that there has been both translation in a meridional direction and rotation of land masses. Thus, Britain is said to have moved a long way northwards in the last 150 million years from a position about 10° north of the equator (roughly the latitude of Southern India) and North America has done the same. England has also rotated through about 35° relative to the direction of present magnetic north and this could probably be interpreted as an increase of the distance between North America and Britain. Other, and sometimes decidedly different, estimates have also been made. There is apparently a postulate that the magnetic and geographical poles have always been associated much as they are now.

Another line of recent research which may be expected to throw light on the history of the oceans is the study by modern methods of the ocean floors. These are covered with oozes and the depth of these are determined by echoes from high explosives detonated at various depths. Echoes, it is accepted, are reflected both from the surface of the ooze and from that of the solid rock on which it rests. From the records it is possible to estimate the thickness of the ooze. A further calculation based on the rate of sedimentation then allows an estimate to be made of the minimum age of a given portion of the ocean. On the whole, the recent results obtained by the Swedish *Albatross* expedition are against the theory of continental drift as applied to the Atlantic and as put forward by Wegener, since the estimates are for a time span of 300 to 400 million years, possibly still more. Very recently actual borings into the sea floor, in fairly deep water, have been made off the Californian coast and it has been suggested that there is no known theoretical reason why borings to considerable depths should not be made into the crust at very considerable oceanic depths. Such might settle many questions at present controversial.

The literature on the subjects outlined above is extensive. The following books and papers may be consulted: Wegener[226], Köppen und Wegener[109], Du Toit[56], Brooks[22], symposium on "The Theory of Continental Drift"[194], Runcorn[166], Chaney[33, 34, 35], Petterson[146], Mayr[131], Edwards[59].

The theory of continental drift, if accepted, obviously solves some phytogeographical problems, even if it leaves many untouched and raises some new ones. It is, perhaps, right to take the floras of South America and

Tropical Africa as the simplest test. Wegener fitted the Brazilian bulge into the Gulf of Guinea and postulated the separation of Africa and America as commencing in the Cretaceous. We do not know when or where or from what the Angiosperms arose but there were certainly many existing families of flowering plants in existence and widely ranging by Cretaceous, even Lower Cretaceous, times while gymnosperms had evolved long before. Palaeobotanically the angiosperms and gymnosperms are crucial for the question of dispersal since their seeds are, with few exceptions, large and heavy compared with the spores of cryptogams. What then are the resemblances and differences found on comparing the spermatophytic floras of Africa and South America? There are about 300 species at most known in the natural or subspontaneous state to be common to the two areas. Many of these are halophytes (some 30 spp.) easily transported by tides and currents, or aquatic and marsh plants (about 100 spp.) often of wide range and frequently dispersed by birds, or pantropical species spread by man. More critical data for our purpose are to be found at the levels of families and genera.

Good[69] lists generic connections across the South Atlantic, excluding pan-tropical genera, as follows:

America, Africa and/or Madagascar, etc.: 27 genera.
America and continental Africa only: 64 genera.
America and Madagascar only: 4 genera.

Some of these genera are wrongly included, though, on the other hand, some can be added. The total is a fairly large one but needs very much more detailed analysis than it has received. At the family level, connections between America and Africa excluding Madagascar are shown by *Bromeliaceae*, *Caricaceae*, *Humiriaceae*, *Loasaceae*, *Mayaceae*, *Rapataceae*, and *Vochysiaceae*, and those between America and Africa including the Madagascan region are shown by *Canellaceae*, *Hydnoraceae*, *Strelitziaceae*, *Turneraceae*, and *Velloziaceae*. While it appears that the lists of genera and families of angiosperms common to South America and Africa can be given as evidence of a former land connection, and, indeed, of continental drift, some of the ranges can be otherwise explained. Thus, the *Bromeliaceae* are American except for *Pitcairnia feliciana* from French Guinea and Chevalier[39] accepts the view that "violent aerial currents" carried the light seeds of a species of *Pitcairnia* from the Caribbean islands, or from more eastern islands that have now disappeared, to West Africa and that isolation then led to differentiation from all American known species. *Rhipsalis* (*Cactaceae*) may have been dispersed by birds or by man, at least, there has been much controversy regarding the history of the present range of this genus. The possibility that some of the South American-African discontinuities are due to

independent migration southwards from some common northern source where the genus or family is now extinct must be kept in mind. It is also important to remember that many genera (and even some tribes and families) are not common to Africa and America. Whether these evolved after separation of Africa and America, if the continents were formerly joined, or if they have died out in one or the other we do not know.

Oceanic Islands

Islands have a fascination for the biogeographer. Their boundaries are definite, the land area is often not too great for a relatively detailed survey, the problems involved are often clear-cut and peculiar. There are, of course, many different kinds of islands: off-shore islands, continental, oceanic, solitary, archipelagos, volcanic, coral, and so on, and they range in size from mere rocks to continents. As showing isolation from continental land masses, oceanic islands allow the investigation of certain phytogeographical problems under almost experimental conditions of abstraction. In particular, those of volcanic origin, with no indication of any former attachment to continental land have unique conditions for the study of the origin and development of the flora. They usually have a natural flora poor in species, relatively rich in endemics, and showing taxonomic affinities in one or more directions. Unfortunately, the flora of many of the islands has been greatly modified by man and sometimes largely destroyed, an extreme example being the indigenous flora of St. Helena.

The famous lecture by J. D. Hooker[94] on "Insular Floras" summarized the floristic characters of a number of islands. He pointed out that they are rich in cryptogams, have many evergreen but few herbaceous plants and fewer or no indigenous annuals. Species are few in proportion to genera and genera in proportion to families, and the total number of species is small compared with continental areas of equal size and similar conditions. Many more oceanic islands have been investigated, or much more fully investigated, botanically since Hooker's time and new developments both within the realm of biology and outside it have to be taken into consideration. Nevertheless, several of the major problems remain much as they were in 1866. These oceanic volcanic islands have, or naturally had, a rich vegetation of a limited number of species. It is extremely unlikely that the ancestors of these species originated by any form of special creation in these islands and they must, therefore, have arrived from other areas, probably continental, either across land that has now disappeared or transoceanically. The efficiency of long distance dispersal has been a matter of controversy. No one disputes that disseminules (spores, seeds, etc.) can be scattered some distance from the parent plant, the distance being commonly a matter of yards to a few miles (see Ridley[161]). The evidence for long distance transport over oceans,

extensive deserts, etc., is indirect or meagre, with one exception. It is generally agreed that ocean currents can transport some disseminules for long distances but these are those either of strand plants or of relatively few species that withstand immersion in sea water for a considerable time. Man, of course, is recognized as the most efficient of all transporting agents but we are here concerned with the floras that originated before the advent of man. The two natural agencies whose efficacy over very long distances is in dispute are wind and birds. There is a little direct evidence of wide dispersal by both but more is difficult to obtain (see Turrill[208]). Modern research is badly needed. Spores and bacteria are certainly carried widely in the upper atmosphere and it is to be hoped that those engaged in aerobiological work will extend their methods and observations to seeds and other disseminules. Cyclones may be important (Visher[218]). Birds are said generally to travel on long distance migrations with empty alimentary systems and with clean feet and feathers. There is, however, an open field for combined botanical-ornithological research here. Migrating birds are now ringed in large numbers. If they could always be carefully examined for attached fruits and seeds and if some such could be attached to them experimentally immediately previous to migration, and if the bodies of dead immigrants (at lighthouses, etc.) could be analysed externally and internally for plant parts, much might be learnt. The question of land connections has been dealt with above and it need only be said now that problems of wide dispersal are also found over many continental areas where they are sometimes at least as puzzling as for oceanic islands.

There is much indirect evidence in favour of some transoceanic dispersal. The richness of many oceanic islands in cryptogams with their light spores, especially of bryophytes and pteridophytes, suggests wind dispersal has occurred for these plants. For seed plants, the poverty in taxa and the mixture of taxa suggest chance dispersal, as does also the absentees which might be expected had there been direct land connections. Sometimes the taxonomic affinities of the flora of an oceanic island, or island group, are correlated with general direction of the wind or with bird migration routes. Finally, we may note that the two hypotheses of dispersal over long distances and of land connections are not mutually antagonistic for both may have happened, one for this island, one for that, or both for the same island.

Given the establishment of a flora on an oceanic island there are the problems concerned with its further development *in situ*. Cytogeneticists and others engaged in population studies now, rightly, stress the pros and cons of isolation. In the evolution and maintenance of taxa (especially of species) isolation means reduced biotic competition, reduced swamping or extermination of mutations since there will be no flow of new immigrants, and absence of hybridization outside a very restricted

population. Compared with a large continental area the agents of natural selection will be different and, on the whole, less intensive. The climate, for example, is usually more equable than in a continental area, while predators, diseases, and pests are often less numerous. Thus evolution may be slower and old kinds or old characters are likely to survive. On the other hand, mutational characters suited to the conditions of an oceanic island, but less suited to those of a continent, will be selected. Some devices for self- or wind-pollination, for vegetative propagation, for certain life-forms (as perennials and not annuals) come under this heading.

The literature on oceanic islands is extensive but extremely scattered. Reference is made here to only a few striking examples: St. Helena (Turrill[207]), Juan Fernandez and Easter Island (Turrill[210]), Tristan da Cunha (Dyer[58]), Galapagos Islands (Stewart[188, 189]; Svenson[193], and references there), Gough Island (Waite[219]), Kerguelen (Turrill[209], pp. 190–4).

Polyploidy and Plant Geography

Polyploids are organisms having an increase in the number of chromosome sets above the normal diploid. It is reasonably certain that in any naturally occurring plant series the plants with the lowest chromosome numbers are more primitive than polyploids presumably derived from them. Hagerup[78, 79, 80] observed a correlation between polyploidy and extreme climates, "those with the higher chromosome numbers are always the ones growing farther north, and thus more exposed to extremes of temperature." Later correlations were found between increases in percentage of polyploidy and other environmental extremes. The subject has grown considerably and useful summary accounts will be found in Stebbins[154], Cain[27], and A. and D. Löve[123]. Reese[156] shows that, on available data, polyploidy increases with latitude from North Africa through Europe to the Arctic. He considers that the main correlation is with the age of the flora: the younger the flora the higher the percentage of polyploids. Those readers particularly interested in the British flora might consult Haskell[83]. Most authors who have written on the ranges and distributions of polyploids conclude that polyploidy confers benefits which enable the species (or other taxon) to extend into less favourable habitats. This is certainly sometimes true but how far wide conclusions are valid is more doubtful. The results as presented are frequently statistical and are sometimes open to criticisms: only parts of floras are included, the chromosome numbers used are based on few reliable counts of wild plants of known origin per species, most of the research has been done in Europe in areas heavily glaciated in the Ice Age, tropical and subtropical floras have been very little examined cytogenetically, and so on. Further, even if it were accepted that polyploidy is, at least on the whole, advantageous in the struggle for existence, there is little

or no agreement as to the underlying causes, that is of the nature of the advantages. Structural, physiological, and genetical advantages of various kinds have all been suggested by different authors. Stebbins[184] said "Perhaps the safest generalization that can be made about polyploids is that they are most numerous in regions that have only recently been open to colonization by plants or that have undergone great changes in their floras in recent times."

However, it must also be said that some authors have failed to find such correlations between polyploidy and ranges as indicate that polyploids can withstand less favourable ecological conditions than diploids. Soó[183] and Heiser and Whitaker[89] are examples and the latter even go so far as to say that generalizations involving polyploidy are probably meaningless. While this last is too sweeping a statement there is no doubt that much more research is needed before the full significance of polyploidy for plant geography is known.

The Future of Phytogeography

For several reasons phytogeography is becoming of increasing importance. The rejuvenation of taxonomy along the lines of the "new systematics" or synthetic taxonomy, the application of data derived from the newer branches of ecology and cytogenetics, the extending realization that man is destroying the natural flora and vegetation of many parts of the world, and, perhaps, one may add, the greater facilities for overseas travel are all stimulating to phytogeographical research. It may, therefore, be worth while to give seriatim some suggestions for extending investigations from which the phytogeographer can reasonably expect new and important data.

(1) Exploration, and further botanical exploration, of certain parts of the world, especially of Indo-China, New Guinea, Amazonia, and the Pacific Islands. Though no part of the earth is over-explored.

(2) The intensification of research on fossil angiosperms. For many taxa existing ranges are the relicts of past ranges and these can only be inadequately inferred in the absence of palaeobotanical data. The excellent work of pollen analysis, in Europe and North America, and more recently in New Zealand and Australia, should be extended to as many countries and as many kinds of deposits as possible.

(3) Cytotaxonomic investigations need to be undertaken in many more phytochoria, with the co-operation of taxonomists and phytogeographers.

(4) Concentrated investigation, including controlled experiments, of long distance dispersal of disseminules is required to replace vague but often dogmatic assertions.

(5) Much more consideration needs to be given to the study of clines

in plant groups. Botany seems out of balance with zoology in the taxonomic and ecological examination of populations over wide geographical areas.

(6) The causes of death and extinction of taxa need investigation extensively.

(7) There is considerable need for definition or re-definition of terms. Thus the word "alpine" is used in at least two senses: growing at high altitudes or restricted in range to the European Alps.

(8) The adequate summarizing of books and papers on phytogeography written in certain languages, especially Russian and Japanese.

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PALAEOBOTANY IN GREAT BRITAIN

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THE establishment of the Royal Gardens at Kew occurred at a time when fossil plants were beginning to attract the attention of geologists and botanists, but it was not until the beginning of the 19th century that any significant contributions were made to our knowledge of extinct plants by British writers. It is appropriate that the important part played by the Jodrell Laboratory in the development of palaeobotany in Britain should be remembered. It should also be recalled that three of the Directors of Kew, Sir Joseph Hooker, Sir Arthur Hill, and Sir Edward Salisbury have all engaged in palaeobotanical research and have made important contributions to our knowledge of the subject. Many accounts have been given of the early development of the study of fossil plants and it is unnecessary to repeat what has already been written on this topic. In this chapter the writer will as far as possible confine his remarks to the contributions that have been made to Palaeobotany, particularly of work on Palaeozoic plants by British workers, starting from the beginning of the 19th century.

Plants are generally much branched organisms occupying a large space and presenting a large surface area. They are rarely preserved in a complete state in contrast to animals, which are relatively compact organisms with a hard outer surface or skeletal structure, or to the complete living plants studied by the systematist. Plants found in the fossil state are usually in the form of fragments, the leaves, stems and reproductive structures being rarely found connected together. This has led inevitably to considerable difficulties in nomenclature even more complex than those which face the systematist in classifying living plants and it is possibly for this reason that geologists, in this country at any rate, have paid so little attention to them. In few cases only is our knowledge of a fossil species at all complete and it is only from the study of very large numbers of specimens that the occasional lucky chance of a connection between leaf and a fructification or leaf and a stem makes it possible to build up our conception of the plant as a whole. This need for the examination of large numbers of specimens accounts for the fact that our knowledge of past floras is very uneven because some geological formations have afforded relatively few fossil plants. The great advances in the subject made by British palaeobotanists in the 19th and first half of the 20th century were largely the result of the industrial revolution when the

demand for coal led to the widespread exploitation of Carboniferous strata and the discovery of great numbers of fossil plants found in the shales brought up from the mines. The most important discovery of all was that of the beautifully petrified plants in the coal-balls found in the seams and roofs in some of the Lancashire and Yorkshire coal mines. We know, therefore, more of the structure of the extinct plants of the Carboniferous than of the plants of any other geological period. This has had a profound effect on comparative morphology, especially of the Pteridophyta and Gymnosperms.

In Britain, palaeobotanical research has been principally carried out by botanists, privately or in botanical institutions. The result has been that research has been mainly concerned with problems of comparative morphology and the evolution of the plant kingdom and less attention has been paid to the use of fossil plants in stratigraphy. Abroad, however, the position was and still is different, and a great deal more attention has been paid to the study of fossil plants by geologists. In this country very little attention is given in geological institutions to palaeobotany and the palaeontology taught is almost exclusively concerned with animal fossils. On the continent of Europe and in America a much larger proportion of those engaged in the geological and mining services are palaeobotanists and palaeobotanical data are used to a much greater extent in stratigraphy than here. This is unfortunate for this country because the geologists have greater opportunities of collecting and are usually better qualified than others to determine the horizon or age of their finds.

While we find fossil plants described in the works of some earlier writers the first important British work is Parkinson's *Organic Remains of a Former World* (1804). In it we find the results of a critical examination of the nature of fossilization and descriptions of a number of fossil plants. However, the rapid advance during the 19th century of the science in Britain and on the Continent was largely due to the work of Henry Witham of Lartington. Henry was the second son of John Silvertop of Minster Acres, Northumberland, by Catherine, daughter of Sir Henry Lawson of Brough in Yorkshire. Henry was born in 1779 and inherited the Lartington estate. He married Eliza, daughter of Thomas Witham of Headlam and by sign manual took the name and arms of Witham. His wife inherited valuable estates. Unfortunately for her, Henry did not confine his pursuits to palaeobotany and before long by injudicious management, and it was said by gambling, lost most of this property. Lartington was fortunately so tied up that he could not dispose of it. In 1831 Witham[15] produced his book *Observations on Fossil Vegetables accompanied by representations of their internal structure as seen through the microscope*. It is the first publication of research in which thin ground sections of rock had been used, and led to great developments in petrology and palaeobotany. Witham obtained these

sections from William Nicol, the inventor of the Nicol prism, who had the assistance of an Edinburgh lapidary in making them. Witham was a fellow of the Geological Society and of the Royal Society of Edinburgh. Although a few years earlier Sprengel in 1828 had shown that the internal structure of silicified *Psaronius* stems, after polishing, could be examined under the microscope, there is no doubt that the advent of the thin slice method was responsible for the great advances that followed in our knowledge of the internal anatomy of extinct plants. Witham produced in 1833 a second version of his book under the title of *The Internal Structure of Fossil Vegetables found in the Carboniferous and Oolitic Deposits of Great Britain*[16].

In Britain the main sources of petrified plant material were the coal balls found in certain Upper Carboniferous coal seams in Lancashire and Yorkshire and Witham's method of making thin sections provided William Crawford Williamson (1816–1895) with the means of investigating the plants contained in them. W. C. Williamson owed much to his early environment[14]. His father, John, who began his career as a gardener was, however, interested in more scientific subjects and was for twenty years curator of the Scarborough Museum where young Williamson had ample opportunity of handling and studying collections of fossil plants and became himself an enthusiastic collector. He made the acquaintance of William Smith and Murchison, founders of English geology, and indeed the former resided with the Williamsons for two years. It was W. C. Williamson who extended Smith's principle that geological formations could be identified by their organic remains and showed that fossils such as Ammonites could be used as zonal indices. W. C. Williamson entered the medical profession but maintained a keen interest in natural history, publishing, when only 16, a paper on rare Yorkshire birds. Later he entered University College, London, where he came under the influence of Lindley. He settled down in practice in Manchester and although in 1851 he was appointed Professor of Botany, Geology, and Zoology, still retained his medical practice. He had published several papers between 1851 and 1868 mostly on Jurassic plants from Yorkshire, but it was not until 1868 that he employed sections in his investigations. He had acquired a knowledge of the lapidary's techniques from his grandfather and uncle on his mother's side of the family and became highly skilled in the art of cutting sections. Sorby, who revolutionized the study of petrology by making use of thin rock sections, did not learn the technique directly from Witham, as is generally assumed, but from W. C. Williamson whom he visited frequently between 1838 and 1840.

Before continuing our consideration of Williamson's activities it is necessary to refer to an earlier very important event, the publication by Adolphe Brongniart in 1822 of his article in *Mémoires du Museum d'Histoire*

Naturelle, entitled "Sur la Classification et la Distribution des Végétaux Fossiles." In this important work he remarks on the disadvantage to the study of fossil plants caused by the lack of precision in the descriptions published in earlier works on the subject and the lack of accurate geological data. He also deplores the fact that no effective scheme of classification had been evolved. In 1828 in his *Histoire des Végétaux Fossiles*[3] he introduced the system of form genera for incompletely known fossil plants and those whose relationship to living plants cannot be determined. He also suggested that palaeobotany should be able, on the one hand, to take its place beside palaeontology as one of the important tools of the geologist in the study of stratigraphy, and at the same time contribute to our knowledge of the nature of extinct plants and floras. He was also a great advocate of comparative anatomy as one of the surest foundations on which to base classification and it is interesting to note that he laid particular stress on vascular structure. He anticipated Williamson in using sections in his examination of the internal structure of Carboniferous plants and describes in his *Histoire des Végétaux Fossiles* the internal anatomy of *Lepidodendron harcourtii* Witham. Brongniart's influence was twofold. He underlined the importance of the use of sections of fossil plants in comparative morphology and in doing so stimulated the great interest displayed in this country by botanists led by Williamson and Scott during the last hundred years. Brongniart also stimulated the interest of geologists in using fossil plants in stratigraphy but, as has already been mentioned, this side of the subject has been largely neglected by geologists in this country and has been left in the hands of the botanists, of whom the most notable were Kidston, Seward, and Arber.

It was when he had passed middle age that Williamson began his well-known work on the structure of Carboniferous plants, especially those found in the coal-balls. He made his first sections about 1850, but it was not until 1868 that he published his first results. Between 1871 and 1893 the Royal Society published nineteen of his famous Memoirs, but, in addition to these, many papers by him appeared in other journals, including his monograph on *Stigmaria* in 1886, published by the Palaeontological Society.

Among the greatest achievements were his demonstrations that Sigillariae and Calamariae were Cryptogams. Brongniart had maintained that these plants which had a cambium and secondary wood could not be Cryptogams and the controversy over this raged for over twenty years. Williamson discovered the fructifications of *Sphenophyllum* and revealed the wide range of structure in the fossil Lycopods. He also discovered that there were plants with a type of structure which he considered was intermediate between that of ferns and Cycads. His output of work was immense and his memoirs are almost entirely illustrated by his own drawings, masterpieces of accuracy. Sir Albert Seward told the writer that when Williamson took up a pencil

his hand was so shaky that it was difficult to believe that he could draw at all, but once his wrist was resting on the paper the tremor completely disappeared and his pencil was completely under his control. He was, in addition, an accomplished water-colour artist and this artistic talent was inherited by his son, John Copley the eminent lithographer. Williamson was always willing to help young botanists and others interested in fossil plants and his "coal hole," as the little den in which he cut his sections was called, was frequently the resort of botanists. Scott and Seward both spent some time at Manchester with Williamson and regarded him with much affection.

On his retirement in 1892 from the Chair at Manchester he settled in London and was fortunate in finding an ideal collaborator in the person of Dukinfield Henry Scott, then honorary curator of the Jodrell Laboratory at Kew. Scott was admirably fitted for this work and three important joint memoirs appeared between 1894 and 1896. Scott[8] was the youngest son of Sir George Gilbert Scott the architect and was born in London in 1868. He was schooled at home by tutors and at the age of fourteen found much to interest him in Hooker's presidential address to the British Association at Norwich. His father had hoped that he would become an engineer but after four years of reading at Oxford for Pass "Mods" and Honours "Greats" and spending three years in preparing for his profession he decided to study botany and was advised by Sir Joseph Hooker to follow Bower and Vines and study in Germany. He then went to University College, London, where he succeeded Bower as Daniel Oliver's assistant. It was there that he met Frank Oliver who became one of his closest lifelong friends. He later in 1885 became Assistant Professor of Botany under Huxley at the Normal School of Science and the Royal School of Mines. During these early years Scott used to spend much time at Kew and Mrs. Herbert Simon, one of his daughters, tells how he rode on horseback to Kew from his Surrey residence and put up his horse at Newens's café, which still exists. He kept a diary which his daughter, Mrs. Paul Wiltshire, kindly allowed the writer to examine in which are recorded his varied activities, the people he met, and the weather with recordings of the rainfall, temperature, and barometric pressure. Later when he was appointed Keeper of the Jodrell Laboratory at Kew he and his family occupied part of the Old Palace at Richmond. After his retirement from active life he lived at Basingstoke, where he still kept up an interest in palaeobotany and in the flora of the surrounding country. Dr. and Mrs. Scott were ideal host and hostess and the frequent visitors from all parts of the world were given welcome and were made to feel part of the family. His daily stroll inevitably included a bridge over the main railway line where he noted with great interest if the expresses were on time or not.

Among other workers engaged in research on the structure of Palaeozoic plants mention must be made of Sir Joseph Hooker who between 1846 and



Fig. 1. Jodrell Laboratory at Kew.

1889 published a number of important papers on Carboniferous fossil plants and their structure. He held for a time the position of Botanist to the Geological Survey of the United Kingdom. In 1848 three papers by him appear in the *Memoirs of the Geological Survey*. They deal with the vegetation of the Carboniferous Period and on the structure of *Stigmaria* and *Lepidostrobus*. In 1853 he described a new species of *Volkmannia*, and in 1889 we find an account by him of *Pachytheca* in the *Annals of Botany*. In 1855 he collaborated with E. W. Binney in a description of *Trigonocarpus*. E. W. Binney himself made some notable contributions to the study of the coal ball flora although his knowledge of botany was slight. By the end of the 19th century, thanks largely to Williamson and Binney, the broad basis of our knowledge of the coal-ball flora was well established and a considerable mass of evidence was available about the major groups of which it is composed.

Scott carried on the work of Williamson in the investigation of the petrified plants found in the Carboniferous rocks of Great Britain and in establishing our now extensive knowledge of the Articulatales and Filicales and other Palaeozoic groups. Scott's *Studies in Fossil Botany* appeared in 1900. In the Introduction he states that his main object was to present to the botanical reader those results of palaeobotanical research which he considered to be of fundamental importance to the botanical reader, and that he did not intend to produce a manual comparable to Seward's *Fossil Plants* or Potonié's *Lehrbuch der Pflanzen Palaeontologie*. *Studies in Fossil Botany* and the later two volume edition (1907, 1908) became the generally accepted text-books in university botanical departments and had immense influence in stimulating research in palaeobotany and the comparative morphology of the Pteridophyta and Gymnosperms.

In 1898 Potonié, in his text-book, established the class of Cycadofilices for plants which exhibited a mixture of fern and gymnosperm characters in their vegetative anatomy. The first and most important of these were *Lyginopteris*, *Heterangium*, and *Medullosa*. In 1903, however, F. W. Oliver and Scott discovered that *Lagenostoma lomaxi*, a not uncommon seed in the coal-balls, belonged without doubt to the same plant as *Lyginopteris*. This information led to the renaming of the group which is now called Pteridospermae, which have fern-like fronds and gymnospermic reproduction. It was soon realized that a very large number, if not the majority, of the fern-like fronds so abundant in the Carboniferous were probably not ferns at all but Gymnosperms.

Much work on the structure of the seeds found in the coal balls in which Professor Frank Oliver, Sir Edward Salisbury, and others took an active part proved that a considerable number of different genera were present. These genera, evidently related, are now included in the Lagenostomales. Another

important group are included in the Trigonocarpales. We now suspect that many of the fern-like frond genera such as *Neuropteris*, *Alethopteris*, and a large number of species of *Sphenopteris*, are almost certainly Pteridosperms, although, in most, conclusive proof of connection with seeds has not yet been obtained.

With the Pteridosperms mentioned above, Scott included a number of families based on the anatomical structure of the stem. It is significant that all are of Lower Carboniferous Age. They are Retinangieae, Calamopityeae, Stenomyeleae, Protopityeae, and Cladoxyleae. Their fructifications and leaves were unknown.

The Cladoxyleae are a remarkably isolated group and practically nothing of importance has been discovered since Scott's time to supplement our knowledge of them. The same applies to the Calamopityeae, Retinangieae, and Stenomyeleae, but recent discovery of a specimen, undoubtedly *Protopitys*, bearing branching sporophylls with large terminal sporangia, some of which contain large spores, most with small spores half the diameter of the large ones and some with intermediate sized spores, suggests that *Protopitys* was pteridophytic as regards reproduction, although it had massive trunks with compact secondary wood of definitely "gymnospermous" type[13].

Williamson had inspired a number of people in the Manchester area with a keen interest in his coal-ball investigations and in the making of sections. Evidence for this is found in the considerable collections of sections of fossil plants in the Manchester University Collections, the best known of which were made by Cash, Hick, Wild, Cunliffe, and Butterworth. After Williamson's death separate professorships were established at Manchester in Botany, Zoology, and Geology. Professor F. E. Weiss[12] was appointed to the Chair of Botany. He was a botanist with a very wide range of interests, but no doubt finding that special facilities for research were offered by the palaeobotanical material in Manchester, investigated some of the extinct Lycopods represented in the collections. His special interest lay in *Stigmaria* and he wrote a number of papers in which he describes several types of Stigmarian branches and rootlets. He was the first to notice that the orientation of the plate of xylem in the lateral rootlet of *Lyginopteris* was such that it lay in the same plane as the stele of the root to which it was attached as in the Phanerogams and not at right angles to it as in the Pteridophyta. It was this observation that convinced Scott that the Pteridosperms were not directly related to the ferns. At the British Association Meeting at Bournemouth in 1919 Scott read a paper on the relation of the seed plants to the Higher Cryptogams and said that as the result of Weiss's discovery he no longer regarded the Pteridosperms as related to the ferns but considered that they must be placed in a distinct phylum. Professor Lily Newton, who was present at the

meeting, remembers being much impressed by the way in which Professor Seward rose and thanked Dr. Scott for his paper and remarked that it was a notable occasion when a man of the distinction of Dr. Scott announced that he had been wrong and had made a mistake in previously relating the Pteridosperms to the ferns. She remembers the delight and applause with which Professor Seward's remarks were received.

Among others who were privileged to work with Professor Weiss was the late Dr. Marie Stopes who was appointed lecturer on the staff of Manchester University in 1904 and in 1909 became Lecturer in Palaeobotany. During this period she spent two years (1907–1909) in Japan carrying out research on Cretaceous plants. She also visited North America in 1911 where she was the first to discover coal-balls in American coal-measures. Near Saint John in New Brunswick she investigated the Carboniferous Flora of the "fern ledges." Her earliest research had been on Cycadean ovules while she was a student with Professor F. W. Oliver at University College, London. No doubt he had suggested this investigation because at that time he was working at the structure of Carboniferous seeds. In 1908 she collaborated with Professor D. M. S. Watson[10] in an investigation of the distribution and origin of coal-balls, a very interesting work on thenature of petrifaction. She wrote the catalogue in two volumes of the Cretaceous Plants in the British Museum (1913). In 1914 she was appointed Lecturer in Palaeobotany at University College and during the war she engaged in research on fuel technology and in collaboration with Wheeler produced a number of important papers including a monograph on the constitution of coal. In 1919 she published a paper[9] in which she gave a scheme of classification of the constituents of coal which is still the basis of the present-day system.

While considerable progress was being made in the study of petrified plant material which has so much increased our knowledge of the morphology of Carboniferous plants, great advances were being made in the study of Carboniferous floras and in its application to geological stratigraphy. Brongniart had demonstrated conclusively that plants could also be used as indications of the age of the rocks in which they were found in the same manner as animal fossils were used by geologists.

In Britain, among the chief workers in this field were Robert Kidston, E. A. N. Arber and, later, Sir Arthur Trueman and Miss E. Dix. Robert Kidston contributed more than any other in this country to our knowledge of the floras and zonal distribution of Carboniferous plants. Born in 1852 he started his career in business but at a relatively early age, being possessed of private means, retired to Stirling and devoted the rest of his life to palaeobotanical work. He was a keen collector and the floor of his study at Stirling had to be strengthened with girders to support the weight of his collections which are now preserved in the Geological Survey Museum in London. He

acted in an honorary capacity as palaeobotanist to the Geological Survey. In spite of having private means he pursued his work on fossil plants with a devoted concentration and persistence rarely equalled. He worked for over nine hours a day with great regularity. It is said that he had a reading desk that could be fitted over his bath. He was a very warm-hearted and generous man and those who were privileged to know him and enjoy the hospitality of his family received much inspiration and encouragement from him. He won an international reputation and was the recipient of many honours.

He had studied in Edinburgh and no doubt was influenced by Professor Hutton Balfour who was the first in Britain to produce a text-book on palaeobotany[2]. Balfour's *Introduction to Palaeontological Botany*, written for students, contains an introduction in which he discusses types of fossilization and describes in detail a slicing machine with a pneumatic chuck for cutting rock sections.

Kidston was mainly interested in the "impression" type of fossil plant, or as we call them now "compressions," which are found in the shales associated with coal-seams and he has described the floras found in most of the British coalfields. From his investigations of these floras he was able to define zones in the Upper Carboniferous in terms of their characteristic fossil plants. He was particularly interested in the apparently sudden change in the flora which occurs in the Roslin sandstone. This floral break between the characteristic floras of the Lower Carboniferous and Upper Carboniferous in Britain has been the subject of much controversy and would now seem to have been due to rather local conditions of sedimentation in the Roslin area because no such sudden change is found on the Continent. He was engaged at the time of his death in 1924 in writing his great work on *Fossil Plants of the Carboniferous Rocks of Great Britain* for the Geological Survey. He completed the first five parts which included the ferns and fern-like plants. It contains 156 plates and 681 pages of text[4]. The photographic illustrations are of a very high order of excellence and the locality and geological information is meticulously recorded for every specimen. He has during the course of his investigations described a very large number of new species and genera. Another very important monograph appeared in 1917 on the Calamites of Western Europe and adjacent regions in which he collaborated with the late Dr. W. J. Jongmans. He was also author in 1886 of *Catalogue of the Palaeozoic Plants in the British Museum*, and collaborated with Colonel Stirling in producing a flora of Stirlingshire.

Although his main interest lay in the study of compressions, he also took an active part in the study of petrifactions, both of Upper and Lower Carboniferous age. His collection of over 3,000 sections was bequeathed by him to the Botany Department in Glasgow. He was modest about his knowledge of plant anatomy and through his acquaintance with Professor

F. O. Bower he formed close friendships with D. T. Gwynne-Vaughan and Professor W. H. Lang when they were on the Staff of the Botany Department in Glasgow. The results of this connection with Glasgow were outstanding. Between 1907 and 1914 Kidston and Gwynne-Vaughan[5] produced that fine series of memoirs on the fossil Osmundaceae which are of outstanding botanical interest in that they give a remarkable demonstration of the course of evolution of the stele in the Osmundaceae from a solid protostele to a highly evolved dictyostelic arrangement. More will be said later of the results of his collaboration with Lang in describing the flora of the Rhynie Chert.

Kidston was a very careful and conscientious worker. Any conclusions which he drew were very securely based on observable facts. Sir Albert Seward told of a conversation he had with Williamson about some debatable matter concerning the interpretation of some fossil plants in which he, Seward, referred to some criticisms by Kidston; Williamson interrupted irritably saying "confound Mr. Kidston and his impressions."

In 1832 Lindley and Hutton refer to the coal formation "which may be considered the earliest in which the remains of land plants have been discovered." Until then the plant remains from earlier formations had by most been regarded as fucoids. Hugh Miller had, however, in *The Old Red Sandstone*, 1841, and in his subsequent books, described land plants as well as fucoids. It is interesting to note that Arber[1] as late as 1920 writes that he considers *Psilophyton* and the other genera associated with it were probably more akin to Thallophyta than to Pteridophyta.

In 1917 Kidston and Lang published the first part of their descriptions of the flora found in the Rhynie Chert[6]. It was the most dramatic and important palaeobotanical discovery of the century. In all, three genera including four species of vascular plants are fully described. They are undoubtedly land plants of simple construction. *Rhynia* and *Hornea* are thalloid in form without leaves or roots. The age was found to be not younger than Middle Devonian, but recent stratigraphical work in the area suggests that a Lower Devonian age is more likely. This is also supported by the simplicity in form of the plants compared to the many highly organized and more complex plants found elsewhere in the Middle Devonian. A fragment of *Nematophyton* found in the Rhynie Chert also suggests the earlier age.

This discovery has had a most profound influence on morphological theories on the evolution of the higher plants. Professor Lang told the writer many years ago that the discovery of the Rhynie plants would lead to much trouble and this prediction has certainly come true. Some remarkable and rather fantastic family trees have been constructed in which practically all the known phyla of vascular plants are grafted on to the Rhyniaceae.

Lignier at a much earlier date had suggested the origin of the megaphyll of the ferns and Angiosperms by the flattening of subordinate lateral branches of an otherwise undifferentiated branching thallus. This idea has been incorporated in Zimmermann's telome theory which today receives wide acceptance. It is interesting to note that Kidston and Lang in 1920 suggest that a consideration of the morphological characteristics of the Rhyniaceae indicate that they are consistent "with the Rhyniaceae finding their place near the beginning of a current of change from an alga-like type of plant to the type of the simpler vascular Cryptogams." Recent work on the Devonian sequence in Eastern North America by Professor Harlan Banks of Cornell University indicates that in it no noticeable floral breaks occur such as occur between the Lower and Middle and Middle and Upper Old Red Sandstone in this country.

Cookson and Lang[7] have described a Silurian flora from Australia in which there is evidence that more complex plants than the Rhyniaceae were then already in existence, which suggests that the origins of most of the phyla of vascular plants must be sought in the Silurian or still earlier periods. Indeed, there is already evidence from spores and some rather ill-defined impressions that vascular plants existed in the Cambrian. Further confirmation of this is, however, required before any definite conclusions may be drawn. It would therefore appear that instead of being near the beginning of a current of change from alga-like types to the simpler vascular Cryptogams the Rhyniaceae were possibly nearer the end of such a trend.

From about 1880 to 1925 may perhaps be regarded as the grand period of British palaeobotany. It covered the latter, very productive, part of Williamson's life and the activities of Kidston, Scott, Frank Oliver, A. C. Seward, F. E. Weiss, D. T. Gwynne-Vaughan, W. H. Lang, and many others. Sir Albert Seward[11] was to have the greatest influence in encouraging the development of palaeobotanical research in this country and abroad. He was exceptionally qualified, having a wide knowledge of both geology and botany. His first papers appeared in 1888 and one of his earliest was on fossil plants as tests of climate. He had spent a year working at Manchester with W. C. Williamson whom he always regarded with great affection. While at Manchester he introduced his fiancée, Marian Brewis, to Williamson who wrote to him that he thoroughly approved of his choice. He contributed to periodicals more than 160 papers and was the author of a number of books including *Fossil Plants* in four volumes (1898–1904) and *Plant life through the Ages* (1931). His very successful book *Geology for Everyman* was completed only two days before his death in 1941. He was also the author of a series of British Museum catalogues of Mesozoic plants. His principal palaeobotanical interests concerned the Jurassic and

Cretaceous although latterly he became deeply interested in Tertiary floras, largely as the result of a most successful collecting expedition to West Greenland with Professor R. E. Holttum in 1921. He has had more influence on modern palaeobotany than any other writer and this is a remarkable achievement when one remembers that he was Lecturer in Botany at Cambridge from 1890–1906 and Professor from then until the date of his retirement. This involved much teaching and, for a considerable period, he was Master of Downing and Vice-Chancellor of the University. He had the unique distinction of having been a President of the Geological Society and a President of the International Botanical Congress. He had great powers of rapid concentration and made good use of the short periods available for palaeobotanical work at times when he had much on his hands with teaching and administration.

His enthusiastic nature made him an excellent teacher. His colleague Dr. Hamshaw Thomas, who for many years conducted courses of palaeobotany for botanical and geological students, was responsible for introducing to British workers modern techniques in the investigation of the compression types of fossils and has enormously widened our knowledge of the Jurassic and Mesozoic floras, particularly those found in the Estuarine Series of the Yorkshire coast. His papers on the Bennettitales and Caytoniales, in which he enables us to reconstruct almost in entirety plants of these interesting groups, are important milestones in the advance of our knowledge of Mesozoic plants. The Caytoniales are an exceedingly interesting group and have provoked much discussion among botanists. Dr. Thomas has suggested that they might possibly have given rise to some of the Angiosperms since, when he first described their ovulate fructifications, he thought that the fruits were closed or "angiospermic." Professor T. M. Harris, who was inspired by Sir Albert Seward and Dr. Thomas to study Mesozoic floras, subsequently discovered that the fructifications were open at the time of pollination. Latterly the Caytoniales have been regarded as a highly evolved type of Pteridosperm and in the opinion of the writer this supports Dr. Thomas's view, for of all the Palaeozoic groups it would appear to show great plasticity in its reproductive parts and is the most likely of all of them to have contained the progenitors of the Angiosperms.

The late Professor Birbal Sahni was one of Seward's most grateful and enthusiastic adherents. When he had to return to India after the years he spent at Cambridge, he was so apprehensive of the strain of parting that he bought a toy monkey, which fitted the hand so that its arms and head could be made to move, and took it to the station with him. He produced it just before the train left and its antics made the parting less emotional and more tolerable. Many years later, on his last visit to this country a year before his death, he had the monkey with him. It had become rather tattered and my

wife performed some plastic surgery on it with a needle and thread. The Sahni Institute of Palaeobotany at Lucknow has a Seward Laboratory and an annual Seward Lectureship.

Today, research in palaeobotany is still actively continuing but less attention is being paid to the Upper Carboniferous coal-ball flora. Williamson and Scott and their followers in this field of activity had by the time of Scott's death almost completed the main work to be done and, owing to the closing down of the mines which produced coal-balls, less and less material became available. The activities of Hemingway and Lomax, the section cutters who provided Scott and Kidston with most of their petrified material and sections, came largely to an end. During the period which followed World War II some of these pits were reopened but little that was new was discovered in the coal-balls which came from them. Now that coal-balls are being found in the United States in unlimited quantities from a very wide area and with even better preservation of the plants inside them, the main centres of research on the Upper Carboniferous coal-ball flora are there and much interesting and important work is being published.

At present there is a revival of interest in the rich deposits of petrified plants found in the Lower Carboniferous of Scotland. The early work of Witham, Kidston, and W. T. Gordon indicated what a wealth of material there is, and it is evidently by no means exhausted. The Lower Carboniferous flora promises much of interest. No seeds or seed plants have so far been found in the preceding Upper Devonian. Three papers on Lower Carboniferous seeds were read at the British Association Meeting at Glasgow 1958. These seeds are evidently of a very primitive type and provide evidence that at this period seeds were evolving from megasporangia by a progressive investment by parts of the surrounding sporophyll which formed integuments and cupules.

So far we have been mainly concerned with investigators of the earlier fossil floras found in the Palaeozoic rocks and there is no doubt that British palaeobotanists were largely responsible for the great progress that has been made, especially in the investigation of the internal structure of extinct types of plant of the Carboniferous and Devonian Periods. There was, however, important work being done on fossil floras of later periods. Reference has been made to the work of the Cambridge School on the Jurassic floras of Yorkshire. Outstanding work on the Tertiary and Quaternary floras has also been done and among many workers the most outstanding have been Clement and Eleanor Reed. Dr. H. Godwin and his fellow workers at Cambridge have for a number of years investigated the Quaternary floras by extracting and identifying the pollens found in peats and sediments from various parts of the British Isles, and have been able to follow the

fluctuations in climate and vegetation that have occurred since the Glacial Period.

There have been considerable advances in the technique of examination of fossil plants. The petrological section method for the examination of petrifactions developed by Witham has been supplemented by the use of peel sections which may provide almost continuous serial sections. This makes it possible to investigate in great detail the internal structure of objects such as small seeds from which the old slicing method could have produced two or three sections at the most, since the width of the slice produced by the cutter was large in relation to the dimensions of the seed. Peel sections can be prepared from any size of petrifaction whereas petrological sections are of limited size and require a high degree of skill in their manufacture.

It is in the technique of examining the compression type of fossil plant that most progress has taken place. Dr. Hamshaw Thomas was largely responsible for introducing to workers in this country the use of maceration methods of isolating cuticles and spores and methods of softening and sectioning with a microtome softened fragments of compression material: and Professor Harris has used cuticles very extensively in his investigations of the Jurassic floras of Yorkshire. He has shown that much of the structure of a highly compressed seed can be deduced from the cuticles isolated from it by maceration. It may provide the cuticles of the megaspore and nucellus as well as of the integument and micropyle. The examination of compression fossils is also considerably facilitated by the transference of the substance of the fossil from the rock to a translucent base. The use of all these methods and various modifications of them have been used not only for Mesozoic fossils but have proved to be of immense value in the examination of fossil plants of all geological ages from the Quaternary to the Cambrian where some of the original organic substance of the fossil is present.

The dating of geological periods by means of the uranium-lead ratio, one of the most important discoveries of the century for palaeontologists, has shown what an immense period of time has elapsed since the first appearance of living organisms in the geological record and the evolution of the world of living things of today. It also provides a useful time-scale of geological events in terms of millions of years. The more recent discovery that radioactive carbon produced in the upper atmosphere is absorbed in the form of carbon dioxide in photosynthesis and used in the construction of the plant tissues has made it possible to estimate the age of vegetable material by measuring the amount of radioactivity in its carbon content. This method can be used to determine the age of materials such as wood, peat, and other materials and its application to quaternary organic deposits by Dr. H. Godwin and his colleagues has met with outstanding success.

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PLANT CYTOLOGY

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CYTOLOGY is the branch of knowledge which deals with the cell. The cell is the minute unit in which living matter, protoplasm, is organized. Cytology is, therefore, of all fields the one which is closest to the heart of the major goal of biology, the understanding of the nature of life.

Though so very small, the cell is of astounding complexity. Within a volume of the order of $1000\mu^3$ (of which there would be a million or so in a drop of water) there is an organized system of a large number of different kinds of molecules, ranging in size from the very simple to the most highly complex. These molecules, each with its own chemical and physical properties, when organized together in the right way, are responsible for what we call life.

The study of the cell is therefore concerned with the range of substances encountered in living matter, but especially with their organization both as a matter of morphology and as regards reproduction of the material of the cell as a whole. Until recently, cytology has depended very largely upon the study of the cell, either alive or dead, fixed and stained, by means of the light microscope. Its limitations have been lifted in various directions, by new sorts of instruments, by new chemical methods, by closer integration with genetics, and by studies of microorganisms.

The nucleus has been regarded as the most highly organized part of the cell, partly because it has hitherto been accessible to more varied modes of experiment and analysis than the cytoplasm around it. The nuclear basis of heredity had to be established before the role of the cytoplasm could be understood. The regular behaviour of the chromosomes has not been paralleled amongst cytoplasmic organelles, and the chemistry of the cytoplasm appears to be more complex. Considerable progress has been made in understanding the anatomy of the cytoplasm, and some inkling of the ways by which the nucleus and cytoplasm interact.

The ultra-violet microscope, with its expensive quartz optical system, extends the resolving power somewhat since it uses shorter wave lengths, but cells have to be examined indirectly by photography and are undoubtedly damaged by the ultra-violet radiation. The phase-contrast and interference microscopes employ optical principles, previously unused in microscopy, which permit many of the constituent parts of the cell to stand out from the

rest while the cell is living, so that they may be studied with respect to their structure and behaviour *in vivo*.

The most spectacular mechanical development in recent years is the electron microscope. This instrument is capable of providing sharp resolution at magnifications at least ten times that of the light microscope. Admittedly, there are disadvantages, such as that the material must be in very thin slices and studied in a vacuum, hence that it is necessarily dead. This is apart from the capital cost of the instrument, the considerable task of maintenance and adjustment, and the fact that it must be used primarily as a photographic instrument. The use of fine-grained film permits considerable useful enlargement. Improved methods of preparation of material for electron micrography include better means of preservation against the distortion liable to result from evacuation and desiccation, and also microtomes which will cut ultra-thin sections. Much of the work has employed fixatives and treatments by which heavy atoms, such as osmium, are selectively incorporated in particular parts of the cell. The reliability of this interesting new development in the morphological study of the cell seems assured by the concordance of fine structure displayed by plant and animal cells, including those of microorganisms, prepared in a variety of ways.

The most striking advances secured by electron microscopy relate to the structure of the cytoplasm, which has proved to be almost incredibly membranous, the membranes being strongly osmophilic. The ground cytoplasm consists of a network of minute channels, the endoplasmic reticulum (Porter and Kallman[29]). This forms a continuous network of cavities, canals, and vesicles, bounded by a membrane about 80Å thick and communicating throughout the cytoplasm from the outer membrane to the nuclear membrane. They are, perhaps, involved in intracellular transport of various substances, and their import to and export from the cell.

The mitochondria are bodies of various shapes, each bounded by a double membrane and enclosing a mass of folded double membranes, the cristae (Palade[28]). These are believed to be the surfaces upon which enzyme systems are organized. The outer double membrane consists of two layers, ranging from 35 to 60Å in thickness, separated by a space of 40–70Å. The interior double membranes, which are mainly oriented perpendicularly to the long axes of the mitochondria and may be folds or diverticula of the inner membrane, range from 40 to 70Å in thickness and are separated by a space of 40–80Å. The actual measurements vary according to cell type and species and, perhaps, may vary with the precise mode of preparation. Other mitochondria have numerous tubules rather than cristae.

The plastid is a prominent feature of many plant cells, particularly those in which it contains chlorophyll. It has a complex, membranous structure

(von Wettstein[35]; Leyon[28]). In colourless cells, plastids are present but are much smaller and somewhat simpler in their structure. The plastid is made up of discs, the grana, embedded in a less well ordered stroma. The grana consist of parallel lamellae and, in the stroma, there are thinner lamellae to which those in the grana are joined in pairs. The lamellae are thought to consist of protein, the spaces between being occupied by lipid. The chlorophyll is probably spread over the lamellae.

The literature upon the fine structure of the cytoplasm as revealed by the electron microscope has become very voluminous; for more details reference may be made to various reviews, such as Jackson and Randall[18], Dalton and Felix[9]. It suffices for our present purpose to have seen the variety of organized structure, mostly organized as plates perhaps made of a mosaic of repeating structures which will provide sites for functions yet to be certainly associated with particular parts. The boundary between nucleus and cytoplasm is of especial importance from the point of view of their mutual relations.

The nuclear membrane is also a double layered structure. The first investigations, by Callan and Tomlin[5], were of dissected nuclear membranes of amphibian oocytes and showed an outer layer which contained pores, about 400Å in diameter, and an inner continuous layer in contact with it. Watson[34] and others have found a somewhat different structure. Two membranes are present, continuous with each other and showing circular pores of about 500Å diameter. The outer membrane is continuous with the membranes of the endoplasmic reticulum, whose space is therefore continuous with that between the nuclear membranes. There are thus two possible paths of exchange between the nucleus and the endoplasmic reticulum, the pores and the perinuclear space linked to the endoplasmic reticulum.

It is of particular interest that Gay[15] has described the production of outgrowths from the surface of the nucleus by the formation of small vesicles as outpocketings of the entire double layered membrane. Serial sections show that these blebs are invariably associated with highly differentiated parts of chromosomes. There is also circumstantial evidence that the blebs are finally freed into the cytoplasm. Perhaps they represent the early stages in the development of cytoplasmic organelles and so a means of transfer of special material from the inside of the nucleus to the cytoplasm. It is clear that the morphological boundary between the nucleus and cytoplasm is not sharp and that ample ways are provided for the exchange of complex as well as simple compounds. Moreover, it appears possible that material may be transferred from the nucleus to the cytoplasm already organized in a lamellar form.

The structure of the chromosomes has been less illuminated by electron

microscopy. First, a brief reference should be made to the structure as observed by ordinary microscopy. This has shown that the chromosomes undergo a cyclical change in form, possessing, in their most extended state in the resting nucleus, a long filamentous form variously coiled and twisted within the restricting bounds of the nuclear membrane. During the prophase of mitosis each chromosome undergoes contraction by assuming a spiral structure. At first the coils are very small and close together but gradually become larger and of greater amplitude as prophase proceeds. It seems possible that there may be several orders of spirals; at least two orders can be demonstrated in chromosomes at meiosis. The thickness of the thread is such that it must be made of a bundle of fibrous molecules, or else be an immensely long, very highly coiled structure. The question of the chemical composition of the chromosomes and its possible chemical organization will be left until later except to state that both deoxyribonucleic acid (DNA) and protein appear to enter into it.

One of the clearest electron microscope examinations of chromosomes so far is of the giant polytene ones in the salivary glands of *Drosophila* (Kaufmann and McDonald[19]). These are generally considered to be a bundle of chromosome threads each similar to that in a normal mitotic chromosome. They show that the chromosome is not bounded by any discernible membrane, but that it is composed of a bundle of clearly delimited, coiled fibrous strands in both the banded and the non-banded regions. The finest strands discernible are about 250Å in diameter, though this may represent more than a single strand. It appears, moreover, that these coiled threads are intertwined in pairs to form a hierarchy of pairs of pairs, but it cannot be stated with accuracy whether they are interlaced or whether they lie side by side without interlocking. The number of strands in the salivary chromosomes is very large and of the order of 1000–2000. Each shows a longitudinal differentiation with apparent chromomeres, which group together to form the bands readily visible by means of the light microscope.

More conventional chromosomes, such as the prophase chromosomes of *Tradescantia*, show a similar series of several orders of helically disposed strands. Each chromosome appears to be divided into two secondary, or half, chromatids and each of these in turn successively subdivided into lower orders of pairs of threads, the smallest clearly defined units in the electron micrographs being about 125Å in diameter. In end view these final units show a rim of dense material surrounding a less dense core. The wall of this ring, which has a thickness of about 40Å, assumedly represents the end view of a pair of coiled threads twining round the central axis which is also about 40Å in diameter. If this interpretation is correct, this ultimate pair of intertwined strands would approach the dimensions of the type of

nucleoprotein system which has been discussed by physicists. Others, such as Moses[27], have described laminated cores in chromosomes.

This view of the structure of the chromosomes, as a bundle of threads, raises some very acute problems. Are all the threads similar? Is there a single master one amongst them, the rest being subsidiary and of different material?

The chromosomes consist characteristically of a combination of protein and DNA (deoxyribonucleic acid), with a small and variable quantity of RNA (ribonucleic acid). The mode of association is debatable. The content of DNA remains constant in amount in the resting nucleus, at the level present at the preceding anaphase and telophase, until it increases in the course of reproduction (Boivin and Vendrely[2]; Mirsky and Ris[26]). The protein varies in character, being largely histone in somatic cells, but largely protamine in sperm. The residual proteins also vary in quantity.

Chargaff[8] and others have shown that DNA has nucleotide proportions, in terms of purine (adenine and guanine) and pyrimidine (thymine and cytosine) bases, which are characteristic of the chromosome complement of each species. There is an equality in number of purine and pyrimidine bases; amongst the bases the adenine and thymine molecules are equal in number, as also are the guanine and cytosine molecules. Together with crystallographic evidence, this has suggested a new model of DNA (Watson and Crick[33]). In this model there are two helical chains joined together by purine-pyrimidine pairs and linked longitudinally by sugar to phosphate to sugar bonds. The possible base pairs are only two, adenine with thymine, guanine with cytosine. The two chains complement one another, so that each side, separated from its partner, can act as a template for assembling the other. DNA could thus be a self-sufficient genetic structure with the protein at least mechanically subordinate.

The characteristic structure, longitudinally differentiated, of a nucleic acid or a polypeptide or a chromosome depends upon the lengthwise repetition of similar though variable units. In a sense, each represents coded information for metabolic action. The reproduction depends upon a precise repetition laterally, the manner of which could be imagined for a nucleic acid or a polypeptide, but the size and heterogeneous composition (DNA and protein) of the chromosome raises additional problems. It is uncertain whether the chromosome is a single ultimate unit, or a coordinated bundle of similar fibres (polynemy), or an organization of one central with a number of peripheral subsidiary fibres, or even whether it might have lateral branches (Schwartz[31]). Electron microscopy suggests polynemy. There is certainly a wide variation in chromosome size and DNA content, ranging over three orders of magnitude, amongst plants and animals. It is difficult to suppose that the numbers of genes vary over so big a range, especially when wide

differences in size (and perhaps in DNA content) occur in related species. Further, different kinds of cells in one organism, such as the red and white blood cell precursors in mammalian bone marrow, have different DNA contents (La Cour[20]).

These considerations tend to support the assumption of a polynemic structure of the chromosome (Darlington[10]). If this is so there are two levels at which chromosome and gene reproduction occur, namely the ultimate unit fibre (presumably an association of nucleic acid and protein) and the whole organized bundle. The first would precede the second, the division of the bundle perhaps being conditioned by instability due to it becoming double sized. Differently sized chromosomes would have different degrees of polynemy and each degree would require a different stability determination. Among other things, a polynemic structure could explain the appearance of a mutation being delayed for several cell generations, though the occurrence of this seems doubtful (Witkin[36]). On the other hand it raises difficulties in respect of the precision of pairing and crossing over at meiosis, and it will be fair to consider other possibilities.

An associated problem concerns the nature of the substance which provides the permanent genetical material of the chromosomes. As an approach to this problem, it is worth turning to the simplest organisms which are available for study, namely the bacteriophages. The best studied one, T2, consists of a head and a tail, the outer part of the head and the tail being made up of protein. The inside of the head is principally deoxyribonucleic acid. When this virus parasitizes a bacterium, it attaches by a special organ at the end of the tail to particular areas of the bacterial cell surface. It then injects its internal material, the DNA, into the bacterium leaving the protein shell of the head and the tail on the outside of the bacterium. Tracer studies, using P^{32} and S^{35}, respectively to mark the DNA and the protein, indicate that virtually only DNA is injected (Hershey and Burgi[17]). Thus the genetic material of the phage appears undoubtedly to be DNA rather than protein.

Other significant experiments have traced the transmission of the DNA to progeny. Levinthal[22], in particular, by marking the DNA of parental phage with P^{32} and studying the distribution of isotope amongst progeny has shown that a large part of the P^{32} present in one parental phage is transmitted half to each of two progeny phage, other progeny not receiving any of the isotope. There is therefore a strong indication that DNA is the significant genetic material in phage. The exact nature of the transmission is such that a parental phage shares its DNA with a progeny phage, so that each receives a half portion of the parental DNA, this half portion thereafter being strictly conserved. These two parts have been correlated with the two parts of the DNA molecule proposed by Watson and Crick[33].

Further highly significant information about the conservation and

reproduction of DNA has been obtained by Meselson and Stahl[25] in bacteria, using *Escherichia coli*. Their method involves the use of bacteria whose DNA has been labelled with N^{15} by growth in the presence of this heavy isotope of nitrogen for a number of generations. This has the effect of increasing the density of the DNA molecules. The density of isolated DNA may be measured in a density gradient on an ultracentrifuge. The density gradient is prepared by the use of a heavy salt, in particular cesium chloride. On prolonged centrifugation the DNA floats at a fixed zone in the density gradient dependent upon its own density, which is thereby measured, and the effect of Brownian movement acting upon its molecules. The greater the size of the individual molecules the narrower the zone. N^{15} labelled DNA, being heavier, floats at a zone which is below that at which normal N^{14} DNA settles.

If *E. coli*, with heavy DNA, is grown in a medium whose nitrogen is only ordinary N^{14}, the density of the DNA, as it changes with the growth of the bacteria, may be studied. At first, a new sort of DNA, hybrid DNA, having an intermediate density, appears in the bacteria. In the course of the experiment only these three sorts of DNA density, heavy, hybrid, and normal, are encountered. At the end of one generation of growth in N^{15}-free medium, all of the DNA is hybrid. At the end of two generations, half is hybrid and the other half is normal. After three generations only one-quarter of the DNA present is hybrid and the rest is normal. The same principles hold for further generations so far as the N^{15}, which is being diluted in the population, can be traced.

The conclusions to be drawn are as follows. The DNA molecule, when it reproduces, divides into two equal parts. At the same time a new complementary half is synthesized for each of the two parental halves, so forming the hybrid molecules, if the parental ones were labelled with N^{15}. Thereafter, at each reproduction, the division occurs so that the part which was derived from the grandparent remains intact. The reproduction of the DNA is therefore strictly semiconservative. This implies a mode of organization and reproduction of the bacterial DNA which is consistent with the structure of the molecule proposed by Watson and Crick; but it is also consistent with a variety of other possible models of bacterial chromosomes, any of which allow of a semiconservative type of reproduction.

That the DNA constitutes the genetic material in bacteria as well as in bacteriophages is demonstrated by the fact that it is the only chemical substance concerned in the process of transformation in bacteria. In transduction, which is meditated by phages, the material transferred by the phage is also presumably DNA.

The argument that DNA is the sole genetic material, rather than a constituent one, has been extended to higher organisms. First, it is a constant

constituent of chromosomes, absent from cytoplasmic organelles, except for special instances, such as kappa in *Paramecium*. Secondly, the DNA shows constancy in amount in different cells of the organism provided they have the same chromosome complements. It doubles in amount once at a fairly specific time in the mitotic cycle, preparatory to mitosis. In tissues which have chromosome numbers different from those normal to the organism, for instance polyploid tissues, the amount of DNA present is greater by a factor equal to the degree of polyploidy. Other substances, for example proteins, which by their considerable diversity of structure have been considered as candidates for the genetic material of cells, are found in general to be inconstant in amount. Perhaps, however, this is merely a consequence of our inability to recognize a specific type of protein, constant in amount, which is obscured by variable quantities of proteins which are not of genetic significance.

The current hypothesis, however, is that DNA is the significant part of the chromosome providing the genetic information. However, between the DNA molecule and the chromosome there appears to be a very considerable gap in respect of size, the chromosome being of the order of 100 times thicker than the DNA molecule. The problem of bridging this gap is a very serious one.

The lamp-brush chromosomes, of amphibian oocytes, have provided a substantial part of our information about the chemical organization of the chromosomes and suggest how the gap may be spanned. These chromosomes are of very considerable size and appear to be made up of a relatively very long slender thread-bearing chromomeres along it. Pairs of these chromomeres, situated at fairly widely separated points along the chromosome, associate and the chromosome thread between is thrown into a loop. The large number of these loops contributes to the fluffy lamp-brush appearance of the chromosome. Individual chromosomes may be characterized by the loops which they show at particular regions. Certain of the loops bear large numbers of dense bodies, sometimes enclosed in a matrix. It is quite clear that the loops are an integral part of the chromosome and that the particular form is simply a consequence of the association of the chromomeres in pairs (Callan[3]; Gall[14]).

One important method of studying the chemistry of chromosomes, and which particular substances determine continuity of the integral structure of the chromosomes, is the use of enzyme digestion. Enzymes may be expected, if they are pure, to attack specific constituents and, by the disintegration or not of the structures, to give information about the disposition of the specific substances. Enzymes, such as trypsin or pepsin, which attack proteins, if used on living chromosomes from newt oocytes, certainly remove material from the chromosomes. The threads become thinner, but they retain their

integral structure. If the chromosomes are treated with RNAase there is removal of other constituents from the chromosomes, notably the granules, small or large, which are attached, in particular abundance, to some of the loops. These granules are rapidly removed and float away under the influence of Brownian movement. It appears that these granules are not themselves RNA but are attached, apparently to the chromosome, by a little stalk which is composed of RNA, so that when this is digested the granules become detached.

The only enzyme which attacks the integral structure of the chromosomes is DNAase (Callan and MacGregor[4]). Within a few minutes after the living chromosomes are put into a solution of DNAase, breaks may be seen at certain places, which are quite at random. More and more of these breaks appear both in the main axis of the chromosome and in the loops, so that the structure is very rapidly broken up into small pieces which float away, the whole being reduced to a suspension of small fragments. It is important to note that these results are obtained only if living chromosomes are used. If fixed chromosomes are used, as has so frequently been done in the past in similar studies, no disintegration by DNAase is observed. Previous results, using fixed material, are therefore all suspect. It therefore seems certain that the chromosomes of, at least, some organisms have a backbone constituted of DNA. Whether this is a single molecular chain or a bundle is something which must be left for future studies to settle. What additional coatings there are around this core, to give it greater thickness, are at present unknown. The possibilities are that there is a layer of protein and even additional DNA attached in special ways.

Considerable progress has been made in knowledge of the metabolism and reproduction of the chromosomes by the use of autoradiography. This is a technique whereby radioactive isotopes are incorporated into cells or tissues, which are sampled at various times, fixed, smeared or sectioned and covered with a layer of photographic emulsion sensitive to ionizing radiations. The incorporation and distribution of the label are studied by mapping the tracks of the ions from disintegrating isotopes with respect to the chromosomes, or other structures. The amount of information which may be obtained in this way depends upon the precise properties of the label used. One that has been used frequently is P^{32}, but the degree of resolution obtained with this isotope is rather limited. It is, however, possible to determine that the phosphorus is incorporated into the chromosome, at a particular stage in the mitotic cycle, which corresponds to that at which the amount of DNA present doubles.

A method of labelling DNA (and therefore chromosomes) specifically is to use tritium incorporated into thymidine, the nucleoside of thymine, a base which is peculiar to DNA and absent from RNA. When the tritium

disintegrates the radiations are extremely soft and are absorbed within a very short distance so that the degree of resolution is extremely high. Taylor *et al.*[32] have used tritiated thymidine to study the reproduction of the chromosome, employing colchicine to recognize the first and the second mitotic cycles after the application of the label.

Their results show that the reproduction of the chromosome is semiconservative, exactly as the reproduction of DNA in phage is semiconservative. When a chromosome, uniformly labelled with tritiated thymidine, reproduces, the two daughter chromatids are found to be about equally labelled with the tritium. However, in the chromosomes at the next mitotic cycle, one of the daughter chromatids is labelled and the other unlabelled. This is exactly comparable to the situations encountered in bacteriophage and in bacteria. However, in the chromosomes there are occasional orderly exchanges between sister chromatids, so that they may be made up of segments of labelled and unlabelled portions. Other work, for example that by La Cour and Pelc[21], suggests that Taylor's description and interpretation may need revision.

Another method which may throw light upon the structure of the chromosome is the study of the patterns of recombination, presumably by crossing over, between closely related genes and between different alleles. This work has disclosed marked differences between intra- and intergenic recombination. Characteristically, intragenic recombination does not show the complementary pairs of recombinants typical of crossing over. Thus, where two mutant alleles have gone into a cross, occasional wild types appear, but, where tetrad analysis is possible, as in fungi, normally no complementary recombinant, with the two mutants together, is found. This situation, first found by Lindegren[24] and called by him "conversion," has been encountered in a number of organisms (Roman[30]). Secondly, additional markers closely linked, one each side of the locus at which conversion is studied, show virtually independent recombination with respect to the conversions. This is entirely different from what would be expected if the recombinants were due to conventional crossing over. If the conversion were a recombinant of conventional type, it would be associated almost exclusively with one of the two possible types of recombination of the outside markers. In practice, the conversions are associated almost equally frequently with the two parental and two non-parental combinations of outside markers, with one of the non-parental combinations being somewhat predominant (Freese[13]; Case[6]).

The situation has sometimes been interpreted as due to a high degree of negative interference. However, the phenomenon is more suggestive of something different from normal crossing over. It appears as though the genes themselves were situated on branches from the main backbone of the

chromosome. Crossing over between different genes may be regarded as a phenomenon of the backbone and conversion as a process, perhaps comparable to recombination in bacteriophage, which occurs in the side chains. If so the absence or virtual absence of correlation between the two events could be understood. What correlation there is could be a consequence of efficiency of local pairing.

The occurrence of recombination, between different alleles shows that these are due to alterations at different sites within the locus. This fine structure of the gene has been demonstrated in bacteriophages, notably by Benzer[1] in the case of the rII mutants of T2 bacteriophage, in *Salmonella* by Demerec[11] and his co-workers and in yeast by Roman[30]. A similar situation appears to be emerging from more detailed examination of particular loci in *Neurospora* (Case[6]) and *Aspergillus*. The data so far seem capable of representation by means of a linear diagram, comparable to a conventional linkage map. This indicates that the information within the gene is disposed in a linear fashion, comparable to the linear disposition of the genes along the chromosome.

It has recently been discovered that many genes are also differentiated longitudinally in a physiological manner. For example, mutations at certain sites produce physiological changes which are recognizably different from those following from mutation at other sites along the gene. The simplest and the most extensive way by which these physiological differences may be recognized is in the fungus *Neurospora*, where certain pairs of alleles put together in a heterocaryon show degrees of complementation (Fincham and Pateman[12]; Giles *et al.*[16]). The complementation results in the heterocaryon being able to dispense with the specific growth factor required by each of the two constituents, though it may not grow so well as the wild type. Further, the enzyme activity is much less than that present in the wild type. The restoration is therefore only partial. Knowledge of the precise manner by which the two alleles, differently altered from the normal, cooperate to produce an effect similar to the normal, would contribute substantially to our knowledge of the organization of the cytoplasm. The occurrence of this phenomenon makes it quite clear that there is at least one intermediate step between the gene and the enzyme system, which it may control in the cytoplasm.

In the heterocaryon the two differently altered genes are in separate nuclei and it seems almost certain that their cooperation must occur through the intermediacy of the cytoplasm. Two general forms of cooperation seem possible. One would be the occurrence of some kind of recombination between the two defective types, thus leading to the formation of a completely normal state which would restore the wild type situation. Against this is the fact that only certain combinations of different alleles are able to

co-operate. If some process of recombination were involved, it is difficult to see how restrictions could be imposed. The second general method involves the assumption that the active material, observedly less active than the wholly normal, is a hybrid substance due to the association of two differently altered materials and that the cooperation is a consequence of chemical interaction occurring presumably at the altered sites. The modes of such cooperation are not known, but might plausibly be supposed to be concerned with the regulation of the folding and the other processes involved in the shaping of enzymes and other active protein substances.

Two points should be made about complementation between two different alleles. It is proving to be extremely common, found wherever any sufficiently large number of independent mutations are analysed. Secondly, in a number of cases the pattern of complementation is complex, dividing a series of alleles into several different groups. So far the pattern of interaction may be represented by a linear diagram in which each is represented as inactivating a certain length of the physiological gene (Catcheside and Overton[7]). In the diagram the inactivated portions are represented as overlapping if two different alleles do not complement, but as not overlapping if two different alleles will complement. With these rules, strictly consistent linear representation of every case has so far been possible.

The next stage in the analysis must be an attempt to correlate this complementation map with a recombination map. The evidence so far suggests that the complementing genes will map in separate regions of the gene, but the non-complementing ones have sites at many positions along the gene, interspersed amongst the sites determining the complementing types (Case[6]).

An outstanding problem in biology is how the information represented in the gene is translated into action represented in the cytoplasm. It has been supposed that the DNA molecules with their sequence of pairs of bases have in them a code which represents, when translated, a sequence of amino acids, which is thereby specified. The discovery of the code, if this is its nature, and its manner of translation into other substances, is a stage in the understanding of the organization of the cell.

It appears that study of the cell, to yield the knowledge that will constitute the cytology of the future, is advancing rapidly in many directions, with results which are sometimes difficult to correlate. Nevertheless, the anatomy, the chemistry, the function, the reproduction, and the differentiation, must eventually come to be understood as a related whole, to constitute an integrated science of the cell.

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GENES, CHROMOSOMES, AND EVOLUTION

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INTRODUCTION

SINCE the publication of the *Origin of Species* a century ago, the study of evolution has become a major focal point of biological science. More than any others, those biologists interested in evolution must assemble knowledge from every possible source, and produce an impartial synthesis of this knowledge based upon careful evaluation of every bit of evidence. In no other field is it possible for the incautious or over-speculative scientist to go farther astray by making dogmatic assertions on the basis of insufficient or one-sided information. The need for this synthesis has been expressed clearly by taxonomists such as Turrill[102], Mason[70], and Constance[33], while the outstanding results which it can achieve are exemplified in Babcock's[8] monograph of the genus *Crepis* as well as the publications of Clausen, Keck, and Hiesey, well summarized in Clausen's[29] admirable essay on plant evolution.

Sources of Information: Taxonomy

The principal fields of biology from which the evolutionist must gather his information may be summarized as follows. His initial source of reference is the great body of data which taxonomists have assembled on the resemblances and differences between organisms in external morphology. Because the number of available facts is so vast, an elaborate system is necessary to classify them, and this system must be based upon relatively objective criteria such as priority of publication and reference to designated type specimens. The rigidity which this requirement imposes is a necessary evil which, however, can be alleviated if taxonomists and other evolutionists agree to recognize, as most of them now do, that such concepts as "type" and "priority" exist solely for the purpose of establishing a stable nomenclature, and cannot possibly have any significance in respect of relationships or evolution. Fortunately a relictual status and eventual extinction are overcoming that species of taxonomist whose chief delight lay in his ability to discover an unused epithet in some century-old tome and to seek immortalization of his own name by resurrecting this antiquity and substituting it for some widely recognized specific epithet. To discard the usage of

priority and nomenclatural type and to substitute, as has recently been suggested[39], a system in which the name of a species might be taken "from the author who has understood the species best," would obviously create hopeless confusion, since even the most objectively minded botanists would often have honest disagreements on this point. Taxonomy is being used to serve the ends of the evolutionist by those who regard the system, in the apt analogy of Constance[33], as a library consisting of labelled pamphlet boxes. These bear names permitting easy identification, but they contain an ever increasing body of information, and can be freely shifted from one part to another of the shelves as determined by the new information which they may acquire.

In recent years, however, evolutionists have realized that the type of morphological information which taxonomists have assembled for the purpose of recognizing and identifying species as readily as possible is not sufficient, even from the morphological point of view, to give us a clear picture of their evolutionary relationships. For this reason they have developed the technique of taking mass collections or population samples[1, 3], and are experimenting with various ways of studying such samples[2, 107]. In addition, most botanists now realize that the internal structure of a plant can often tell us more about its relationships than its outward appearance. The success of this type of approach has been brilliantly demonstrated by Bailey and his associates in their studies of the most primitive living angiosperms, the Magnoliales[9, 10, 11, 12, 21], by Boke[16, 17, 18, 19] on the Cactaceae, by Dormer[43, 44] in the Leguminosae, and by Carlquist[22, 23, 24] in the Compositae, to mention a few of the more recent contributions to this field.

Taxonomists and morphologists have, however, increasingly recognized the fact that their data can reflect revolutionary relationships only very imperfectly, since they are based entirely on external appearances, or phenotypes, whereas evolutionary change must be based upon changes in the hereditary constitution or genotype. Genetics has taught us that a clear distinction between genotype and phenotype is essential to an understanding of evolutionary relationships. Despite the scepticism which apparently is still held on this point by some authors, such as Fothergill[47], such experiments as those of Clausen, Keck, and Hiesey[30] and particularly Stubbe and his associates[97, 98] have rendered highly unlikely the possibility that direct modification of the phenotype by the environment can have any importance in evolution, as has been supposed by Lamarck as well as by some botanists of the present day, particularly in the U.S.S.R. For this reason, such wide variations in leaf form as can be induced in the arrow-head (*Sagittaria latifolia*) by varying the water level in which the plants are grown, must be disregarded by the evolutionist except as examples of the plasticity of phenotype which can be established by natural selection under certain special

environments. Furthermore, the fact must be recognized that comparable phenotypic differences which in some species can be induced by environmental modification, in others come about only through an altered genotype. This fact tells us that similarities or dissimilarities in the outward appearance of plants in their natural habitats are not a sure guide to their genetic and evolutionary relationships.

This leads to the inevitable conclusion that genetics is an indispensable source of information for evolutionary syntheses. In assembling and evaluating such information, furthermore, we must realize the fact that similar phenotypic differences may be based upon entirely different genetic properties in different groups of organisms. An example is the pappus of the composite family. In one species of the tarweed tribe, *Layia platyglossa*, Clausen[29] has noted the fact that the difference between a floccose or plumose pappus and one with simple bristles is conditioned by two pairs of genes, of which opposite alleles may exist even in the same population. On the other hand, the floccose type of pappus persists with such regularity in other genera of the family, such as *Scorzonera* and *Tragopogon*, and is there associated with such distinctive features of morphology, anatomy, and cytology that we can hardly escape the conclusion that in these genera pappus plumosity is conditioned by a gene system, presumably polygenic, which is much more stable and complex than that in *Layia*, and which can be altered only with some difficulty.

Chromosomal differences are so closely associated with genetics that the concept of cytogenetics has often proved to be more useful to evolutionists than either cytology or genetics alone. Taxonomists must, moreover, be reminded of the fact that chromosomal differences are not of the same nature as the usual differences in external morphology; they are not just additional taxonomic characters. Because they bear the genes, chromosomes, under the influence of natural selection, control the way in which complexes of genetic and phenotypic characteristics are distributed to populations, as well as the way in which they segregate to produce the variation pattern found in any population. Furthermore, chromosomal differences are instrumental in building up barriers of hybrid sterility between species, and thus delimiting species with a finality which is rarely accomplished by morphological and genetic variation alone. This point will be illustrated in detail by patterns of chromosomal variation to be presented below.

Developmental Morphology and Morphogenesis

A field which up to the present has contributed far too small a share of knowledge to our understanding of evolutionary relationships is that of developmental physiology in relation to morphogenesis. Knowledge of this field is essential for a complete understanding of the connection between

morphological and genetic differences, since it alone can bridge the gap between gene and character. The width and complexity of this gap is just beginning to be realized. The rapid advances of biochemical genetics during the past fifteen years have shown us clearly that the primary action of genes is on chemical processes, and that genes can affect adult characteristics of form only by altering the pattern of interaction between these processes in development. The idea which was held by some of the earlier Mendelian geneticists, namely that the appearance of a new phenotypic trait requires the origin by mutation of a new type of gene, is thus shown to be far too naïve and inadequate. This fact is further emphasized by the demonstration of Smith[85] and others that transgressive segregation from an interspecific hybrid can establish entirely new types without mutation, and by Gajewski[50], Grant[56], and others that "macro-recombination" of gene systems belonging to different species can produce entirely new variation in respect of such basic characteristics as the number of parts of the flower.

Although our information is far too scanty to permit more than the most tentative working hypotheses on this point, the latest studies of morphogenesis and developmental physiology[53, 104, 105] suggest to the present writer that the structural differences upon which students of the evolution of the higher plants have traditionally laid the greatest emphasis, such as nodal anatomy, the structure of the inflorescence, the number of sepals, petals, stamens, and carpels per flower, the degree of union of these parts, and the nature of floral symmetry—all these are probably determined by an intricate pattern of balance between gene-controlled cellular states which promote on the one hand intense mitotic division of undifferentiated meristematic cells, and on the other hand slowing down and cessation of cell division accompanied by cell enlargement and differentiation. The genes probably control these processes at least in part through the medium of growth controlling substances. Differences in the developmental pattern can be produced by altering the concentration of these growth substances, the time when they are released, or the rate at which they diffuse through the plant body. Taken in this context the diffusion-reaction theory of Turing, as applied to plant development by Wardlaw[105] and Melville[74], has great potential significance. It tells us that small quantitative differences in the concentration time of production or rate of diffusion of growth substances, such as could be produced by differences in dosage of genes having similar primary actions, could alter the developmental pattern, and thus produce profound and apparently qualitative changes in the adult characteristics of the organism. The complexity of this phase of gene action has been well brought out by Waddington[103], whose conclusions must be carefully studied by plant and animal evolutionists alike.

In spite of our lack of knowledge of this subject, therefore, we know

enough to be very cautious about speculating on how many or what kind of genetic changes are necessary to originate a new species, genus, family, order, or class.

Floristics and Plant Geography

The types of information already reviewed tell us chiefly about those internal characteristics of plants which relate them to each other. Evolution, however, is determined only in part by such relationships. Natural selection, the only recognizable guiding force of evolution, results from the interaction between the population and its environment. Consequently, the ecological and geographical relationships of species must be fully understood before the evolution of their variation patterns can be interpreted. By means of such knowledge, situations which at first sight seem illogical and incomprehensible can often be explained by applying a few basic principles. An example is the series of morphological, ecotypic, and cytological variation patterns noted by Clausen, Keck, and Hiesey[31] in their survey of ten different plant groups along a transect across central California (fig. 1). The authors report that each of the ten groups contains a similar series of ecotypes, adapted to the sequence of extremely different climates which prevail along the transect. On the other hand, the relative distribution of diploid and polyploid chromosomal types along the transect is different for every group, and the reasons for such differences are not readily apparent. Darlington[39], reviewing the situation, suggested that it could be explained by assuming the absence of geographic barriers, an assumption which is contradicted by the topography of the transect itself, since it contains mountain systems almost as high as the Alps, and equally long and continuous. The climatic changes caused by them are as great as those between London and Rome.

If, however, one examines separately the entire geographic distribution of each of the ten groups concerned, and relates this to the geological and floristic history of western North America, the chromosomal patterns can be reasonably explained on the basis of two well-known and widely accepted generalizations: The first is that the flora of any region, particularly one having a diversity of local climates as does California, contains elements derived from several geographically different sources. The second is that polyploids, because of their new adaptive properties, are likely to be most successful in colonizing habitats new to the group concerned.

The principal centres of differentiation of the ten groups concerned are evident from available monographic studies. Three, those in *Penstemon*[63], *Aster*[34], and *Viola*[29], occur primarily in the mountain regions to the east and north of California. All of these contain diploids in the eastern part of the Sierran transect. *Penstemon* sect. *Spermunculus* contains no polyploids in California, although several of these have evolved farther to the north and

east. The Californian diploid occupies chiefly montane and subalpine meadows, habitats which are similar in all of the mountains of western North America. *Aster* is poorly known cytologically but the morphological

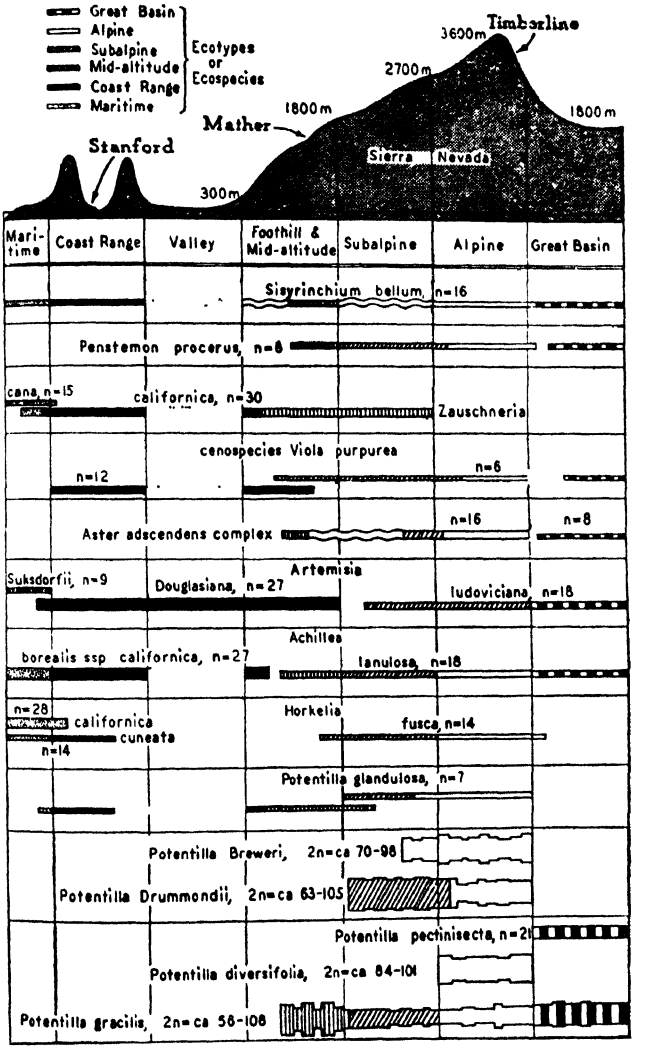


Fig. 1. Patterns of ecotypic and chromosomal variation within and between species, as shown by ten groups in an east-west section through California (from Clausen, Keck, and Hiesey, 1941).

similarity between the Sierran tetraploid and forms from the Rocky Mountains suggests that it originated in the latter area, and entered California as a tetraploid, probably under the influence of the Pleistocene glaciation of the Sierra Nevada. In *Viola* the tetraploid of the foothill region has morphological characteristics which suggest its origin by amphiploidy from the

montane diploid and another diploid species, *V. pedunculata*, one of the commonest violets of the maritime zone.

Three other groups, *Zauschneria*, *Potentilla glandulosa*, and *Horkelia*, belong to the endemic Californian flora, and are adapted primarily to the Mediterranean type of climate which prevails there. All have been studied more or less in detail by Clausen, Keck, and Hiesey[30]. *Zauschneria* is a polyploid complex containing three diploid species with widely separated and localized geographic distributions in coastal southern and central California, northern California, and Utah. These are undoubtedly relictual types, which have generated a large number of intermediate and highly successful tetraploids, by means of which *Zauschneria* was able to enter the new ecological niches made available by the extensive climatic changes which California has undergone during recent geological epochs. *Potentilla glandulosa* not only contains a wealth of ecotypes adapted to nearly all of the climatic extremes found in California, but in addition the studies of Clausen and Hiesey[32] have shown that progeny from hybrids between these ecotypes are fully fertile and can produce by gene recombination new types with entirely new adaptive properties. Because of the enormous amount of variability which *P. glandulosa* can generate at the diploid level, it has apparently been able to keep up with California's changing climates without resorting to polyploidy. The third Californian group, *Horkelia*, is closely related to *Potentilla*, but unlike *P. glandulosa*, its species are rather specialized in their edaphic requirements, and have narrow geographic distributions. Consequently, a considerable amount of speciation has taken place in *Horkelia* at the "diploid" (though originally tetraploid) chromosomal level of $2n = 28$. In the North Coast Ranges, which is the centre of species diversity, two "tetraploid" species with $2n = 56$ have evolved, but these have remained less widespread than the "diploids."

The remaining species belonging to a primarily American genus, *Sisyrinchium bellum*, is probably tetraploid as compared with other species of the genus, and belongs to a polyploid complex which is best developed in the south-eastern United States and South America. It probably entered California as a tetraploid, and already equipped with enough genetic variability to enable it to cope with the diversity of climates found there.

The remaining three groups, *Achillea*, *Artemisia*, of the *A. vulgaris* complex, and species of *Potentilla* related to *P. gracilis*, are all peripheral representatives of widespread holarctic polyploid complexes, which almost certainly originated and had their principal development in Eurasia. They agree with each other and differ from the American groups listed in having degrees of polyploidy at the hexaploid level or higher. *Artemisia* and *Achillea* agree also in having a tetraploid form in eastern California and eastward, plus a hexaploid form in coastal California. In *Artemisia*, the hexaploid is an

amphiploid between the tetraploid and a coastal Californian diploid, while the hexaploid *Achillea* seems to have been derived entirely from tetraploids.

The historical factors which might explain the present distribution of these ten groups are by no means completely known, but enough has been learned about them so that the contribution of this type of evidence towards clarifying the story of their evolution has become amply evident.

Paleontology

Finally, the evolutionist must, whenever possible, consider the evidence from the fossil record. The great weakness of this evidence lies not only in the scanty and irregular distribution of fossils of land plants, and the fact that the parts preserved, which consist mostly of leaves and pollen, are different from those ordinarily used by the taxonomist for identification. In addition, the species most often found as fossils are trees, which are poorly adapted to cytogenetic investigations, so that correlation between the cytogenetic relationships existing among modern populations and the history of their progenitors as determined by the fossil record will always be a formidable task.

Nevertheless, some of the more recent paleobotanical studies are providing valuable background information for interpreting the evolutionary history of contemporary groups. Most significant are the extensive studies made by Chaney[27, 28] and Axelrod[4, 5, 6, 7] on the Tertiary floras of western North America, in which the similarity between whole communities of the Tertiary and modern floras has been found to be great enough so that reasonably accurate inferences can be made about the climatic and ecological conditions prevailing when these fossil communities were living. These comparisons tell us that nearly all of the contemporary species of trees in western North America have existed in essentially their present form, at least in respect of phenotype, for periods of at least five to thirty million years, but that the geographic distribution of the various species, as well as the way in which they have been associated into communities, has been radically altered. They thus reveal a phenotypic stability of evolutionary lines over long periods of time which might not have been suspected without such evidence. Although our knowledge of the Tertiary floras of Eurasia is far less detailed than that of western North America, all the evidence which we possess points to similar conclusions about them[26, 35, 60, 66, 75, 76, 79, 80].

Whether this phenotypic stability of woody plants has been accompanied by an equal degree of genotypic and chromosomal stability cannot be decided directly, but the available evidence points strongly in that direction. As pointed out elsewhere[87] (p. 234), the genetic and chromosomal differentiation of woody plants usually lags behind their phenotypic differentiation. In Quercus, for instance, fertile hybrids can be produced between an

evergreen, shrubby species with entire leaves (*Q. wislizenii*) and a deciduous tree with large, deeply lobed leaves (*Q. kelloggii*). In sycamores and chestnuts fertile hybrids have been obtained between New World and Old World species, suggesting that little genetic differentiation has occurred during the millions of years which separate these species from their common ancestor in the holarctic Tertiary forests.

On the other hand, systematic, cytogenetic, and distributional studies of numerous groups of herbaceous and some woody species native to western North America suggests that evolution in them has been going on far more rapidly. In addition to the ten examples listed above, strong evidence is available from the tarweed tribe of Compositae[29], the genera *Clarkia*[68], *Gilia*[56], *Ceanothus*[69] and many others. Since these herbaceous and shrubby types have left few or no fossils, such inferences about them can never be directly verified. There is, nevertheless, one bit of fossil evidence which supports the hypothesis that herbaceous species can evolve more rapidly than the woody members of the same community.

Direct fossil evidence for more rapid evolution among herbaceous groups is provided by two series of fossil seeds. One of these is of the water plant, *Stratiotes*, in Britain[26], and the other is of grass seeds belonging to the tribe Stipeae in the Great Plains of North America[45]. The latter example is particularly instructive. The grasses concerned were very abundant during the Miocene and Pliocene epochs, from 20 million to about 2 million years ago. Their seeds occur by the thousands, and are so well preserved that many details of the hulls, including the type of hairs or bristles which they bore, can easily be seen. Now, however, they are wholly extinct, except that types closely resembling them are found in the plains of southern South America, where they are placed in the genus *Piptochaetium*[87] (p. 527).

Since these modern *Piptochaetium* species of South America all have the chromosome number $2n = 22$, it is likely that this number existed also in the plants which bore the Tertiary fossil seeds of North America. On this basis, the only living North American species usually placed in *Piptochaetium*, *P. fimbriatum*, is tetraploid, since it has the somatic number $2n = 44$[38]. The primitive number $2n = 22$ does exist, however, in *Stipa avenacea*, a species found in the woodlands of eastern North America[54]. The section *Podopogon*, to which *S. avenacea* belongs, is placed next to *Piptochaetium* by Elias[45] and the resemblance of *S. avenacea* to certain South American species of *Piptochaetium* with the same chromosome number as well as to some of the fossil species is reasonably close. One can suggest, therefore, that *S. avenacea* is an offshoot of the Tertiary Great Plains species which has been preserved until modern times because it inhabits a relatively stable forest habitat. On the plains themselves, the dominant grasses of the Tertiary Period became

replaced by more advanced types, including three species of *Stipa*, *S. comata*, *S. spartea*, and *S. viridula*. All of these are polyploids, with somatic chromosome numbers respectively of 46, 46, and 82. Their external morphology suggests that they have been derived at least in part from the Tertiary species which formed the fossils. In this example, therefore, synthesis of evidence from systematics, cytology, and paleobotany suggests to us that in the tribe Stipeae the North American plains, which are central to the group and which experienced the greatest amount of environmental change, also were the scene of active evolution, including polyploidy and perhaps also hybridization. In the peripheral areas, in which the environment changed less, the modern species are less altered from their Tertiary ancestors.

Although the chromosome number of extinct species can, of course, never be known directly, inferences about it can sometimes be made from a study of their fossil remains. In this way some idea can be obtained about the conditions under which some important steps in chromosome evolution took place. An example is the study of cell size, particularly the stomatal apparatus in fossils of *Sequoia* and *Metasequoia* found in Japan, and comparison with the dimensions of their living counterparts. By such studies Miki and Hikita[77] were able to infer that the polyploid number $2n = 66$, which distinguishes the coast redwood (*Sequoia sempervirens*) of California from all other members of the family Taxodiaceae, already existed in the Tertiary Japanese counterpart of this species. If comparable information could be obtained on fossil sequoias of other regions and of earlier geological epochs, a reasonable estimate might be obtained of the time and place when the polyploid *Sequoia* arose.

Another possible source of information on the origin of polyploids is from studies of the sizes of pollen grains. In many groups pollen grain size is closely associated with polyploidy[87] (p. 303), so that valid inferences on chromosome number can be made from measuring the pollen grains of herbarium specimens, provided that these can be compared with living plants of which the number is actually known. In view of the fact that the characteristics of pollen which distinguish modern species are becoming much better known[46] while discoveries and analyses of fossil pollen are also greatly increasing in number, the combination of these two types of data for the purpose of tracing out the ancestry of polyploid complexes would seem to be a valuable new avenue of approach, which deserves attention.

THE MAJOR PROCESSES OF EVOLUTION

The information which has been provided during the past half century by the various fields of botany just reviewed can be synthesized to give us a reasonably accurate picture of the basic processes which determine the

rate and direction of evolution. Four of these are essential, at least in the higher plants: mutation, genetic recombination, selection, and reproductive isolation. To understand evolution, we must learn as much as we can not only about each of these processes in itself, but also about the interrelationships between them.

Mutation

The concept of mutation, in order to have the greatest possible significance to evolutionists, must be defined in the broadest possible terms, as was done by Mayr, i.e.[85]: "A mutation is a discontinuous chromosomal change with a genetic effect." With such a definition, mutation must be considered at three levels, those of the gene, the chromosome, and the chromosome set or genome. The boundaries between these levels are hard to define, and some of the mutations at one level are very similar in their effects to those at the level above or below. In progressing from mutation at the level of the gene to that of the chromosome and finally the genome, we note principally a shift in emphasis. Gene mutations alter primarily individual developmental processes, and so have specific effects on individual phenotypes. Chromosomal and genomic mutations, on the other hand, alter either whole series of different processes, or affect the relationships between them. They are, therefore, most likely to have a series of generalized effects on the phenotype. Furthermore, they tend to bring about a new organization of the hereditary material, which contributes to the reproductive isolation of the mutant individual, and thereby to the origin of species.

Gene mutations must be considered in two aspects, first the type of change which they involve, and second the effects which they have on the organism. To understand the first aspect, we must know something about the composition and organization of the hereditary material itself. Fortunately, co-operation between biochemists and geneticists has in the past few years given us a much clearer picture of this material. Genes and chromosomes apparently consists of three substances, desoxyribosenucleic acid (DNA), ribosenucleic acid (RNA), and proteins of the histone type. The recent findings of Fraenkel-Conrat[48, 49] on tobacco mosaic virus suggest that all of these substances are essential for biological and hence genetic activity, and that they must be organized in a particular way. Variation in the chemical composition of DNA derived from different organisms[100], plus the demonstration that this substance can bring about a specific type of hereditary transformation in pneumococcus bacteria, suggests strongly that DNA is the component which confers on genes their specificity. One way in which genes differ from their neighbours in the same nucleus, as well as from their alleles on homologous chromosomes, probably lies in the structure of the DNA molecule. According to the model of this molecule made by Watson

and Crick[14, 106], it is a long, flat, spirally wound ribbon, whose borders consist of a constant alternation of phosphate and sugar groups. They are connected by a core consisting of pairs of purine and pyramidine bases, joined together by hydrogen bonds. Four kinds of base pairs exist (adenine-thymine, thymine-adenine, guanine-cytosine, cytosine-guanine), and these may follow each other in any sequence. According to Beadle[14], the particular sequences set up in a particular molecule of DNA may be imagined as a sort of Morse code, which transmits a particular "genetic message" to the cell. One type of gene mutation, therefore, can be visualized as a change in the order of base pairs in the DNA molecule, which causes it to transmit a different "message."

This, however, by no means exhausts the possible types of genetic changes which would pass as gene mutations according to all of the experimental tests usually applied to detect them. As Stadler[86] first pointed out, the only practical working definition of a gene which we have is "the smallest segment of the gene string that can be shown to be consistently associated with the occurrence of a specific genetic effect." To show this association between the gene and its effect we rely on three different types of tests; those from linkage and crossing over, from mutation, and from the action of the gene in development. Comparison of the results of these three types of tests in maize, *Drosophila*, and *Neurospora* tell us that in these organisms the gene can be defined in different ways according to the tests applied, and in all probability consists of several molecules. Furthermore, numerous cytological studies have shown us that under certain cellular states, such as at the prophase of mitosis or meiosis, the chromosomes possess regions which stain heavily ("heterochromatin") alternating with those which stain more lightly ("euchromatin"). These regions have different genetic effects. The heterochromatic regions contain few or no genes with easily recognized Mendelian properties, but their differentiation appears to contribute rather to the quantitative differences between organisms. The euchromatic regions probably contain genes with all types of effects. The difference between heterochromatic and euchromatic regions lies in the behaviour of their nucleic acid molecules, and may be related to the organization of nucleic acid and protein molecules relative to each other as much as to the chemical structure of the molecules themselves. We can thus imagine that submicroscopic changes in this organization would have genetic effects, and so would qualify as gene mutations.

Finally, the analysis of pseudoallelism and related phenomena in *Drosophila*, maize, and *Neurospora*[14, 86], has shown that many of the so-called gene loci in these organisms are actually compound structures, which may be separated into smaller units by rare crossing over. At least in maize the plant can suffer the loss of part of such a locus without deleterious effects. Furthermore,

the activity of "alleles" of such loci depends upon their position relative to other alleles. Hence in pseudoallelic loci, which probably exist in all higher plants and animals, rearrangements (deficiencies, duplications, inversions) of chromosomal segments so small that they cannot be detected with the usual microscopic and genetic techniques also can qualify as gene mutations.

From the foregoing analysis, we reach the conclusion that gene mutations consist of all those chemical and physical changes of chromosomes which occur at the submicroscopic level.

The effects of gene mutations on the organism are equally heterogeneous. They range all the way from such drastic alterations as the transformation of a two-lipped into a radially symmetrical flower in the snapdragon (*Antirrhinum*) or from of a compound to a simple leaf in the garden pea, down to effects which are so slight that they blend into the modifications of the phenotype normally produced by the environment. Although mutations with all sorts of effects are from time to time favoured by selection and thus contribute to evolutionary change, the great majority of the mutations which contribute to evolution have relatively slight but cumulative effects. This is shown by the analysis of segregation in progenies of hybrids between widely different subspecies or between interfertile species such as the recent studies of Clausen and Hiesey[32] on *Potentilla glandulosa* and of Gajewski[51] on *Geum*. In these progenies, all of the characteristics by which the parents differ segregate according to more or less complex ratios, showing that two or more, and most often a large number of genes is involved. The greatest influence exerted by a single gene difference is to produce a clearly recognizable difference in flower colour or a distinct notch on the upper margin of the petal. In *Potentilla*, all of the characteristics which adapt one race to the mild subtropical climate of California and another to the rigorous environment which prevails at timberline in the Sierra Nevada are governed by many genes, each with a slight, hardly detectable effect.

Although the vast majority of the gene mutations which contribute to evolution are undoubtedly those with slight effects, the possibility still exists, as has been suggested by Goldschmidt[53], Gustafsson[58], and Stubbe and Wettstein[99], that occasionally mutations with large effects may become established by selection, and may exert an influence on the course of evolution far out of proportion to their numbers. In the flowering plants, such mutations might be expected most often as the basis of radical alterations in the structure of the flower or the inflorescence. The fact that few or no intermediate conditions exist between radially symmetric and zygomorphic flowers, between corollas with separate and with completely united petals, and between the head of the Compositae and more conventional types of inflorescences, might be taken as evidence that mutations

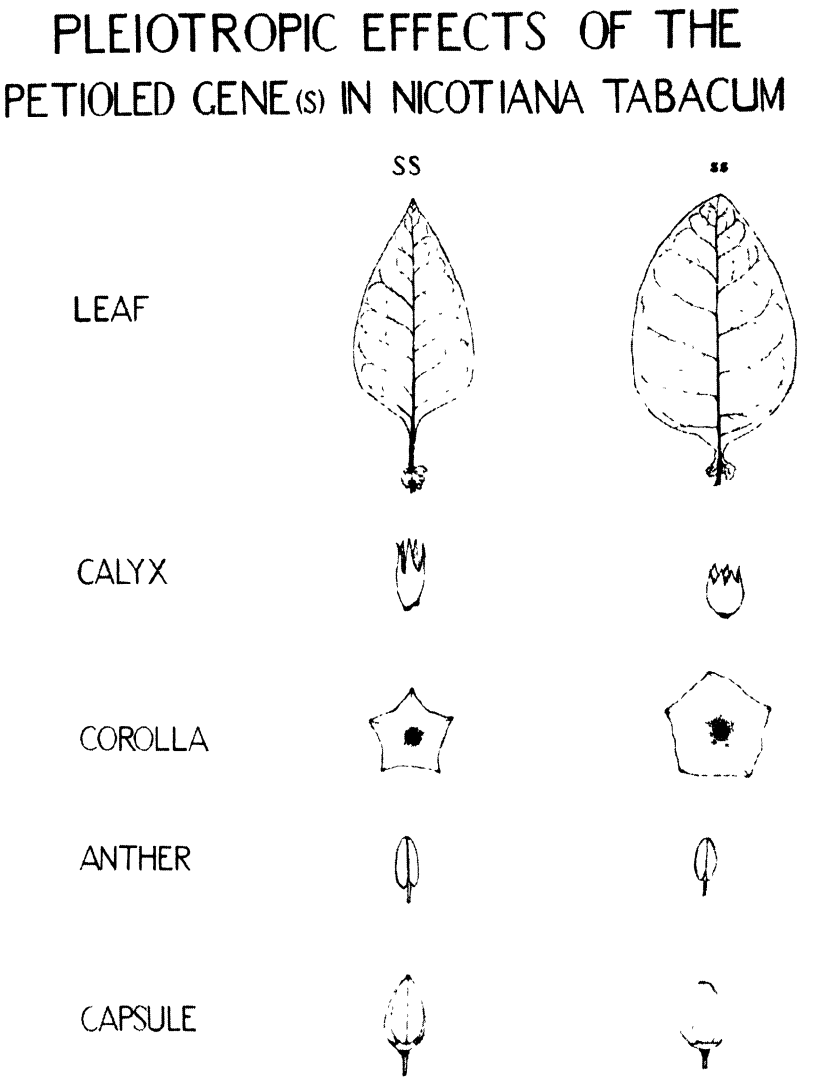


Fig 2 Diagram showing the effects of the "petioled" gene in *Nicotiana tabacum* on leaves, calyx, corolla, anthers, and capsule.

with large effects contributed to these highly significant differences. Unfortunately, species which are separated by such radical differences as these are usually so distantly related to each other that fertile hybrids between them cannot be obtained, so that this point is very difficult to test experimentally. One example which points towards the importance of genes with large effects is that of the columbine (*Aquilegia*). Gajewski (unpubl.) has recently found from F_2 progeny of hybrids between the spurless columbine of Asia (*A. ecalcarata*) and various species with normal spurs, that the presence of a spur is determined in some species by a single dominant gene and in other species by two such genes. Differences in length of spur, on the other hand, are governed by many genes with small effects.

One feature of gene mutation which is of particular significance to evolution is that many mutations, perhaps a majority of them, affect several characteristics of the adult phenotype. This phenomenon, known as pleiotropy, results inevitably from the complexity of the developmental processes which lie between the gene and the adult character. Although most if not all genes affect only one primary process of cell metabolism, each primary metabolic change takes place in cells of diverse types all over the body, and so is bound to produce different but related effects on different organs. An example is the gene "petioled" in *Nicotiana* (fig. 2). This gene produces leaves with longer petioles and more acuminate tips, calyces with longer, narrower sepals, corollas with more acuminate lobes, stamens with longer anthers, and longer, narrower seed capsules. All of these multiple effects probably result from a single initial difference; the "petioled" gene produces greater elongation in all of the appendicular organs.

Pleiotropic effects may influence greatly the selective value of a mutation. One can easily imagine mutations with pleiotropic effects, some of them advantageous, some neutral, and some even harmful. Because of pleiotropy, therefore, the action of natural selection is likely to be indirect, and characters which have no selective value in themselves can become established due to the secondary effects of genes which are valuable to the organism for completely different reasons.

The gene mutations which contribute to evolution, therefore, do not produce a new adaptive type in one step, as De Vries and other early Mendelian geneticists believed. They are, rather, the building stones which must be combined in particular ways to produce adaptive variation. For this reason, the mechanisms of recombination in populations play as important a role in generating the variation upon which selection acts as the mutations themselves. Few if any mutations play a significant role in evolution at the time when they arise. Rather, they may be added to the assemblage of genic differences already present in the population, and so may serve to enrich or replenish its "gene pool."

Gene Recombination

Gene recombination has thus been elevated to a role as important as that of mutation in producing adaptive variation in higher plants and animals, and one which has an even greater immediate significance to the selective process. This has explained clearly nature's apparent "urge" towards cross-fertilization, which is so manifest in the elaborate forms of flowers, studied already by Darwin[40], as well as the genetic systems for self-incompatibility, which are equally complex in a different way[67].

Once the evolutionary basis was understood for nature's apparent "insistence" on cross-fertilization in many species of plants, a rational foundation was laid for solving the problem of why many species of plants which escape this "dictate" of nature by means of self-fertilization or even by the negation of sex through parthenogenesis and related phenomena, nevertheless manage to become highly successful and widespread, and can even evolve whole series of species at these reduced levels of genetic recombination. The first steps towards its solution were taken by Darlington[37] and Mather[71], who pointed out that cross-fertilizing populations contain a large store of hidden variability, in the form of recessive genes held in the heterozygous condition, and that most of this variability is inadaptive. Because it is continually being brought out by recombination, it reduces the immediate fitness of the population. On the other hand, hidden variability is valuable insurance which, by generating constantly genotypes not perfectly adapted to the environment which the population occupies at any particular time, increases the probability that some recombinations will be adapted to new environments which the population may be called upon to face. Every population must, therefore, strike a compromise between the immediate fitness but evolutionary rigidity which results from self-fertilization or asexual reproduction, and the lowered immediate fitness but greater evolutionary flexibility which is produced by cross-fertilization. Data have been presented elsewhere[87] (chap. 5)[89], which show that genetic systems involving self-fertilization, parthenogenesis, and other devices which promote immediate fitness are in the higher plants always secondary, having been derived from systems having a maximum flexibility because of cross-fertilization. They occur principally in populations which occupy temporary or pioneer habitats, such as annual weeds. The immediate fitness of such populations helps them in the rapid colonization of newly available habitats.

The reversion from cross- to self-fertilization may also take place in connection with long-distance dispersal. Baker[13] has shown that in genera of Plumbaginaceae the species found in or near the Eurasian centre of distribution for the family are predominantly cross-fertilized because of floral dimorphism, but that in America and other regions remote from the original centre self-pollination prevails. This situation is easily explained if we assume

that new colonies of the species are occasionally built up from a single individual grown from a seed which has been accidentally transported for a long distance. Under such conditions, a plant which could produce vigorous, well adapted offspring from self-fertilization would have an obvious advantage over one which required pollen from another individual of the same species. Surveys of the distribution of self- and cross-fertilization in several other genera have shown that this relationship is a general one. Plant geographers have thus been provided with a valuable additional criterion for determining centres of origin and dispersal. Its reliability is probably greater than that of many other criteria used for this purpose, since it is directly associated with the capacity for long-distance migration and establishment. This provides another reason why monographers should pay much more attention than they have to the question of whether the species with which they are dealing are predominantly cross- or self-fertilized.

Recent studies of the genetics of animal populations, particularly those of Dobzhansky[41] and his associates on *Drosophila*, have demonstrated experimentally that natural selection may promote the restriction of recombination in certain chromosomal segments by means of inversions which in the heterozygous condition inhibit crossing over. One can logically infer, therefore, that many of the inversions which exist in plant populations are maintained for the same reason. Under some circumstances, as in *Oenothera*[36, 87], heterozygosity for translocations serves the same purpose. Cytologists are therefore coming to the conclusion that the numerous chromosomal rearrangements which exist in plant populations, and which often contribute towards the origin of species, as will be brought out below, have been established not by chance but because of their particular selective advantage in tying together adaptive gene combinations.

The Significance of Hybridization

The demonstration that gene recombination supplies the population with essentially all of the genetic variation which it requires to become adjusted to a new environment by means of selection carries with it an important corollary. Any method by which recombination can be suddenly and drastically increased will have a particular value for the population when it is faced with a radically new environment, and so will have a profound effect on evolution. This shows us the basic importance of hybridization, if we define this process as crossing between individuals belonging to differently adapted populations[92].

Hybridization, as defined in this broader sense, is of three types: occasional outcrossing between the pure lines of a predominantly self-fertilizing species, crossing between completely interfertile but differently adapted races or ecotypes of the same species, and crossing between species which are

reproductively isolated from each other. Although all possible intermediate conditions exist between these three situations, typically they have such different consequences that they must be considered separately.

Analysis of the variation pattern in species with predominant self-fertilization, such as *Bromus carinatus*[59], *Microseris douglasii*[25], and *Myosurus* spp.[95] has shown that these species consist of a multitude of genetically homozygous pure lines, each of which breeds exactly true to type for hundreds of generations, and occupies a specific, often rather restricted ecological niche. Because of genetic uniformity and homozygosity, each line has a minimal gene pool, and by itself would have little capacity for evolution in response to a changing environment. From time to time, however, crossing occurs between members of different lines, and the resulting hybrids, which often exhibit hybrid vigour or heterosis, segregate in later generations to produce a host of new lines. Many of these are either completely inadaptive or have limited adaptive values, but some of them may become equally or more successful than the parental lines, particularly if the environment is changing. In a predominantly self-fertilizing species, therefore, the variation of the gene pool exists in a potential form[71] represented by the genetic differences between the pure lines, and is released by occasional hybridization. For the taxonomist, such species have a characteristic and easily recognizable variation pattern. Each line can often be recognized by distinctive characteristics, and seems to constitute a species within a species. The concept of "microspecies," or "jordanons" was developed in species of this type, such as *Erophila verna*, and in fact can have validity only in them, or in groups in which asexual reproduction alternates with the sexual methods.

A second type of hybridization is that between differently adapted but completely interfertile populations. This has been designated by zoologists "secondary intergradation." It can produce a temporary increase in the size of the gene pool which is of particular significance because the environmental changes which bring together previously isolated races or subspecies are likely to provide also new habitats into which the products of hybridization can enter. An example is *Potentilla glandulosa* subsp. *hanseni*, which probably arose from hybrids between subspp. *reflexa* and *nevadensis*[30, 87]. It occupies meadows in the central Sierra Nevada of California, a habitat which resulted from changes in drainage produced by the action of the Pleistocene glaciers.

In terms of storage and release of variability, hybridization between ecotypes and between pure lines of a self-fertilizing species have much in common. In both situations the total gene pool of the species is divided into compartments, which in one case are inherent in the reproductive system of the species and in the other result from varying response of segments of the species population to different environments. Hybridization, by breaking

down the barriers between these compartments, releases stored or potential variability.

The same function on an even larger scale is accomplished by hybridization between species. Here, however, the release is more or less greatly hindered by the barriers of hybrid sterility and other forms of reproductive isolation which usually separate valid species. In some instances, these barriers can be overcome by genetic segregation alone, aided by a selective agent which strongly favours an intermediate type. A striking example of this has been found by Straw[96] in certain Californian species of *Penstemon*. Strong circumstantial evidence of various sorts points to the conclusion that a widespread species of southern California (*P. spectabilis*) with somewhat two-lipped, purplish blue corollas, is derived from hybridization between one species (*P. grinnellii*) that has widely two-lipped, bright blue corollas and another with narrowly tubular bright red corollas (*P. centranthifolius*). The parental species are kept apart largely by the fact that one is normally pollinated by large carpenter bees (Megachilidae) and the other by hummingbirds (Trochilidae); the hybrids are formed from rare accidental cross-polination by other agencies. Although the F_1 normally has no pollinating agent to which it is well adapted, it is fertile when pollinated artificially. The species *P. spectabilis*, which strongly resembles the F_1 hybrid and is probably derived from it by segregation and selection, is regularly pollinated by wasps of the genus *Pseudomasaris*. In this instance, therefore, a new type of pollinating agent "captured" the F_1 hybrid and, while promoting its successful increase in an intermediate ecological niche, insured its reproductive isolation from the two parental species.

This method for the origin of species by hybridization is, of course, confined to those plants which have flowers highly specialized for pollination by animal vectors, and in which hybrids between species having highly differentiated flowers are nevertheless fertile. This condition exists, however, in a number of families, such as the figwort (Scrophulariaceae), mint (Labiatae), and orchid families, so that examples like the one just described are probably not uncommon.

Two other methods of stabilizing and rendering fertile the products of hybridization are of much greater general significance in the higher plants. One of these is introgression, as discussed by Anderson in a number of works[2]. This involves the regular succession of hybridization, backcrossing of the usually partly sterile hybrid to one of its parental species, and selection of the back cross derivatives. By this means, blocks of genes or chromosomal segments belonging to one species can be transferred to the genetic background of another. The new genotypes thus produced often have different adaptive properties from either of the parental species, and so can extend both the variability and the geographic distribution of the recurrent parental species.

The fact must be emphasized that because of the permanence of genes the effects of introgression, if they widen the range of adaptability of the recurrent species, can become evident far beyond the original locality of hybridization, and can persist for thousands or millions of years after the original crossing took place. The introgressed populations can, therefore, behave like good subspecies or ecotypes of the recurrent species. A striking example of this is the red cedar (*Juniperus virginiana*) of the eastern United States[2]. The typical form of this species exists on the geologically and floristically ancient Appalachian Plateau, but it has produced four different races or subspecies in the south-eastern, south-western, north-western, and northern portions of its range. Each of these subspecies varies in the direction of another valid species of *Juniperus* with which *J. virginiana* hybridizes in the regions concerned.

Hybridization and Polyploidy

The best known method for the stabilization of interspecific hybrids is by doubling the chromosome number or amphiploidy. This process is

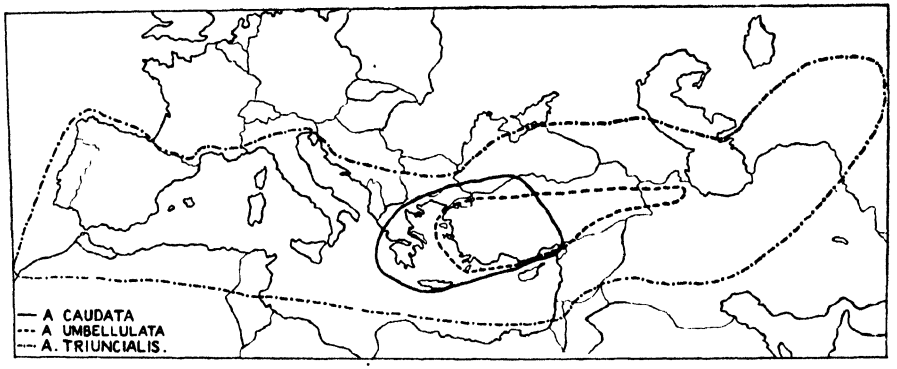


Fig. 4. Map showing the distribution of *Aegilops triuncialis* and its diploid ancestors. After Kihara, 1954.

now so well known and is so fully discussed elsewhere[87] that an extended discussion here is not needed. A particularly clear example is in the genus *Aegilops*, or goat grass, of the Mediterranean region (fig. 3), as described by Kihara[64]. The two diploid species *A. caudata* and *A. umbellulata* have completely different seed heads, associated with differentiated and easily recognized chromosomal sets. *Aegilops caudata* is distributed from Greece to western Asia Minor, while *A. umbellulata* overlaps with it in Asia Minor and continues eatward to Iran (fig. 4). The amphiploid *A. triuncialis* combines both the morphological and cytological characteristics of *A. caudata* and *A. umbellulata*. It occurs over the entire range of both of its diploid ancestors, and extends farther both to the eastward and the westward. In addition, it has become extensively introduced into California.

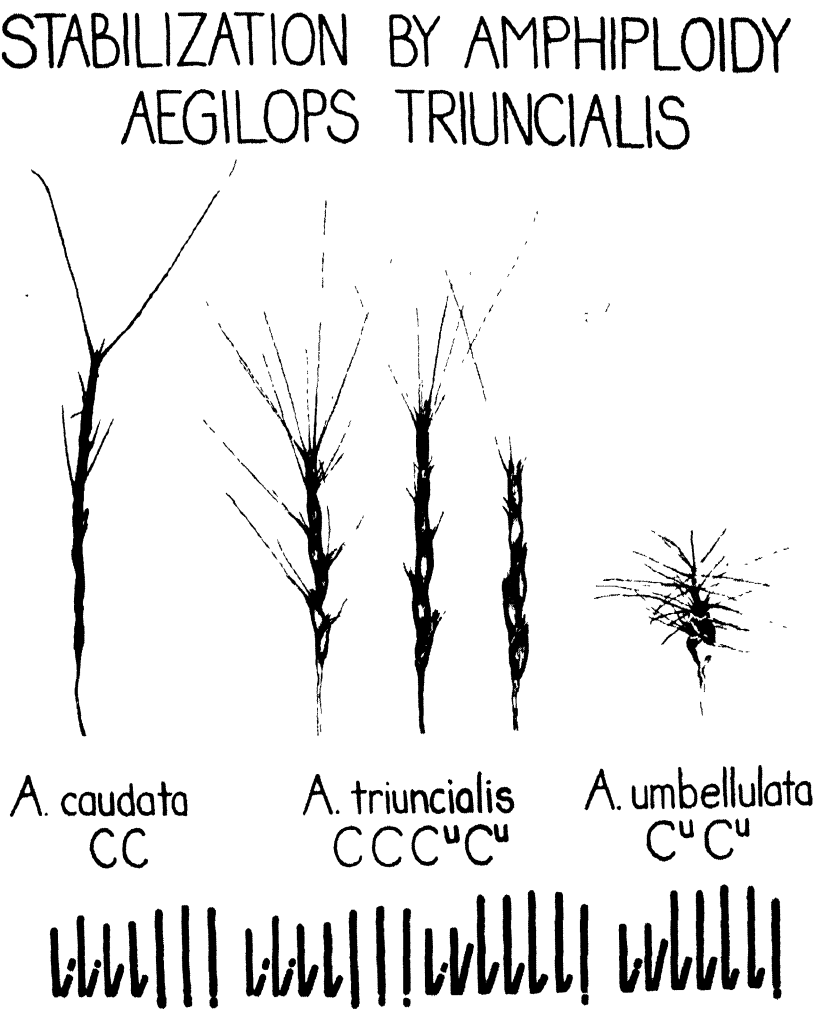


Fig. 3. Diagram showing the amphiploid species *Aegilops triuncialis* and its diploid ancestors, *A. caudata* and *A. umbellulata*. In part after Kihara, 1954.

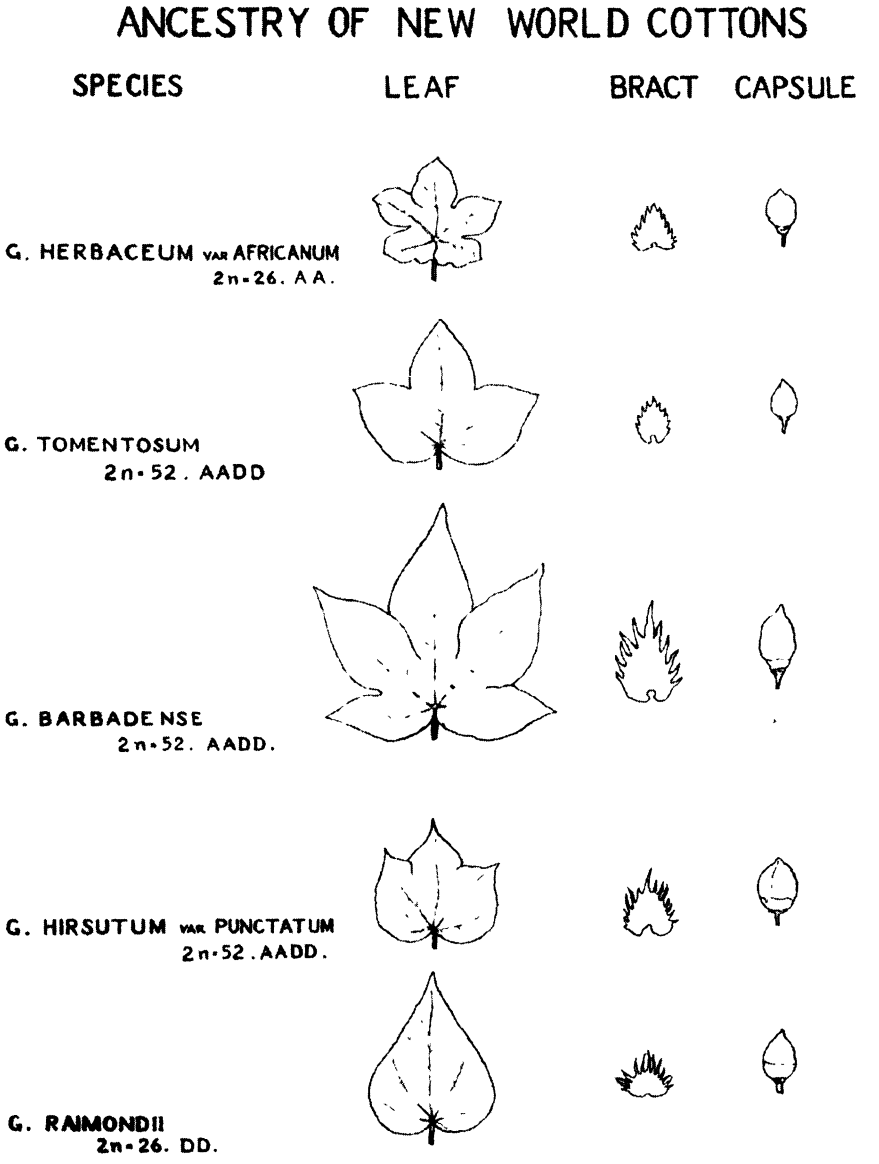


Fig. 5. Diagram of the morphological characteristics of *Gossypium herbaceum*, *G. raimondii* and one of the New World tetraploid species, *G. barbadense*. (Redrawn from Hutchinson and Stephens, 1947.)

Aegilops triuncialis is an amphiploid of relatively recent origin. Its parental species are still in contact with each other over a wide area, and F_1 hybrids between them might still be found. It is primarily a weed of disturbed ground, and to my knowledge has never been recorded from an area undisturbed by man. Since the region where its parents overlap is one of the oldest sites of human cultivation, a likely hypothesis is that *A. triuncialis* originated with the dawn of cultivation, and has acquired its wide distribution because of its weedy tendencies.

The majority of amphiploids are so old that their parental species are no longer in contact, and in many instances one or both parental types have become extinct. Amphiploids which live in different regions from their ancestral species are of particular value to the plant geographer. Their ancestry can be inferred by morphological comparison, particularly through the use of Anderson's[2] extrapolation methods, and if the plants can be raised under cultivation these inferences can be verified experimentally. In this way, the strongest possible evidence can be obtained for the existence of two species, the ancestors of the amphiploid, in regions from which one or both is now absent. When this evidence is added to other evidence from plant geography and paleontology, a reasonable hypothesis can often be constructed as to the time and place when the amphiploid originated. In this way cytogenetics can provide concrete evidence to assist the plant geographer in reconstructing the past migrations of floras.

The author has elsewhere[87] presented such examples in the genera *Iris*, *Oxycoccus*, *Bromus*, *Oryzopsis*, and *Gossypium* which have strengthened hypotheses already developed about the geological history of the flora of North America. That of *Gossypium* is worth repeating here, since it involves the origin of a well-known crop plant, cotton, and may clarify the connections between the floras of the Old and New World. Moreover, new evidence has been obtained during the past eight years which points even more strongly than before toward the hypothesis of ancient origin of the amphiploids which the author has advanced.

Hutchinson and Stephens[62] have reviewed carefully the cytogenetic evidence which shows with almost complete certainty that the tetraploid cottons of the New World are amphiploids derived from hybridization between one diploid species (*G. raimondii*) which is now confined to Peru and another which belongs to the Afro-Asiatic group of cultivated diploid cottons. This evidence is summarized in figs. 5 and 6. The hypothesis of Hutchinson and Stephens, that the amphiploid originated through the transport of the Asiatic diploid *G. arboreum* to Peru by prehistoric man, is now made even more improbable than before by the discovery of Gerstel[52] that the chromosomes of the New World tetraploids are similar to those of the African *G. herbaceum* rather than to *G. arboreum*. Furthermore,

Hutchinson[61] has found that *G. herbaceum* exists as a truly wild species in Africa, while *G. arboreum* is known only in cultivation. The possibility that *G. herbaceum* could have been transported from Africa to Peru by prehistoric man is so remote as to be not worthy of serious consideration. This leaves as the only reasonable possibility the hypothesis of the present author, that an ancestral diploid similar to *G. herbaceum* was once much more widespread, and extended into North America over the Siberian-Alaskan land bridge,

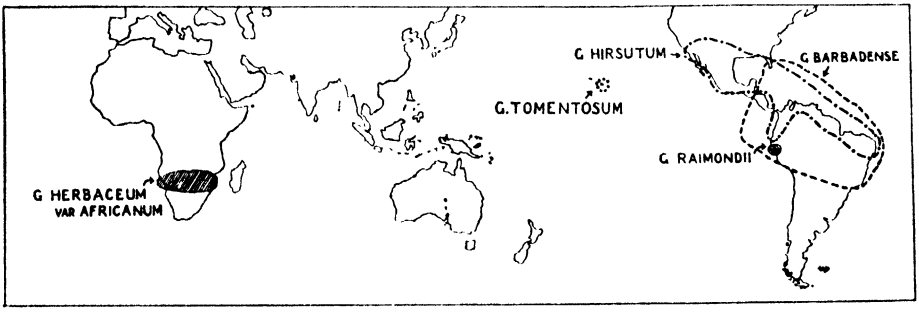


Fig. 6. Map showing the distribution of the wild forms of the diploid species *Gossypium herbaceum* and *G. raimondii*, and both wild and cultivated forms of the New World tetraploids. (From Hutchinson and Stephens 1947, and Hutchinson 1954.)

which in the early part of the Tertiary period apparently served as a migration route for many types of plants and animals which are now confined to tropical or subtropical regions. The hybridization and amphiploidy probably occurred at this remote period in North America. Subsequently, climatic changes caused the extinction of *G. herbaceum* in North America and Asia, and permitted the survival of *G. raimondii* only in its present southern refuge. Meanwhile, the derived tetraploids maintained themselves in tropical America and spread even to Hawaii.

The example of *Gossypium* thus provides for an herbaceous genus, which because of its perishable structure cannot be preserved in the fossil record, evidence for a past history of migration similar to that which paleontologists have shown to exist for woody genera of which fossil remains have been preserved[27]. Intensive studies of other pantropical herbaceous genera will probably reveal additional examples of this type.

The percentage of polyploids among the flowering plants as a whole is between 30 and 35 per cent. On the basis of indirect evidence now available, the author estimates that more than half of these, or at least 20 per cent of the existing species of angiosperms, arose by amphiploidy from hybrids between pre-existing species which were distantly related to each other. In addition, many natural polyploids arose from hybrids between more closely related ancestral forms. In some instances, as in *Zauschneria californica*[30],

the ancestors were species so closely related to each other that their chromosomes were almost completely homologous, giving to their tetraploid derivatives many characteristics of an autotetraploid. Others, such as the common cocksfoot or orchard grass (*Dactylis glomerata*), are derived from hybrids between completely interfertile ecotypes of the same species, and thus are autopolyploids in their cytogenetic constitution in spite of their hybrid origin[94].

In such polyploids, chromosome doubling has a different function from its role in amphiploidy. In the origin of such species as *Aegilops triuncialis* and tetraploid cotton the principal result of polyploidy was to render fertile a vigorous but sterile hybrid. In cocksfoot, on the other hand, diploid hybrids between widely different ecotypes are both vigorous and fertile. The autopolyploids derived from such hybrids may, in fact, be less fertile than their diploid progenitors. Their advantage lies in other respects. First, their vigour may be increased through the acquisition of gigas characteristics. Second, their polyploidy acts as a buffering mechanism to preserve their intermediate condition from excessive segregation[88]. Finally, they can acquire new variability through natural crossing with related diploids. Zohary and Nur[108] have shown that in Israel, where diploid and tetraploid forms of *Dactylis* occur together in abundance, the occasional triploid hybrids between them serve as one-way bridges for conveying genes from diploids to tetraploids. These triploids are surprisingly fertile, since the amount of seed which they produce is between 15 and 20 per cent of that produced by the adjacent diploid and tetraploid plants. Although much of this seed germinates weakly, and many seedlings fail to flower, about half of the progeny are vigorous and reasonably fertile. All of these successful progeny are tetraploid or pentaploid.

With the demonstration that even autopolyploids may have resulted from hybridization between differently adapted diploid types, the question arises as to what proportion, if any, of natural polyploids are derived from a single diploid population. This question becomes even more acute when we realize that artificial polyploids from well-adapted diploid varieties of cultivated plants are usually inferior to their progenitors, and that the successful breeding of autopolyploid varieties generally requires crossing between different strains[88]. Although many cytologists have assumed that evolution by polyploidy often involves the appearance of a tetraploid in a single population, followed by its divergence from its diploid ancestors by means of mutation and selection[39], the writer knows of no example of a recently evolved natural polyploid for which this explanation is the most probable one.

The point must be emphasized that the evolutionary history of a polyploid complex cannot be safely postulated until it is thoroughly understood

throughout its area of geographic distribution. A glaring example of the errors which can be made because of insufficient knowledge is the discussion by Darlington[89] of the origin of the Jerusalem artichoke, *Helianthus tuberosus*. He postulates that this hexaploid species arose by autopolyploidy from the diploid *H. annuus* and that the change from the annual to the perennial growth habit occurred by selection of aberrant perennial forms of the latter species. Kostoff, however, showed many years ago[65] that *H. tuberosus* is an auto-allopolyploid of the constitution AABBBB, the A genome being homologous to that of *H. annuus*. If one consults the floras of North America, where *Helianthus* is native, one finds that perennial species of this genus far outnumber annual ones, and recent cytological studies have shown that many of these are diploid and tetraploid (Heiser, unpubl.). Although the exact species which contributed the B genomes of *H. tuberosus* has not yet been identified, it probably belongs to the rhizomatous group with the tetraploid *H. decapetalus*, the diploid *H. giganteus*, and several others. All of these are much more similar to *H. tuberosus* in both external morphology and adaptive requirements than is *H. annuus*. From all of the available evidence, therefore, we reach the conclusion that the perennial, rhizomatous condition was already predominant in certain diploid ancestors of *H. tuberosus*, and was merely preserved in the polyploid species.

Natural Selection

Numerous experimental studies, chiefly on populations of animals and micro-organisms, have established beyond doubt the fact that natural selection is the chief and probably the only process which directs evolution, including both adaptations of populations within a species and the major trends of evolution at higher levels. This great body of evidence is thoroughly reviewed elsewhere[41, 84, 87]. The present article will attempt only to explore the implications of this fact to students of evolutionary relationships in the higher plants.

Perhaps its greatest significance lies in its implication that all of the principal differences between races, species, and higher categories have evolved under the guidance of natural selection, and therefore are in some way connected with adaptation. This runs counter to the thinking of many taxonomists, who have supposed that many of these differences and particularly those on which the taxonomist relies the most for diagnostic purposes, have no adaptive significance, and so could not have arisen under the influence of natural selection. Such thinking, however, is based upon too narrow a concept regarding both the nature and extent of adaptive differences and the connection of such differences with selection.

If we think of adaptation principally in terms of the ability of a plant to survive in a particular habitat, we focus our attention on such characteristics

as leaf size, internode development, and growth rhythm, which being greatly modified by the external environment, are the least reliable for the taxonomist, and may be impossible to determine from herbarium specimens. Adaptation, however, depends only partly upon the survival of the individual plant; the propagation of the race is equally important. For this reason, the adaptive nature of the reproductive structures is equally or more important to evolution than that of the vegetative parts. The relative constancy of these structures is well-known, and recent experimental work has shown that this constancy itself may be promoted by natural selection.

An example is the position of the stamens and stigma in species of *Primula* with dimorphic flowers, as studied by Mather[72]. The fact that successful pollination of primrose flowers depends upon an exact correspondence in the position of anthers and stigma in the two types of flowers was shown already by Darwin[40]. In *Primula sinensis*, Mather demonstrated that the difference between the pin and thrum types of flower depends principally upon a group of tightly linked genes, located upon a particular chromosomal segment. As long as normal cross-pollination prevails and the populations are maintained in the heterozygous condition, floral structure is very constant, both between the flowers of a plant and the plants of a single population. But in artificially inbred lines, the resulting genetic homozygosity has brought about a reduction in constancy or homeostasis, and the position of stamens relative to stigma has become more variable between the flowers of a single plant. Mather interprets these results to mean that heterostyly has "been built up gradually with gradually increasing efficiency, by the accumulation, under the action of selection, of the balanced set of genes upon which it depends."

Constancy of flower structure in response to the activity of insect and other pollinating agents is widespread among the more specialized families of flowering plants and provides many of the most reliable characteristics by which their species are distinguished. This was shown by Grant[55] as a result of his statistical study of the characters used in diagnostic keys. It is equally evident from detailed studies of such insect pollinated genera as *Ophrys*[93].

One of the objections which has been raised to the hypothesis that the elaborate forms and colours of flowers have evolved in response to the activity of pollinating agents is that many flowers have such characteristics in spite of the fact that they are normally self-pollinated. Examples can be found among species of *Vicia*, *Medicago*, *Trifolium*, *Phaseolus*, and numerous other genera of Leguminosae, certain northern species of *Ophrys*, and many others. This fact can be explained if we assume that species with predominant self-pollination are always derived from cross-pollinating ancestors, an assumption which is supported by a variety of evidence[89]. The structures

which have evolved in connection with cross-pollination become modified for self-pollination by means of the smallest possible number of structural changes. They are then maintained in a constant form because further mutational changes are likely to destroy their harmony of development as well as the efficiency of self-pollination, and so are rejected by selection.

An additional series of adaptive differences is associated with mechanisms for seed dispersal. The first fact to note in this connection is that selective pressure for efficient seed dispersal is much greater in some species than in others, depending upon their length of life and their capacity for vegetative propagation. For instance, the writer has elsewhere shown[87] (p. 141) that in the grass family the evolution from the rhizomatous through the caespitose perennial to the annual habit of growth has been accompanied by the elaboration of increasingly complex and efficient means of seed dispersal. Next, we must consider the relationship between the habitat of the species and the availability of a particular seed-dispersing agent. We can expect to find adaptation for wind dispersal more commonly in species adapted to open plains or high mountains, or in forest trees of temperate regions, while woodland species are more likely to possess adaptations for dispersal by animals. This relationship is well illustrated by Gajewski's[51] monograph of *Geum* and its relatives. This group contains at one extreme species in the subgenera *Sieversia*, *Neosieversia*, and *Oreogeum*, as well as the related genus *Dryas*, which occupy alpine or arctic habitats, and have large, plumose persistent styles, adapted for wind dispersal of the seeds. At the other extreme are the forest-inhabiting genera *Waldsteinia* and *Coluria*, with small, deciduous styles, whose seeds have either no obvious means of seed dispersal or else are equipped with oil glands, which presumably promote dispersal by ants. The large subgenus *Eugeum*, which is intermediate and appears to have been derived by amphiploidy from the other two, possesses styles of various intermediate types, which because of their adherent hairs are well adapted for dispersal by animals. In this group, therefore, the principal diagnostic characters separating the genera and sub-genera are associated with different methods of seed dispersal, each of which is adjusted to the habitat of the species concerned.

Mechanisms for seed dispersal must also be adjusted to seed size, a factor which, in turn, is critical for the establishment of the seedlings in the correct habitat. Salisbury[82] has provided clear evidence of this fact for British flowering plants, and the writer has made similar observations on the flora of California. In the drier climate of the latter area, large seeds are particularly valuable to species which colonize areas of loose soil, since the great quantity of food stored in them permits the seedling to develop a large root system, which is essential for securing moisture before the photosynthetic surface has become well developed. The dispersal mechanisms of the seeds of

annual grasses found in California and the Mediterranean region, which embody the most important diagnostic characters of the species and genera, are closely associated with seed size, and hence with the ecological niche of the species concerned. For instance, ripgut brome (*Bromus rigidus*) has a seed 2·5 cm long, one of the largest in the family. This is associated with its aggressive colonization of loose, sandy soils by means of a strong, deep root system. Transport by animals of this large seed is secured through the possession of a stout awn, nearly twice the length of the seeds, as well as a pointed callus at the base of the lemma. In another species of *Bromus*, the common soft chess (*B. mollis*), a considerably lighter seed is associated with colonization of heavier soils by means of a relatively small root system. This seed is easily transported by animals through the soft hairs which cover the lemma, and so has a broad, thin lemma bearing a relatively small awn and a flattened base.

Some methods of seed dispersal have brought about the establishment by selection of a whole complex of characters affecting the entire plant. The distinctive characters of the common primrose (*P. vulgaris*), such as the great reduction of the main stem and the elongation of the peduncles, are associated with the adaptation of its seeds for transport by ants. This property of myrmecochory, as shown many years ago by Sernander[83], has brought about comparable modifications in many of the forest-loving herbs of Europe. In melic grass, for instance (*Melica* spp.), the club-shaped rudiment at the apex of the spikelets, since it contains a fatty substance, serves as an attractive mechanism for ants. This rudiment also provides taxonomists with their best diagnostic characters for identifying the species of *Melica*. In the genus *Trillium* Berg[15] has recently shown that an entire phylogenetic sequence of modifications of stem, peduncle, capsule, and seeds has been brought about by selection for increasingly efficient seed dispersal by myrmecochory.

The above discussion has aimed to point out only a few of the ways in which characters which at first sight appear to have no connection with adaptation can by careful study be found to be strictly adaptive, and to have evolved through the direct action of natural selection. In recent years, a tendency has developed to regard with considerable scepticism attempts to find selective values for character differences. In general this has had a healthy effect in counteracting an earlier tendency on the part of naturalists toward excessive speculations in this field. On the other hand, an extreme negative attitude towards adaptiveness is also harmful in retarding our understanding of evolution, particularly when it leads to excessive speculation about internally directed genetic tendencies, often termed "orthogenesis," for which no direct evidence can be produced. Particularly damaging is the commission of what may be called the "fallacy of omniscience." This

fallacy is embodied in the argument of a botanist that because he can see no possible way in which a particular character can have a selective value, therefore it has none. Such reasoning carries the hidden implication that the author is able to detect all of the ways in which a particular character might possess an advantage. Since the studies of Haldane, Fisher, Wright, and others[41] have demonstrated the effectiveness of very small selective advantages, such as the ability for 1000 zygotes of a successful type to reach maturity as compared to 999 of the unsuccessful type, no naturalist can hope to be acquainted with all of the means by which such slight advantages could be acquired.

The problem is made more difficult by the demonstration that pleiotropic effects of genes are widespread. This means that many individual characteristics which by themselves have no selective value can become established by the indirect action of selection, because the genes producing them have other adaptive effects. This and similar considerations have led Dobzhansky[42] to the conclusion, with which the present author fully agrees, that we should not attempt to explain adaptiveness or evolution by selection entirely on the basis of individual traits. These are simply manifestations of a complex, well-integrated pattern of developmental processes which must be adaptive as a whole. In many instances the most important basis of its adaptiveness is hidden in the interior of the organism, or in its effects on early stages of development, which are rarely observed. The fact that one genotype is superior to another in a particular environment has been demonstrated repeatedly in a great variety of organisms, but the reasons for this superiority are often very difficult to determine.

The Origin of Isolating Mechanisms

The final basic process of evolution is the origin of those mechanisms of reproductive isolation responsible for the separation of species. Since this is a very large subject in itself and has been treated in detail elsewhere[87, 91], it will only be summarized here. In the first place, every barrier of reproductive isolation is based upon traits of external morphology or internal genetic organization which permit free exchange of genes through interfertility between populations of the same species, while hindering or completely preventing gene interchange between populations belonging to different species. These traits are usually based upon genes or chromosomal segments which give fertility in the homozygous condition but sterility when heterozygous. Any particular barrier, furthermore, is conditioned by a large number of genetic differences. Numerous analyses of hybrids between partially interfertile species have shown that the isolating barriers which separate them are in the F_2 and later generations fragmented into a large number of separate components, which segregate more or less independently

of each other. In many instances, moreover, their segregation is independent of the segregation for the morphological differences which separate the species. This makes it possible for the descendants of a partly sterile interspecific hybrid to retain an intermediate phenotype, but nevertheless to acquire a new homozygous combination of the sterility producing factors so that they have regained fertility. This situation has been realized in hybrid *Amaranthus* populations of northern California[101] and in *Helianthus* populations of the same region (author's unpublished results). The significance of

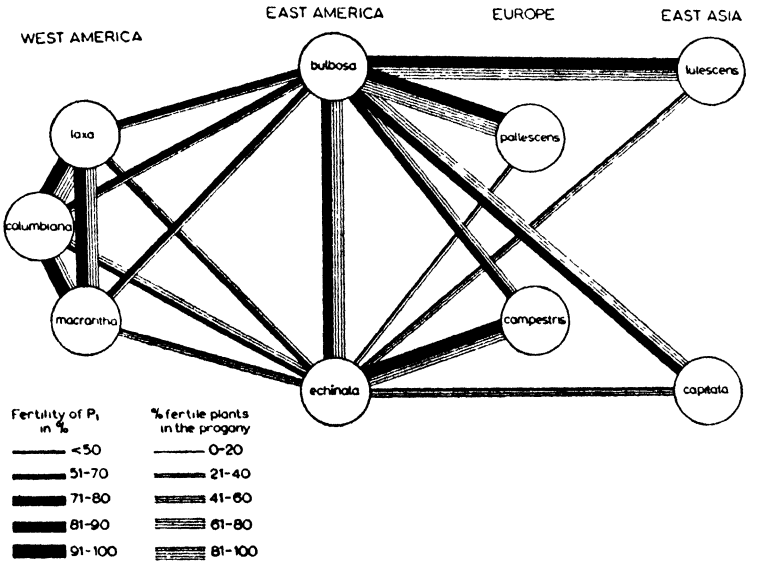


Fig. 7. Diagram showing the degree of sterility in hybrids between certain representatives of the *Luzula campestris* complex. From Nordenskiöld, 1956.

this fact in connection with the origin of new species by hybridization without chromosome doubling is obvious, and has been discussed elsewhere[91, 92].

The next important fact is that barriers of reproductive isolation often exist between individuals or populations of the same species. A simple situation of this nature is one in which hybrids between populations A and B as well as between B and C are more or less fertile, but A and C when crossed directly behave like good species and produce a highly sterile F_1 hybrid. A relatively complex example of such a situation has been found by Nordenskiöld[78] in *Luzula*, part of which is illustrated in Fig. 7. Similar examples exist in *Bromus*, *Oryza*, *Holocarpha*, *Layia*, *Clarkia*, *Gilia*, and probably many other genera.

This situation, embarrassing as it is to the biosystematist who might hope to be able to delimit species on the basis of genetic criteria more reliable than those of external morphology, is nevertheless of great significance in

helping us to understand the origin of species. It tells us that reproductively isolated species have not been evolved at a single step, but by the gradual accumulation of a complex of genetic factors promoting reproductive isolation. In order to become reproductively isolated from each other in this fashion, populations must usually if not always be separated spatially, and studies of the distribution patterns of borderline species show us that this is generally true. Furthermore, the establishment of so many genetic differences between two populations is very hard to imagine without the aid of selection, and several ways by which natural selection can indirectly promote reproductive isolation have been postulated. Experimental demonstration of their action in actually establishing a species isolating barrier is badly needed; here lies one of the major unsolved problems connected with the origin of species.

CONCLUSION

This discussion ends where it began, with the conclusion that of the major processes governing evolution in the higher plants—mutation, recombination, selection, and isolation—no single one can be considered to be of primary importance above the others. All of them must be studied from the observational and descriptive as well as the experimental and historical points of view. The final synthesis of information must combine a healthy scepticism about the value of what is known with an encouraging optimism about what will be discovered in the future.

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VIRUSES

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THE Royal Botanic Gardens were already well into their second century before viruses were known to exist, and it is only within the last twenty or so years that the numbers, prevalence, and importance of viruses in flowering plants have come fully to be appreciated. This belated recognition does not mean that they are recent creations; although the distribution and prevalence of some have undoubtedly been increased by modern methods of travel and of agriculture, virus diseases are not afflictions peculiar to our times, and it can safely be assumed that the Gardens at Kew have never been free from them. No doubt most were brought in unwittingly, but a few, such as "broken" varieties of tulip and variegated *Abutilon*, were probably deliberate introductions, because horticulturists have long been attracted by the strikingly beautiful flowers and leaves (fig. 1) of these infected plants.

There is little surprising in the fact that knowledge about viruses developed only slowly until recently, for it is less than 100 years since the germ theory of disease was firmly established and this theory itself left a legacy of prejudice that tended to hinder advances in knowledge of viruses. In the first flush of success at finding the causes of many important diseases, it was confidently thought that, for each infectious disease, there would be found a specific bacterium, fungus, or some other parasitic organism, which could be identified under a microscope and cultured on artificial media. The event usually taken as the discovery of viruses might have been expected to shake this belief, but it did not because Iwanowski, who first showed in 1892 that the cause of tobacco mosaic could pass through bacteria-proof filters, failed to appreciate the potential significance of his result and continued to assume that the disease was caused by a bacterium. True, a different conclusion was reached by Beijerinck, who soon confirmed the fact that seemingly sterile filtrates of sap from mosaic plants were infective and, impressed by this and other differences he noted from the behaviour of bacteria, he suggested that mosaic was caused by a novel type of entity, which he attempted to characterize by calling it a "*contagium vivum fluidum*." Precisely what he meant by this, except perhaps that the virus was small enough to give stable solutions, is uncertain, but the conflicting conclusions of Iwanowski and Beijerinck set the stage for disputes about the nature of viruses that have continued almost till today.

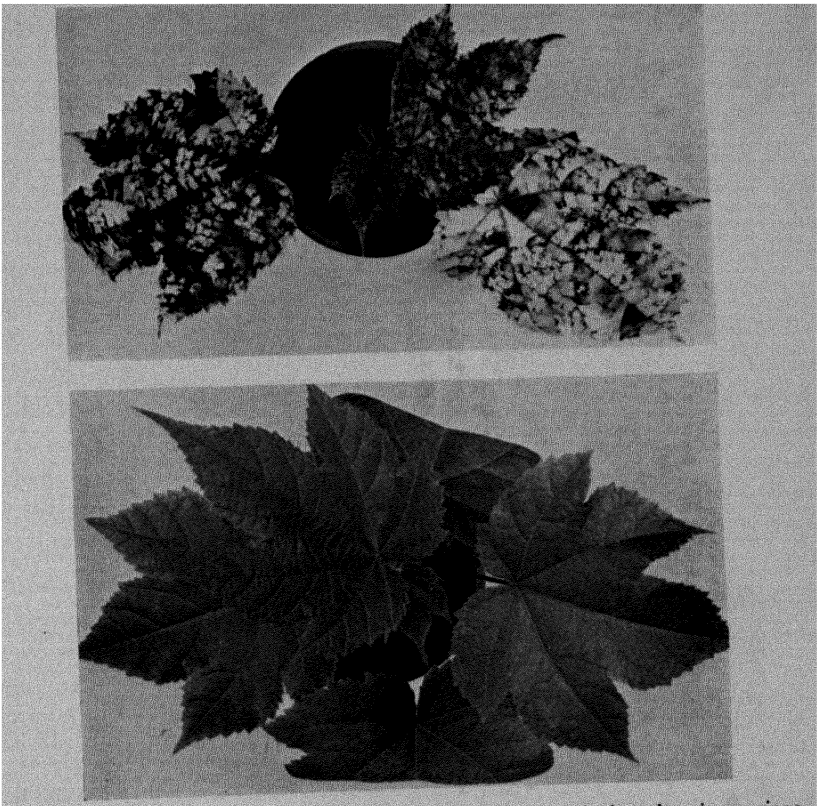


Fig. 1. *Abutilon striatum* (Dicks) plants of the same age; upper plant showing variegation was raised from a cutting taken from an infected plant kept at ordinary glasshouse conditions; lower green plant raised from cutting freed from infection by keeping a variegated plant at 36°C continuously for 28 days. (B. Kassanis. Heat therapy of virus-infected plants. *Ann. appl. Biol.*, 1954, 41, 470.)

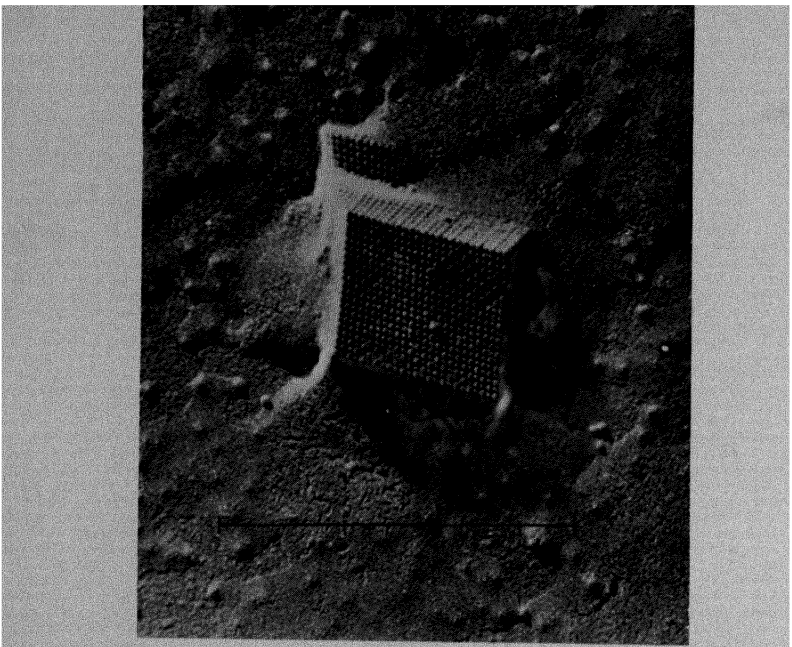


Fig. 2. Electron micrograph of a minute crystal from a preparation of the Rotha sted tobacco necrosis virus showing the arrangement of the particles in a thr dimensional lattice. (R. G. W. Wyckoff. Viruses and macromolecules studied w the electron microscope and ultracentrifuge. *I.R.E. Trans. Med. Electron.*, 19 *PGME-6, 49.*) (*Photograph supplied by and reproduced by permission of Dr. R. G. Wyckoff, National Institute of Health, Bethesda, U.S.A.*)

diffraction, which gave, not only the first direct and precise measurements of particle sizes, but also important information about the internal structure of the particles. Not only were the individual particles sufficiently uniform in size to fit into crystalline lattices (fig. 2), but each particle was composed of many similar sub-units arranged in a regular manner in space to give a fixity of structure that contrasts vividly with the continuously varying arrangements of the varied components inside living cells.

In their chemical simplicity and regularity of internal structure, viruses obviously resemble some of the individual constituents of cells more closely than they resemble whole cells. However, the new knowledge did not settle controversies, and views about viruses continued to differ so widely that, while some biologists continued to call viruses "organisms," some chemists, over-impressed by the seeming homogeneity of their purified preparations, unhesitatingly called them "molecules." Although such wide differences seemed irreconcilable, they were in large part imagined rather than real, reflecting different attitudes of mind and philosophic approaches rather than matters of fact, and they were exaggerated by the misuse of words. Nothing discovered about viruses ever justified the use of either word; "organism" implies an independent existence and a complexity of organization that there was never any reason to associate with viruses, and "molecule" implies a chemical exactness that fits ill with the mutability of viruses and that cannot be demonstrated with particles that are only a fraction the size of virus particles.

Such extreme views overlooked the fact that viruses are not unique in failing to fit neatly into the category of either organisms or molecules. Cells contain many constituents that are equally difficult to classify; some of these, such as chromosomes, plastids, and mitochrondria, are larger than viruses, and others, such as the cytoplasmic nucleoproteins, of comparable sizes or smaller. If analogies for viruses are to be sought, they are most probably to be found among such normal cell constituents, some of which resemble viruses chemically, in as much as they are built from the same aminoacids, purines, and pyrimidines, and some in their behaviour, in as much as they seem to be self-reproducing. No bizarre component has yet been identified in any plant virus and there is no reason to conclude that the viruses are synthesized in a manner that differs significantly from that of "normal" nucleoproteins. The distinctive characters of viruses are their infectivity and pathogenicity, or, in other words, their ability to reproduce in and affect cells to which they are not intrinsic, and these differences from other cell components with basically similar composition are presumably conferred by specific arrangements of nucleotides and peptide chains.

The old disputes about the nature of viruses are largely over; no longer is it seriously argued that they are parasites using other organisms as sources

of food or that they are self-replicating molecules. The differences have been composed into the current concept of virus diseases being primarily derangements of the host's nucleoprotein metabolism, with the relationship between virus and host being such an intimate affair that their activities combine and the viruses in effect become determinant parts of the cells they infect. The infected cell is the operative unit in virus production, with the virus depending on its host, not simply for a supply of food, but also for many of the synthetic mechanisms whereby its component units are made, and in so far as it has any independent activities these are to direct the manner in which these units are fitted together.

That the multiplication of plant viruses is not simply the direct and repeated replication of initially infecting particles has become obvious only recently. For 20 years or so after tobacco mosaic virus was first identified as a nucleoprotein, the whole particles seemed to be required to initiate infection, but they are now known not to be the minimum infective units. Tests with fragmented virus have shown that preparations consisting largely, and possibly exclusively, of the nucleic acid can infect susceptible cells and lead to the formation of new virus, and there is growing evidence that this is also true with other viruses. The virus protein, then, does not multiply; if there is a component that directly replicates it seems to be only the nucleic acid, whose presence in a host cell suffices, not only to produce more of itself, but also to determine the synthesis of the appropriate protein with which it combines to give complete virus particles. Further evidence that the protein plays a little or no role in determining the course of synthesis in infected cells has come from experiments in which components from strains of tobacco mosaic virus that cause distinctive symptoms, or have distinctive aminoacid compositions, were mixed. Treating tobacco mosaic virus with alkali disrupts it and produces protein fragments that will recombine with infective nucleic acid to give infective particles morphologically resembling the original virus. Protein from one strain will combine with nucleic acid from another, and when particles containing components derived from two different strains are used as inoculum, the resulting symptoms, and the type of protein that is made in infected cells, resemble those characteristic of the strain from which the nucleic acid came.

THE MORPHOLOGY OF VIRUS PARTICLES

The development of the electron microscope, especially when combined with the "shadow-casting" technique, which makes virus particles opaque to electrons by coating them with a thin film of metal, made possible direct observations and measurements of the sizes and shapes of virus particles. These observations confirmed earlier conclusions, drawn from the physical properties of purified preparations, that some plant viruses have anisometric

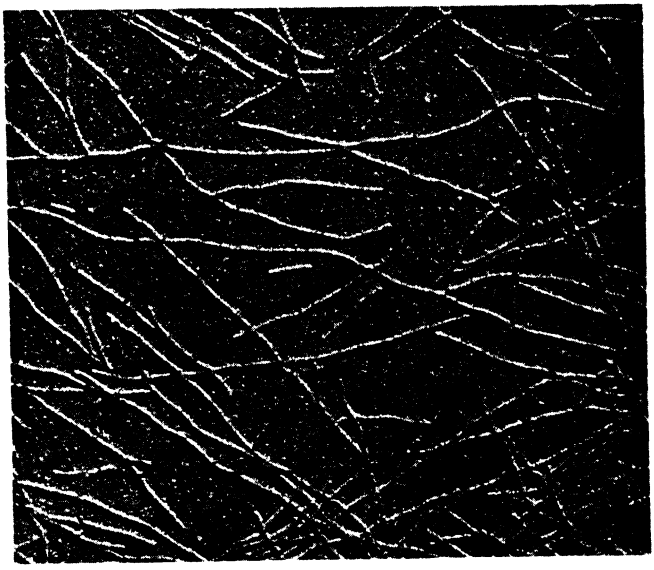


Fig. 3. Electron micrograph of purified preparation of potato virus X, showing the long, narrow, flexible particles. (*Photograph by Mr. H. L. Nixon, Rothamsted Experimental Station.*)



Fig. 4. Electron micrographs of: (top) a normal particle of tobacco mosaic virus; (middle) a partially degraded particle from a preparation treated with a detergent, showing threads containing nucleic acid projecting from the ends of rod where the protein has been dissolved away; (bottom) a small piece of tobacco mosaic virus protein seen end-on and showing a hole in the centre. (R. G. Hart. Electron-microscopic evidence for the localization of ribonucleic acid in the particles of tobacco mosaic virus. *Proc. net. Acad. Sci., Wash.*, 1955, 41, 261. *(Photographs supplied and reproduced by permission of Dr. R. G. Hart, Virus Laboratory, University of California, Berkeley, U.S.A.)*

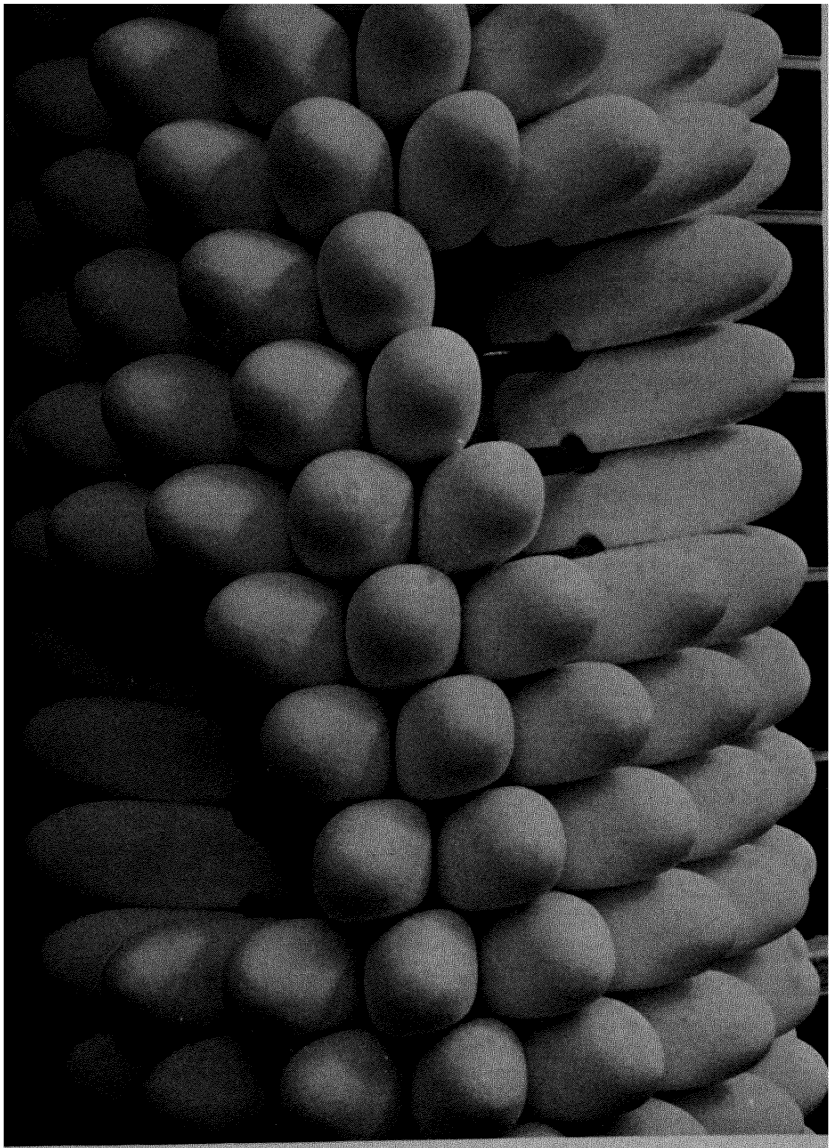


Fig. 5. Model of part of a tobacco mosaic virus particle made by Dr. Rosalind E. Franklin and Dr. A. Klug showing the spiral arrangement of the protein sub-units, which in two places have been removed to show the position of the nucleic thread in the protein. (*Photograph supplied by and reproduced by permission of Dr. K. Klug, Birkbeck College, London.*)

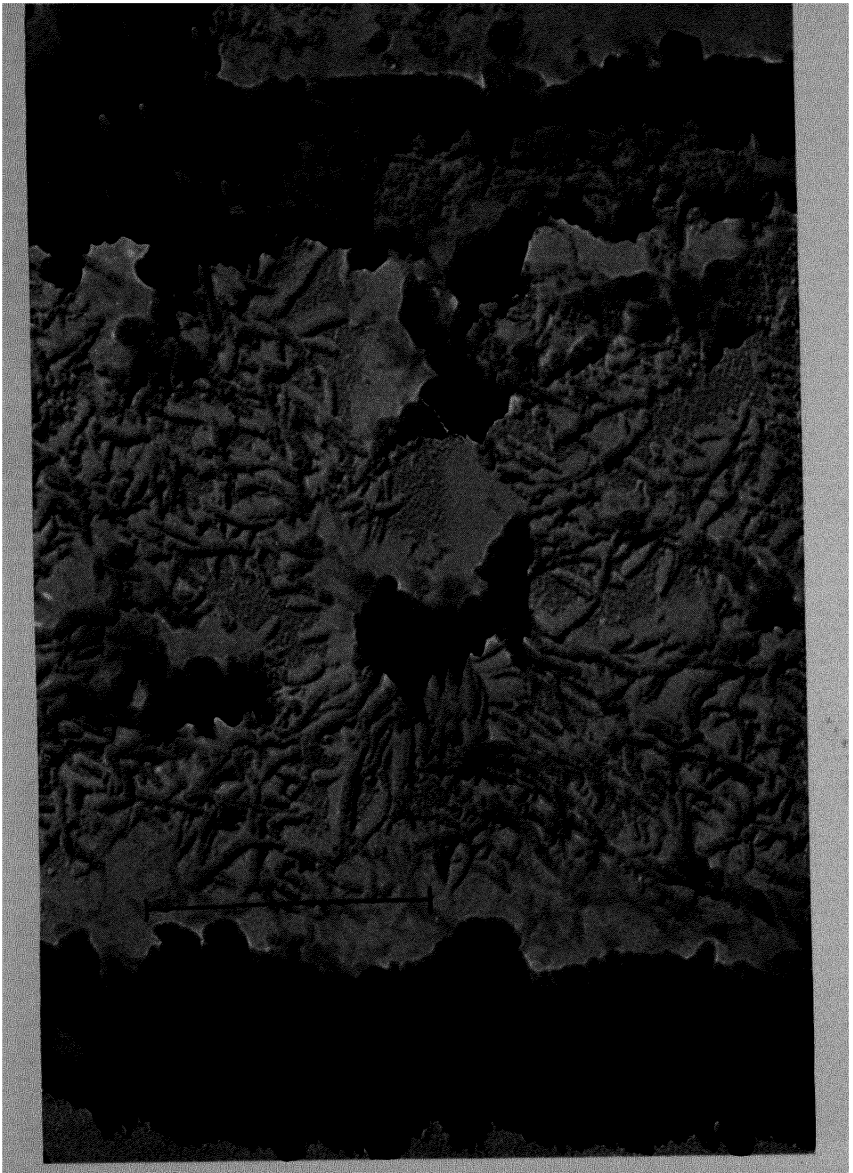


Fig. 6. Electron micrograph of a longitudinal section through a portion of a hair cell from a tobacco leaf infected with tobacco mosaic virus. The rod-shaped virus particles are the predominant components of the cell, which contained in all more than 10,000,000 particles. (Nixon, H. L. An estimate of the number of tobacco mosaic virus particles in a single hair cell. *Virology*, 1956, 2, 126.)

particles and that others are spherical or approximately so. They gave the additional information that some with anisometric particles, of which tobacco mosaic virus is one, are seemingly rigid rods, whereas others, such as potato viruses X and Y, are more thread-like and flexible (figs. 3 and 4). They also showed that, although each anisometric virus has particles of a uniform width, about 15 mμ for tobacco mosaic virus and 12 mμ for potato virus X, their lengths vary greatly; one length is usually far more common than any other, and the most usual for tobacco mosaic virus is about 300 mμ and for potato virus X of about 500 mμ. Most of the spherical viruses occur in particles of a uniform and characteristic diameter, which varies with different viruses from about 20 up to 80 mμ. The Rothamsted tobacco necrosis virus is exceptional in giving particles of two sizes, one about 18 mμ and the other 37 mμ in diameter. It is likely that some of these viruses are polyhedra rather than true spheres.

Some bacteriophages (viruses that attack bacteria) are morphologically more complex than any yet found infecting flowering plants. Shaped like sperms or tadpoles, with a pronounced head and tail, they have minute threads resembling flagella protruding through the tails; their heads are larger than most plant viruses and, when prepared critically for examination, seem undoubtedly to be polygons and not spheres. As with the plant viruses, the only constituents identified in them are nucleic acid and protein, but the nucleic acid is of the deoxyribose type instead of the ribose type that occurs in all the plant viruses yet analysed, that is to say it contains a different sugar and thymine instead of uracil. It seems, too, less appropriate to call the bacteriophages nucleoproteins, for there seems no close combination between the two components; the head is apparently a bag of protein containing all the nucleic acid, and the tail is also protein but of a different serological type from that of the head.

Despite the apparently gross morphological differences between plant viruses and bacteriophages, the two may share some structural similarities. For example, the spherical particles of turnip yellow mosaic virus seem also to carry their nucleic acid inside a wrapping of protein. Evidence for this comes from the fact that extracts from infected plants regularly contain two kinds of specific particle, both of the same size, with the same electrophoretic mobility and the same serological activity. They differ in weight and so can be separated by differential centrifugation. The heavier ones contain protein and nucleic acid; the lighter ones are protein only and are not infective. As electric charge and serological specificity are properties determined by the surfaces of particles, the similarities in these properties provide good evidence that the outside of the heavier ones consists of only protein and that their nucleic acid is carried internally.

Similarly, in the rod-like tobacco mosaic virus the nucleic acid also

occurs towards the centre of the particle. When this virus is appropriately treated with a warm detergent, the particles break down from their ends; the protein peels off leaving a core of material protruding from the ends of the particles, material that is largely even if not wholly nucleic acid because it is destroyed by pancreatic ribonuclease but not by proteolytic enzymes (fig. 4). Also, when this virus is disrupted with alkali, which separates the protein from the nucleic acid, some of the protein fragments produced are of the same general size and shape as the cross section of the virus particles, and when seen end on they show central holes, presumably the sites of the nucleic acid in intact particles (fig. 4). When they are acidified or precipitated with ammonium sulphate, such protein fragments recombine to form rods resembling virus particles. X-ray studies of such rods and of intact virus have given much information about the position of the nucleic acid and about the general structure of the particles. The seemingly rigid rod is a hollow tube, with a deeply grooved exterior. The inside of the tube is lined with a thin layer of protein, and the nucleic acid has its phosphate-sugar back-bone at a radial distance of about 4 mμ from the centre of the tube, where it is deeply embedded in protein. The protein is composed of sub-units, which various lines of evidence suggest to be of a size equivalent to a molecular weight of about 18,000, and these are regularly arranged in a spiral about the long axis of the tube, with probably 49 sub-units in three turns of the spiral, and the chain direction of the nucleic acid is related to the spiral arrangement of the protein sub-units. Fig. 5 is a photograph of a model of tobacco mosaic virus showing what current knowledge suggests about its structure.

Much more is known about the structure of tobacco mosaic virus than about that of any other, but there is no reason to think that it is exceptional. Indeed, all those that have been examined critically have been found to contain protein sub-units arranged in a regular pattern, and there is some evidence that some others with rod-shaped particles are also hollow tubes.

Different viruses contain characteristically different ratios of nucleic acid to protein; the anisometric ones are only 6 per cent or less of nucleic acid, whereas in different ones with spherical particles the proportion of nucleic acid ranges from about 18 per cent to 40 per cent. The nucleic acid of all the plant viruses yet analysed contains the same four purines and pyrimidines, but each contains them in characteristic proportions. These proportions are constant in different strains of one virus, although the aminoacid composition of different strains may differ. The aminoacid composition of unrelated viruses, however, differs more than does that of different strains of one virus.

There are several treatments that inactivate spherical viruses but not those

with anisometric particles; such treatments destroy infectivity without disrupting the particles or destroying their serological activity, so they seem to act on the nucleic acid rather than the protein. Whether this difference in behaviour of the two viruses depends on their structural differences, that is whether the protein arrangement in anisometric particles better protects the nucleic acid from effects of the environment than in the spheres, or whether it depends on the different quantities or intrinsic stabilities of the nucleic acids in the viruses, is unknown.

THE PROCESS OF INFECTION

Current ideas on what happens when virus particles infect higher plants are greatly influenced by the behaviour of bacteriophages, about which there is much more precise knowledge. To assess whether it is at all possible to extrapolate from results with bacteriophages, similarities in behaviour must be established, and on first sight it is the differences that are most obvious. For instance, in addition to containing different kinds of nucleic acid, there is the striking difference between them that, whereas plant viruses seem able to invade their hosts only through wounds, bacteriophages do so unaided. They do this by attaching themselves tail first to susceptible bacteria, at first loosely but then soon irreversibly. The tail then seems to make a hole in the cell wall, through which passes the nucleic acid, but little if anything else, and the empty head and tail remain attached to the outside.

For the first half of the period between infection and the time when the bacteria would lyse and liberate new bacteriophage particles, extracts made by artificially disrupting cells are not infective, and neither serology nor electron microscopy detects any material that can be directly related to bacteriophage particles. This "eclipse" phase, however, is not one of inactivity. The nucleic acid metabolism of the bacteria changes, with infections by some bacteriophages that contain 5-hydroxymethylcytosine, to such an extent that this substance is now made though it is not by uninfected bacteria. Coincident with or soon after the change in nucleic acid metabolism, the protein synthesis also takes new directions. Infective extracts are first obtained early in the second half of the period between infection and lysis, at the time the first fully formed bacteriophage particles become evident, and from then on infectivity and the number of such particles both increase linearly with time until the bacteria burst. Shortly before infective particles are formed, material with the serological specificity of the bacteriophage becomes detectable and electron microscopy also then shows the presence of, first, particles of a size similar to that of bacteriophage heads and, next, some with tails but still lacking nucleic acid and infectivity. These are almost certainly precursors of mature bacteriophages, and have themselves

been built by the accretion of specific sub-units synthesized earlier. The various components are made separately, the nucleic acid perhaps by replicating itself, but the proteins by a synthesis they do not direct, and the new bacteriophage particles are formed by a final process of assembling components that is essentially different from multiplication.

With the plant viruses there is no direct evidence that infection necessitates the separation of the protein from the nucleic acid; nor that the protein plays any active part in initiating infection comparable to that of the bacteriophage's tail. Indeed, that the protein is not essential is shown by the fact that preparations of nucleic acid from tobacco mosaic virus can be infective. However, these preparations are only a fraction as infective per unit of phosphorus as is intact virus, and they rapidly inactivate in conditions harmless to normal virus. The infectivity of the nucleic acid can be stabilized and increased by recombining it with protein. This increase could mean no more than that the protein protects the nucleic acid from inactivation by ribonucleases or other hazards encountered when it enters cells, but it could also mean that the protein plays some more active role in establishing the nucleic acid safely in some essential multiplication site.

There is evidence from many kinds of experiment that viruses become unstable soon after they are inoculated to leaves, and most of this is compatible with the idea that an initial step in infection involves the nucleic acid separating from the virus protein. For instance, rubbing leaves with pancreatic ribonuclease soon after they have been inoculated with a virus prevents infection from occurring, but rubbing a few hours later does not. Also, one of the first detectable effects of infection is an increased resistance of the virus to inactivation by ultraviolet radiation. When leaves are inoculated with intact tobacco mosaic virus, this increase occurs only after some hours, whereas with nucleic acid as the inoculum it occurs almost immediately. The increase is most plausibly interpreted as meaning that the virus, or at least its infective part, has become protected from inactivation because it is now associated with other material that absorbs ultraviolet radiation, and the fact that the nucleic acid does so sooner than intact virus is *prima facie* evidence for the idea that the delay with intact virus represents the time taken for some system in the host cell to disrupt the virus into protein and nucleic acid.

Evidence of changes in the state of potato virus X particles soon after they enter leaves comes from experiments on photoreactivation, that is the ability of visible light to counteract the damage done by ultraviolet radiation. The extent to which irradiation decreases the infectivity of virus preparations depends on the conditions to which plants are exposed soon after they are inoculated, and is much less when plants are kept in the light than when they are kept in darkness. Exposing the irradiated virus preparations to

visible light does not affect their activity, so the effect is obviously indirect, operating through some light-sensitive system in the host, most likely the same system that counteracts damage by the radiation to leaf cells. By exposing plants inoculated with irradiated virus to periods of light and darkness at different times after inoculation, two changes in the state of the infecting particles can be detected. At first the virus is unaffected by light, but about 1 hr after inoculation many particles become photoreactivable. If, though, the leaves are not exposed to light within the next hour, the particles lose their newly acquired ability to respond to light and are permanently inactivated. Again these results cannot be interpreted certainly, but they fit readily into the story of nucleic acid becoming freed from protein and thus able to be photoreactivated, but simultaneously becoming susceptible to inactivators that destroy it unless it is in a state that allows it immediately to become established and influence cell metabolism.

Similarly, although there is no conclusive evidence that the nucleic acid and protein are produced separately in infected plants and then finally assembled into complete virus particles, there is much that is compatible with the idea. Obviously, once the requisite materials exist, their assembly calls for no very complex process, for fragments of protein produced by exposing tobacco mosaic virus to alkali readily reassemble and recombine with nucleic acid *in vitro* to give rod-shaped, infective particles. There is, too, little doubt that at least the requisite protein occurs free in extracts from infected plants. When such extracts are centrifuged at speeds greater than 50,000 rev/min, the virus sediments but the supernatant fluid still contains some protein that is serologically related to tobacco mosaic virus. This contains little or no nucleic acid, and in many ways resembles the protein fragments produced by disrupting the virus with alkali, including the ability to aggregate and combine with nucleic acid to form long infective rods. Experiments in which infected leaves were exposed to $C^{14}O_2$ gave results suggesting that these small proteins, like the protein-only particles that have already been mentioned as occurring in extracts from plants infected with turnip yellow mosaic virus, are more likely to be precursors of virus particles than to be break-down products from virus particles, but the point is not yet fully established. Similarly, there are claims that, when tobacco mosaic virus is multiplying rapidly, leaves contain more virus nucleic acid than can be accounted for in the number of mature virus particles present, but the evidence is not conclusive.

Despite the many uncertainties, the similarities between the behaviour of tobacco mosaic virus and the bacteriophages are enough to suggest/that, even though there may be many differences of detail, the two probably multiply by processes that do not differ fundamentally. As these two differ chemically and morphologically more than any two plant viruses are known

to differ and yet behave so similarly, it seems safe to assume that many other viruses about whose multiplication nothing is now known also infect and multiply in broadly similar ways.

When leaves of suitable plants are inoculated with a virus and then assayed at intervals for their virus content, there is a period during which either no virus is detected or the infectivity of successive extracts falls. The time at which newly-produced virus becomes detectable depends greatly on the temperature, but it is not until many parenchymatous cells are infected at each infection site. As only epidermal cells are probably infected by inoculation, and infection spreads from the epidermis to deeper cells in about half the time needed to detect new virus, the virus produced in the first cycle of multiplication apparently passes undetected, which is not surprising as the ultimate content of particles per infected cell is of the order of a million, and more than this number is needed per ml of inoculum to get an infection in the test plants used for assays.

Once new virus becomes detectable, the amount in successive extracts increases rapidly, partly because the amount in already infected cells continues to increase for a day or more, but mainly because an increasing number of cells becomes infected. In their ability to move from cell to cell within plants unaided, plant viruses show obvious similarities to bacteriophages invading a whole bacterial culture from one or a few initially infected cells, and it is this ability, rather than the property of multiplication in cells to which they are introduced, that makes them economically important. Many plants, which are now considered to be immune from given viruses, may be susceptible to the extent that the viruses multiply in any cells that become infected at inoculation, but if there is no spread to adjacent cells the plants would show no symptoms and, as we have already commented, multiplication in these initially infected cells would be undetectable. Viruses that do spread from the initially infected cells in some hosts are often restricted to a few hundred cells around the infection site, usually but not always in necrotic local lesions, and in these hosts such viruses are of little or no economic importance. Considering how important is this ability to spread from cell to cell, our ignorance about the process is lamentable. There is no evidence to show whether the virus proteins play any active part, such as does the bacteriophage's tail, in spreading plant viruses from cell to cell; indeed, it is unknown whether the viruses move as nucleoprotein or nucleic acid. It is generally assumed that the movement between adjacent cells occurs along plasmodesmata, but this is not established and viruses seem to move through tumourous tissue growing in cultures, in which there is doubt whether plasmodesmata occur, at about the same rate as they move through leaves. By analogy with the bacteriophage protein, which on its own can lyse bacteria, it is reasonable to expect that the proteins of plant

viruses also have specific activities and they may be responsible for the type of symptoms shown by infected plants.

Individual viruses multiply and spread from cell to cell at different rates, but these differences are small compared with those between the concentrations ultimately achieved in cells by different viruses. Some, of which tobacco mosaic virus is an example, reach high concentrations that, provided conditions remain constant, are maintained over long periods. This virus can amount to one-half or more of the total protein in infected leaves, and, as Fig. 6 shows, the virus particles become the predominant components in the cytoplasm of cells; the hair cell, of which Fig. 6 shows a section of only a part, was calculated to contain about 6×10^7 virus particles.

Only viruses that are unusually stable *in vitro* reach high concentrations *in vivo*, and it seems that, once such virus particles are formed, they are largely divorced from the cell metabolism; that the divorce is not complete, however, is suggested by the fact that their numbers can be increased or decreased by altering the conditions under which infected plants are kept. The viruses that are less stable *in vitro* fall into two types. One, of which potato virus Y is an example, reach a maximum concentration that, although small compared with tobacco mosaic virus, is maintained for long periods; these, like the "normal" nucleoproteins, are probably continually being broken down *in vivo* and the constant amount maintained in constant growing conditions represents a balance struck between degradation and continuing synthesis. The second type, of which alfalfa (lucerne) mosaic virus is an example, reach a high concentration in newly-infected cells, but their concentration then falls rapidly with increasing time; it seems possible that infection with these may stimulate cells to produce virus inactivators, but if this happens the inactivators are not sufficiently active in ordinary growing conditions to free plants from infection. Plants infected with this second type of virus usually first show severe symptoms, which decrease in severity with increasing time as the virus content falls. With viruses that maintain a steady concentration, symptoms also usually continue at their initial level of severity.

In infections of any given plant with a specified strain of a virus, the intensity of symptoms shown is correlated with the virus content of the plants, and changes in growing conditions, such as the temperature at which infected plants are kept, that affect the virus content, also correspondingly affect the symptoms. There is, though, no correlation between the severity of symptoms produced by different viruses or virus strains and the extent to which they accumulate in infected tissues. In tobacco, for example, there are strains of tobacco mosaic virus that cause only a very mild disease, though a kilogram of leaf may contain as much as 4 g of the virus, whereas tobacco etch virus causes a crippling disease although it does not reach more than

one-thousandth this amount. Hence symptoms do not happen simply because aminoacids and nucleotides, which might otherwise have gone to make normal nucleoproteins, have been diverted into virus, but represent specific interactions between metabolic processes of the host and activities peculiar to individual viruses and virus strains.

THE SPREAD OF VIRUSES

Viruses are important and prevalent only in plants in which they cause systemic infections, that is, in plants in which they can move from one infection site to invade all or almost all the vegetative tissues. In such plants, too, it is usual for viruses to survive for as long as any vegetative parts of the plant remain alive. Hence, when perennial plants once become infected with a virus that does not cause a lethal disease, they remain perpetually infected, and even when they themselves may not be seriously affected, they provide continuous reservoirs of viruses that are harmful for other plants. Also, any method of vegetative propagation, whether natural, by bulbs, corms, tubers, runners, and the like, or artificial, by cuttings and grafting of scions, will perpetuate in the progeny any viruses present in the parent plants from which the vegetative parts came. By contrast, it is rare for viruses to invade either the pollen mother cells or the egg cells and, although a few viruses are seed-transmitted this is exceptional and most plants raised from seed start their lives virus-free. It is largely for the reason that sexual reproduction usually cleanses plants from their virus diseases whereas vegetative reproduction does not, that the first enjoys the reputation of being an intrinsically invigorating process and the second of being debilitating. Also, the abandonment after some years in cultivation of desirable clonal varieties, which are often said to have "degenerated," "become senile" or "run-out," is usually the result of their becoming infected either with a virulent virus or with a number of viruses that together cripple the variety.

Plants are much less well equipped than animals to deal successfully with virus diseases. They resemble one another in as much that the older they are the more viruses they are likely to have been infected by, but there the similarity ceases. When animals contract a virus disease that is not lethal, they produce antibodies against the virus and not only recover from the attack but are usually immune from a second one. Thus, each disease may be an unpleasant occasion, but it does not last long, happens only once, and rarely do any two happen together. Plants are not so fortunate; they do not recover from their "nursery" ailments, but once infected they remain so, and at any one time they have all the virus diseases they have contracted during their whole lives. Stocks of many clonal varieties reach the state comparable to that of a, fortunately mythical, person who simultaneously and continuously had mumps, measles, chicken pox, influenza, and the

common cold. It is small wonder that they are "debilitated" and crop poorly, or that it was the virus diseases of such plants as the potato, strawberry, and raspberry that first demanded research on methods of control.

The mechanism whereby most viruses are prevented from invading the seed is unknown, but the rate at which clonal varieties lose their vigour made some such mechanism an evolutionary necessity, otherwise the many species in which virulent viruses spread rapidly could not have survived. It may be relevant that apical meristems also seem to resist invasion; some viruses do not occur in this region at all, and those that do are in much smaller amounts than in older, differentiated cells. Hence, it seems that conditions in dividing cells, perhaps the synthesis of nucleic acids for the new nuclei or cytoplasmic components, may preclude either the entrance of viruses or their survival should they enter. Some indirect evidence for the idea that the synthesis of host nucleic acids may be concerned comes from the fact that leaves also resist infection, by viruses to which they are normally susceptible, while they are recovering in visible light from the effects of exposure to ultraviolet radiation, which presumably mainly damages nucleic acids.

Some of the plant viruses are soil-borne and may have methods of survival yet to be discovered, but most viruses have only a fleeting existence outside of their hosts. As we shall see later, a few can survive indefinitely in insects, but the survival of most depends on the survival of infected plants. Most annual plants raised from seed not only start life virus-free, but when they become infected they also provide only temporary sources of infection for other plants. Viruses that infect only such plants must have both an efficient method of spread and a continuous and over-lapping succession of such plants to ensure their survival. Most have avoided this necessity by having in their host range perennial plants, or species that are propagated vegetatively, and in which they are safely perpetuated for as long as the plant or clone remains alive. No doubt some viruses have been introduced into new regions by the distribution of living annual plants, but this is probably unimportant compared with the number of occasions viruses have been moved over long distances in living tissues of plants used for vegetative propagation. Similarly, the sources of viruses for annual plants are, as often as not, perennials, biennials, or vegetatively propagated plants, in which the virus has survived through the period when the annuals were not growing.

SPREAD BY ANIMALS

Different viruses spread from infected to healthy plants in a variety of ways, some from simple mechanical contact between the two, but most of the known ways demand the intervention of a third party, usually an animal. Man's most important behaviour has probably been to carry infected plants

over long distances and so introduce viruses into places they otherwise would never have reached, but he also does much transmitting from plant to plant. This he does most efficiently by such practices as grafting and budding, which are infallible and are the only methods known whereby many viruses are spread, but he also often unwittingly acts as a vector of such readily transmissible viruses as tobacco mosaic and potato X, which he gets on his hands, tools and clothes in juice from infected plants and then transfers to healthy plants.

Most other vectors of viruses are more discriminating than Man. Those so far discovered are mostly insects, and mostly among types that feed by sucking rather than biting, but some viruses can be spread by biting insects and some by other kinds of arthropods, such as mites. Transmission is a specific action and not something any insect can do. There are two kinds of specificity; one kind is reasonably called group specificity and defined by the general statement that no virus transmitted by individuals of one insect group, say the aphids, has also been transmitted by individuals of other groups, such as the leaf-hoppers, white-flies, mealy-bugs, or thrips. The second kind, species specificity, is shown to very different extents by different viruses. Some of the viruses that are transmitted by aphids can be transmitted by many different species, whereas others are transmitted by only a few, as are most of those that have leaf-hoppers as vectors. Even those viruses that can be transmitted by many species of aphids, however, show some vector specificity, for they are not transmitted by all the species that are vectors of other viruses, and some species transmit them more readily than do others.

The behaviour of different vectors differs greatly, and here we can do no more than outline extremes. The differences are most clearly shown in the lengths of time insects take to become infective after starting to feed on infected plants and for which they remain infective. At the one extreme are viruses that can be acquired when aphids feed for a minute or less and can then immediately be transmitted to a healthy plant; vectors of such viruses soon cease to be infective, usually within less than an hour when they feed and within a few hours when they fast. Aphids that have been fasting before they feed on an infected plant transmit these viruses more readily than those that have not, provided that their stay on the infected plant is brief. Increasing their stay decreases their chances of transmitting, a seeming paradox, for the longer they feed on an infected plant the more virus they might be expected to imbibe. However, these viruses seem to be imbibed mainly from the epidermis, and the explanation may lie in the fact that fasted aphids are more likely than unfasted to imbibe from the epidermis, and that after probing for more than a few minutes the stylets penetrate through the epidermis into deeper tissues from which these viruses are less readily

obtained. Only the small amount of virus that is retained in the tips of the stylets seems to be transmitted to healthy plants, which may explain the rapid loss of infectivity and the fact that it is lost more rapidly when aphids feed than when they fast. As all the viruses whose vectors show this type of behaviour can be transmitted by the manual inoculation of sap from infected plants, this sort of transmission might seem to demand no other explanation than the mechanical carriage of infective juice in the aphid's stylets. However, this explanation neglects the specificity of the transmission; not only do aphids fail to transmit some viruses such as tobacco mosaic and potato X, which are the most easy to transmit by inoculation of sap, but with some viruses the specificity is such that a given species of aphid may transmit one strain but not another. Also, there are many examples of viruses changing so that they lose the ability to be transmitted by an aphid that previously was a good vector. Such facts combine to suggest that there may be specific configurations on virus particles that determine whether or not they are absorbed on and retained in an appropriate manner by the stylets of a given aphid species.

The other extreme of behaviour is shown by a few aphid-transmitted viruses and perhaps by all that are transmitted by leaf-hoppers, white-flies and thrips. Most of these viruses are not transmitted by the mechanical inoculation of sap; their vectors need to feed for more than a few minutes on infected plants before they acquire such viruses, and then there is a further delay before they can transmit to healthy plants, but once they become infective many remain so for long periods, some for the remainder of their lives. The "latent" period between acquiring virus and being able to infect another plant varies from as little as one hour with some to several days with others. Transmission of all these viruses seems to require that they pass through the gut wall of the insect, enter the blood and reach the salivary glands, from which they are injected into plants with the saliva secreted by the feeding insects. With viruses such as potato leaf roll and beet curly top, which have latent periods of not more than about a day or so, this period is reasonably assumed to be the time taken for virus ingested from infected plants to circulate around the insect. The length of time vectors of these viruses remain infective increases with increasing length of time they feed on infected plants, and it seems that their vectors contain only the amount of virus they acquire while feeding on infected plants.

With viruses, such as wound tumour and aster yellows, which have latent periods of several days, the position is quite otherwise. Provided their vectors feed long enough to acquire virus, extending their stay on infected plants does not increase their ultimate ability to transmit. There is unequivocal evidence that several of these viruses multiply in their insect vectors, and with these the latent period seems analagous to the period between infecting

plants and the development of infectivity or symptoms; that is, it is the time for ingested virus to become established and multiply enough to become obvious. Nothing is known of the chemical constitution of the viruses that multiply in both plants and insects, but of the few that have yet been examined in the electron microscope, each has the same gross morphology when formed in the two kinds of organisms. The vectors of some of these viruses not only remain infective for as long as they live, but they also transmit virus through their eggs to some of their offspring, and so provide a lasting source of virus. Fortunately, this behaviour is exceptional; the young produced by insects carrying most viruses are born virus-free and become infective only as a result of feeding on infected plants.

The fact that most viruses with latent periods in their vectors are not transmissible to plants by mechanical inoculation of sap is not attributable to their intrinsic instability *in vitro*, because many of them can be successfully inoculated to their vectors. Two explanations can be offered for the failure of mechanical inoculation to infect plants: (1) plant hosts may be more resistant to infection than insect hosts, and the inocula so far used may contain too little virus to infect plants; (2) only deep-seated tissues, perhaps the phloem, may be susceptible to infection by small doses of virus, and these tissues would be reached by the feeding insects but not when leaves are rubbed.

THE CONTROL OF VIRUS DISEASES

The major advances in controlling virus diseases have been with vegetatively propagated plants grown as clonal varieties, notably the potato, strawberry, raspberry, and hop, and are indicated by the health certification schemes now operated to ensure that stocks destined for propagation are free from serious virus diseases. In the United Kingdom, for example, potato crops meant to supply seed tubers are grown separately from the main crops, usually in the north and west, where the climate is less favourable than it is in the south and east for the aphids, mainly the peach-potato aphis, *Myzus persicae* Sulz., that spread potato leaf roll and Y viruses, the two that here are most important in affecting the yield. Aphids arrive later on potato crops in the north and west than in the warmer and drier south-east; they are also fewer and move less often. Because the aphids arrive late, the crops can be examined and any diseased plants identified and removed before viruses spread from them to their neighbours, a practice that maintains the health of stocks there but is valueless in the south-east. Most English farmers now regularly buy new stocks of certified seed potatoes from Scotland or Ireland and as a result the great losses of crop previously sustained have been almost wholly eliminated. The cost of potato virus diseases in the United Kingdom is no longer to be reckoned in lost tons of tubers, but in the cost

of new seed tubers and their transport to the individual growers, in total, a sizeable annual bill of more than £5,000,000.

As most of our common virus diseases are spread by insects and there are now insecticides that deal effectively with most kinds of insect pests, it might seem that problems of controlling virus diseases were solved. Unfortunately, this is not so, for the control of insects as vectors of viruses is more difficult than their control as pests. There has been some success with some virus diseases, but with others the benefits from spraying have been too slight to suggest that current insecticides will be generally useful. It is worth considering what factors limit their usefulness.

The incidence of virus diseases in a crop can increase in two ways, (1) because plants become infected by insects arriving already infective and (2) because insects spread viruses from infected plants in a crop to their healthy neighbours. As no current insecticide kills rapidly enough to prevent incoming aphids from feeding on the first plants on which they alight, spraying will not stop spread by method (1) and the extent to which it is affected will differ with different viruses, depending on their method of transmission and the behaviour of their vectors. Obviously it cannot be expected to decrease the number of plants that become infected by viruses whose vectors remain infective for only short periods, because the insecticide will not kill incoming aphids before they have done all the transmitting of which they are capable. With viruses whose vectors remain infective for long periods, however, there are better prospects of some effect, particularly when the vectors are insects that move frequently, because although the insecticide may not kill incoming insects quickly enough to prevent them from infecting the first plants on which they feed, it can prevent them from infecting a series of plants, which they otherwise might do.

Similarly, with the second method of spread, the effect of persistent insecticides depends greatly on the virus-vector behaviour. Spraying can almost completely prevent the spread from plant to plant within crops of viruses whose vectors require some hours or days to become infective, but it is much less effective against viruses whose vectors become infective immediately after a brief feeding period on infected plants. Hence, when potato crops are protected with a suitable persistent insecticide while aphids are active, the spread of leaf roll within the crops can be stopped, whereas that of potato virus Y may be unaffected or only slightly decreased, even though both viruses are spread by the peach-potato aphid.

To assess whether spraying is likely to control a virus disease, it is necessary to know, therefore, not only the habits of the vector in transmitting, but also something of the epidemiology. In summary, the possibility of control is worth putting to test when most of the spread is from infected to healthy plants within a crop, and particularly when the prevalent viruses are of the

type that have latent periods in their vectors; but when spread is mainly into the crop by insects that acquire viruses elsewhere, or the viruses have no latent periods in their vectors, then spraying a crop with insecticides is likely to be of little or no avail.

Even this limited use of insecticides has become possible only since the discovery of substances that remain active for some days after they are sprayed on plants, for substances that effectively deal with insects as pests are not necessarily also those useful against insect vectors. To control a pest requires only that its numbers are kept below the level at which their feeding directly damages plants, which with aphids means, in effect, limiting the numbers of wingless ones that are produced within the crop. But wingless ones are relatively unimportant as vectors of viruses. The spread of viruses cannot be computed from knowing the number of potential vectors and of the initial sources of infection, for spread requires that an insect moves from infected to healthy plants and the activity of the insects is an equally important factor. Of two aphid species, equally able to transmit a virus in transmission experiments, one that moves more than the other in field crops will do more spreading of viruses than the other even though it occurs in much smaller numbers; sugar beet crops, for instance, can be blackened with *Aphis fabae* without yellows becoming prevalent, whereas a much lighter infestation with the more active *Myzus persicae* can infect whole crops. That winged aphids spread viruses between crops is too obvious to need stressing, but they also do most of the transmitting from plant to plant within a crop, although they are numerically only a small part of the total population. To deal with aphids as pests, all that is necessary is to spray after the infestation has started, to keep the population of wingless ones reaching harmful levels. But to control aphid vectors means protecting the plants with an insecticide that will kill winged ones when they arrive in the crop, which is a much more difficult task. Nevertheless, there have been some successes; for example, careful spraying of sugar beet has decreased the severity of yellows attacks and given increased yields that represent handsome returns on the cost of spraying; similarly, spraying has controlled leaf roll in potato crops in south and east England and allowed home-saved tubers to be used as seed at less cost than that of buying new seed.

The use of insecticides to control virus diseases is still in its infancy and there is no doubt that it will increase. However, until substances are found that kill more quickly, and remain active on or in plants for longer, than those currently available, it is vain to expect that insecticides will provide adequate and economic answers to all virus diseases. At present, for many virus diseases, the only control measures that can be advocated are sanitary precautions that apply generally to the control of other kinds of infectious diseases; to destroy sources of infection, to use resistant or tolerant varieties,

to plant only healthy stock, and to plant it as far as possible from infected stocks. There are some simple precautions that are valuable in checking the spread of some viruses, such as raising sugar beet plants for the biennial seed crop in barley, which protects the beet from invasion by aphids, but it would be out of place to itemize such things in a general article such as this.

Fortunately the provision of healthy planting material is now an easier matter than it was. Not only are there better methods for diagnosing infection, particularly serological tests, which can give unequivocal answers rapidly, but there are also methods whereby virus-free clones can be regenerated from infected varieties. Many viruses that maintain themselves indefinitely in plants growing at normal temperatures cannot do so at temperatures between 35 and 40°C. Keeping either tubers or growing plants continuously in such conditions for some days or weeks has freed various kinds of plants from many different viruses (fig. 1), and the clones so produced have been multiplied to replace the infected ones previously in cultivation. Usually heat therapy is applicable only to producing initial stocks for multiplication, but with sugar cane, in which a brief dip in hot water is enough to free infected cane from ratoon stunting virus, the treatment is now given routinely to material for large-scale plantings.

Although heat therapy is widely applicable, viruses are individual things and not all of them are inactivated completely *in vivo* at temperatures their host plants can withstand. Another treatment has been devised to free plants from some of these, based on the knowledge that viruses often fail to invade the apical meristems of infect plants. Thus a virus-free clone of the potato variety King Edward, of which all commercial stocks contain paracrinkle virus, has been produced by excising a stem apex, which was cultured on agar medium until it grew into a plantlet able to feed through its own roots. Meristem culture, like heat therapy, has not succeeded in eliminating all the viruses against which it has been tried, and the happy position has not yet been reached in which it is possible to say that no useful variety of any plant need any longer be abandoned because the whole stock has become virus-infected. However, that position may not be far off, for combining the two treatments, so that the virus content is decreased by high temperatures before meristems are exercised, may succeed when neither treatment does alone. Also, there are other methods than heat treatment that affect virus concentration, and these may find uses in combination with either heat treatment or the culture of apical meristems. For example, although as yet no fully successful chemotherapeutic treatment for infected plants has been developed, some analogues of purines and pyrimidines, of which thiouracil and azaguanine have been most studied, not only greatly interfere with the multiplication of various viruses, but can decrease the

concentrations of some in infected tissues; their potential applications are too obvious to need stressing.

FUTURE DEVELOPMENTS

Knowledge about viruses and virus diseases now accrues at an unprecedented rate, which is likely to increase rather than decrease in the near future. Even a few years ago present ideas about the structure and multiplication of viruses could not have been forecast, and it would be only vain now to engage in crystal-gazing in the hope of anticipating what new concepts will come from future discoveries. What is, perhaps, more useful is to pose some of the problems and questions that most urgently need answering.

First, virus composition; to tell any general story, it is still necessary to extrapolate from knowledge on only a few of the many known viruses. As these few differ in many respects and yet all have a similar general composition it is probably a safe assumption that many others are also nucleoproteins, but it would still be rash to assume that all are. And, even if all plant viruses are nucleoproteins, do they all contain ribose nucleic acid? For example, do some of the viruses that multiply in their insect vectors resemble those that cause diseases in insects and contain deoxyribose nucleic acid? This last question may soon be answered, but the chemical composition of many viruses seems likely long to remain unknown, for they are so unstable and occur in such small quantities that the chances of obtaining enough of them by current techniques in a state suitable for analysis seems slight. However, new techniques may well overcome what now seem insurmountable difficulties.

Secondly, the process of infection and virus multiplication: a plausible story can now be told of the infecting virus particles being disrupted into nucleic acid and protein, of the nucleic acid becoming a part of the host system, multiplying and determining the synthesis of protein with which it then combines to give new mature particles. But is it true? Some more direct evidence than any yet produced is needed before it can be accepted as certain that infection with plant virus entails the protein and nucleic acid separating. And if it does, where does it happen? At the cell wall or the edge of the cytoplasm? Or as a necessary preliminary to entering some specific cell component such as the nucleus, plastids, or mitochondria? Further what protects the virus nucleic acid from nucleases and other inactivators contained in host cells? And, a question that has implications extending far beyond pathology, although perhaps more likely to be answered from virus research than elsewhere, how does the structure of nucleic acid influence the arrangement of aminoacids to yield specific proteins?

Thirdly, the spread of viruses: despite the many discoveries, the ways in which some viruses spread from plant to plant are still unknown, and

new kinds of vectors almost certainly still await discovery. Most pressing, perhaps, are the problems raised by soil-borne viruses, whose prevalence and importance are becoming increasingly obvious. How do they persist and spread? We have little knowledge except that one virus affecting the vine seems to be transmitted by nematodes; but this is only a start, and the organisms in soil may prove to be a source of virus vectors as varied as those known to be active above ground.

Fourthly, the control of virus diseases: much has been achieved, but much more still remains to be done before the immense losses from virus diseases can be prevented. This is true even with annuals and short-lived crops, but it is perhaps for dealing with virus diseases of trees that new measures are most needed. Diseases in annual crops at most mean only a loss of that year's income, but infection of trees means a total capital loss when the disease is fatal and a continuing annual loss of crop when the disease is chronic. The losses from such diseases as swollen shoot of cacao, phloem necrosis of elm, peach yellows, and many other killing or crippling diseases of other fruit trees, are beyond computing. Some of these diseases may yield to new developments in the use of insecticides to control vectors, but it is perhaps for tree diseases more than any others that work on chemotherapy is demanded. The fact that most of the substances that show some promise in this direction damage the host plants need not be too discouraging; to save the life of a fine elm, or to restore a fruit tree in its prime to its full cropping power, is well worth some cost and some temporary setback to growth.

Research on viruses and virus diseases clearly presents plenty of problems, and of a variety to attract workers with a wide range of interests and training. Their solution presents a challenge that cannot be avoided, for not only will it increase production and enable the expanding human population to be fed, but it will also do much to unravel many of the processes, such as replication and protein synthesis, that are basic to biology.

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BACTERIA

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INTRODUCTION

1. *What are Bacteria?*

It will be observed that this article is entitled "Bacteria" and not "Schizomycetes," although this is supposedly the correct name of the group, whereby they are defined as a class of fungi characterized by being capable of reproducing solely by binary fission. But since the bacteria are quite distinct from the true fungi, and most decidedly do not confine themselves to reproduction by simple fission, the name and the classification are alike inappropriate. Let us, then, refer to them as bacteria.

It might be rather less than tactful to go too deeply, at this point, into the question of whether bacteria are plants at all, but if the definition of a plant (is there a definition?) is sufficiently elastic to include the fungi and the blue-green algae, especially the latter, there is no reason why it should not include the bacteria. Indeed, the only real qualification for inclusion in the vegetable kingdom is the rather negative one of being quite ineligible for the animal kingdom. A good case might be made out for the establishment of a few more independent kingdoms, including one for the bacteria, but this is hardly an auspicious occasion for insisting upon it.

Bacteria are among the most versatile and adaptable of all the main biological groups. They include photosynthetic and chemosynthetic autotrophs; saprophytes capable of decomposing any imaginable organic materials; parasites, pathogens, and symbiotes of plants, animals and other protista; and even predators. Many bacteria double two or more of these roles.

In morphology, bacteria may cover a smaller range than the animals or the green plants, but it is by no means as small as once was believed. The simplest, but probably not the most primitive, bacteria are tiny coccal cells (most cocci, by the way, are *not* single cells[4]) without external structures. The most complex bacteria are probably the *Streptomyces*, which superficially resemble small moulds, having multiple cells, subterranean and aerial hyphae, and chains of spores. Indeed they have often been claimed to be true fungi, but their cytology[21] and the chemical composition of their cell walls[11] are both quite decidedly bacterial in pattern.

Bacteria do indeed have certain typical characteristics whereby they may

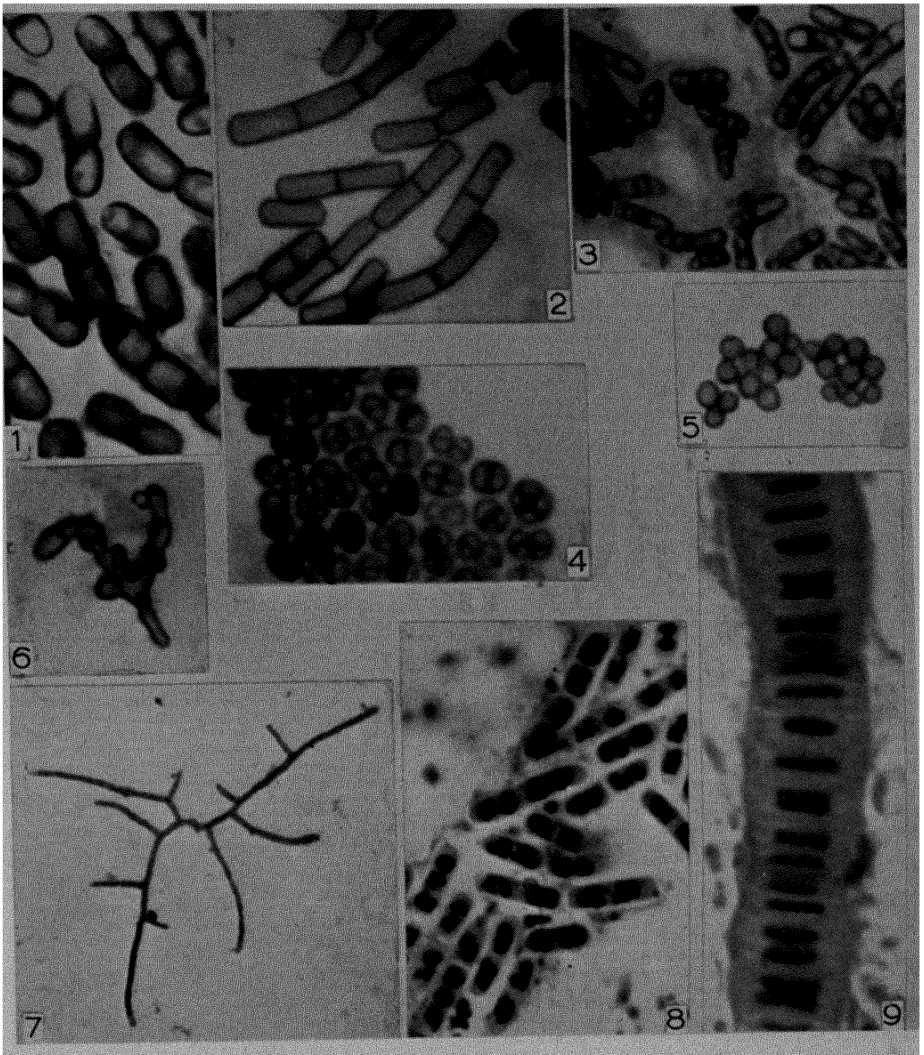


PLATE 1

Figs. 1–6. Cell walls of bacteria. Stained by Hale's method. × 3000 (reduced to 8/10).

Fig. 1. *Azotobacter chroococcum*, showing ingrowth of cross-walls at cell division.

Fig. 2. *Bacillus cereus*, moderate multicellularity.

Fig. 3. *Corynebacterium diphtheriae*, extreme multicellularity.

Figs. 4, 5. Gram-positive cocci, multicellular and unicellular types.

Fig. 6. *Bifidibacterium bifidus*, showing budding and branching.

Fig. 7. *Mycobacterium lacticola*, colony impression, showing branching. Fuchsin. × 500 (reduced to 8/10).

Fig. 8. *Bacillus cereus*, nuclear bodies by Robinow's modification of the Feulgen reaction. Paired transverse nuclear rods are seen; one or two pairs to each cell (compare fig. 2). × 3000 (reduced to 8/10).

Fig. 9. *Oscillospira* sp., nuclear bodies, as in fig. 8. Because of the large size of this micro-organism the nuclei are well seen as paired rods. × 2000 (reduced to 8/10).

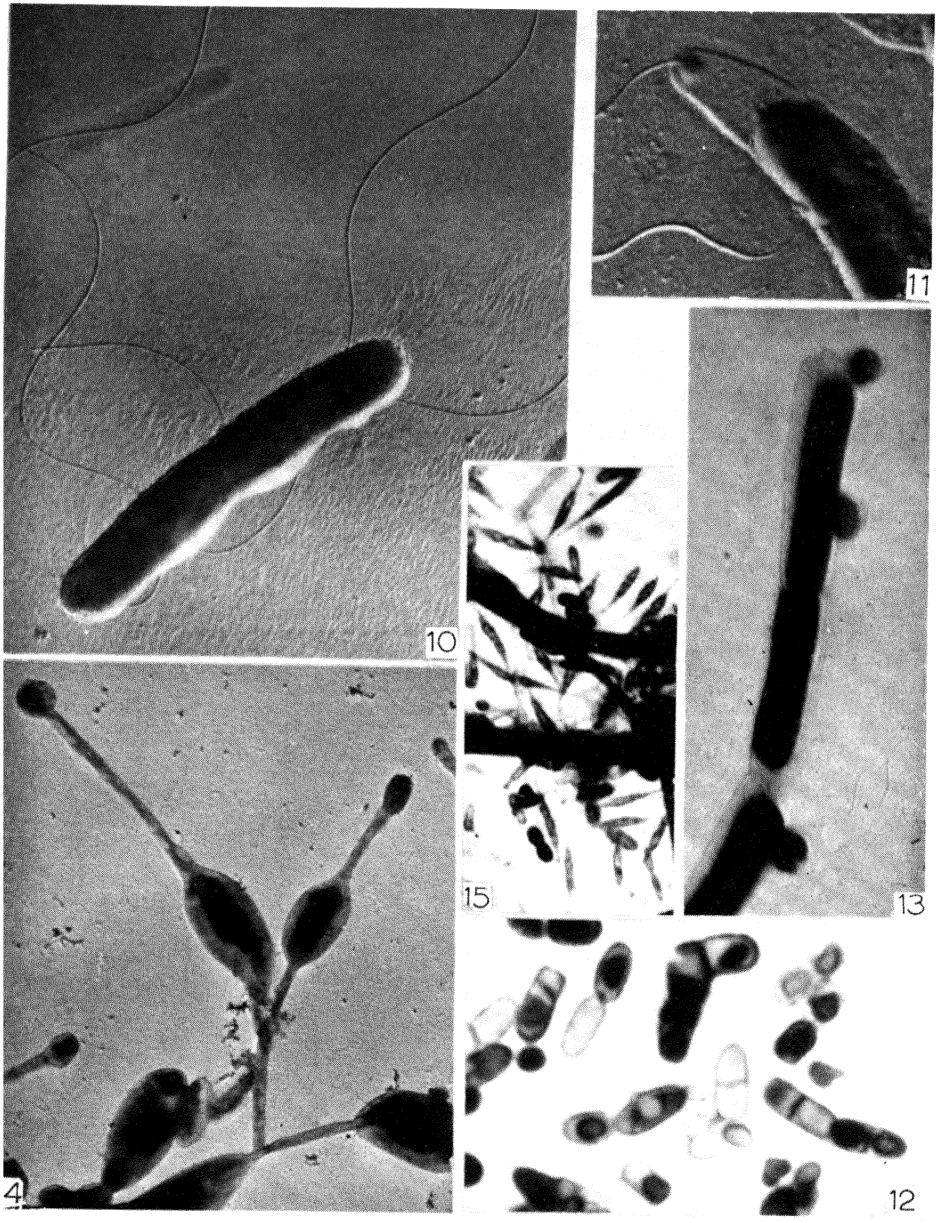


PLATE 2

Figs. 10, 11, 13, 14. Electron micrographs, gold-shadowed. Figs. 12, 15, photomicrographs.

Fig. 10. *Bacterium coli*, unicellular bacterium with peritrichous, unifibrillar flagella. × 16,000 (reduced to 8/10).

Fig. 11. *Spirillum* sp., showing blepharoplast near cell boundary. × 20,000 (reduced to 8/10).

Fig. 12. *Azotobacter chroococcum*, showing endospores. Janus green. × 3000 (reduced to 8/10).

Fig. 13. *Rhizobium* sp. with swarm cells. × 10,000 (reduced to 8/10).

Fig. 14. *Rhodomicrobium vanneilli*, a stalked autotroph, reproducing by budding. × 10,000 (reduced to 8/10).

Fig. 15. *Caulobacter* sp. attached by their stalks to filaments of *Sphaerotilus discophorus* (an iron bacterium), unstained, × 1500 (reduced to 8/10). Compare diagram 3, E.

also highly diagnostic of the group, they are monofibrillar and the blepharoplast is on or near the cell membrane (Plate 2, figs. 10, 11). Bacterial flagella are aligned *away* from the direction of motion. Complex flagella, midway between these and the compound flagella of other protista are found in certain spirilla, which for this and other reasons are believed, at least by the present writer, to be primitive forms[4]. Reproduction by more complex methods than budding or fission is common in bacteria. Many species produce tiny motile gonidia, and almost all have a resting or distributive stage which may be more or less spore-like (Plate 2, figs. 12, 13), and some stalked sessile aquatic bacteria show alternation of generations between sessile and mobile stages (Plate 2, figs. 14, 15). These general questions of life-history and reproduction have been discussed at length elsewhere[4], and a very much greater selection of typical appearances might readily be illustrated, if to do so were not rather beyond the scope of this article.

2. *The Relationship of Bacteria to Other Groups*

In the preceding section it has been indicated that bacteria have been regarded as a class of fungi and, simultaneously, as related most closely to the blue-green algae, but that neither of these suggestions is capable of standing up to very close examination. To obtain a clearer idea of the relationship between bacteria and other living organisms it is of importance to consider the interrelationships of bacteria among themselves. One of the best-known schemes designed to produce a workable classification of bacteria, based upon evolutionary principles, is that of Kluyver and van Niel[22]. This commences with the superficially attractive assumption that the simplest morphological type of bacterium, a coccus, may be considered to be the primitive, ancestral form, from which rod-shaped, spiral and branched bacteria are independently derived. However, this hypothesis neglects the fact, which was not well understood at that date, that most cocci are very far from simple in morphology (Plate 1, fig. 4) and may be subdivided into quite a large number of tiny cells, and at the same time, they tend to be nutritionally rather specialized and exacting, which is an improbable character to find in a primitive ancestral group. Apart from this consideration, the theory of Kluyver and van Niel appears to require a dual or multiple origin for such fundamental and widespread organelles as flagella and spores, which is again rather unlikely.

The autotrophic bacteria, whether photosynthetic or oxidizers of iron, sulphur, or nitrogen, might reasonably be supposed to be among the more primitive members of the group, and among these the great majority are either spirilla, vibrios, or pseudomonads[7], that is, more or less spiral, polar flagellate bacteria. This is the morphology of most aquatic bacteria also, and as was mentioned in the previous section, some of these have

just as all other groups except the blue-green algae seem to have done (Diagram 1).

The bacteria share, however, with the blue-green algae alone of the five major developmental lines, the absence of a mitotic spindle. Plants, animals, and fungi alike have each their own characteristic type of spindle, although

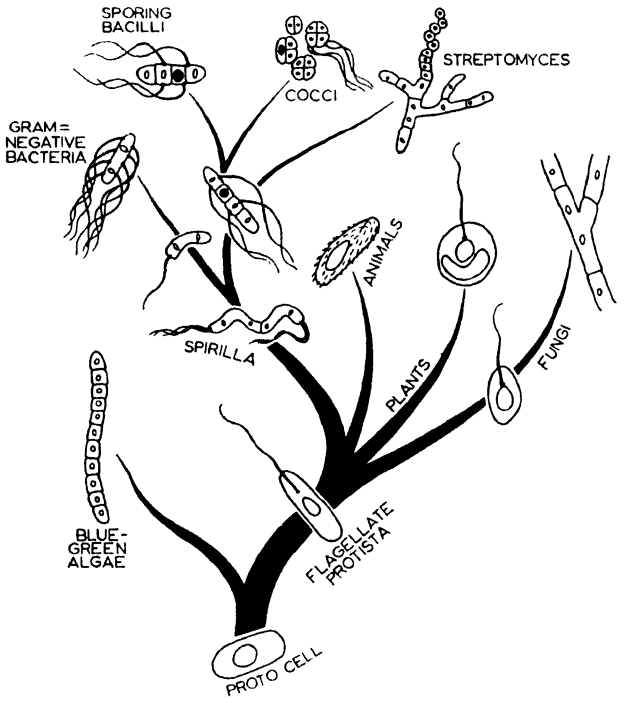


Diagram 1. The relationships of bacteria to other living groups (suggested scheme). Explanation in text.

in some cases, for example, the yeasts, it may have been lost secondarily. Nevertheless, although the possession of a spindle is characteristic of all these flagellate groups it is not found in the euglenids[24], and may therefore be assumed to have been evolved at a later date than the flagellum itself. The role of the blepharoplast as a mitotic centriole provides a hint of what may have been the order of events. It is certainly true that in the two major groups which have evolved without mitosis, the blue-green algae and the bacteria, the former have no flagella, and hence no blepharoplasts, whereas the latter have blepharoplasts which are most closely associated, not with the nucleus but with the cell envelopes (Plate 2, fig. 11). It has been claimed on various occasions that bacterial nuclei divide by a typical mitotic process, the most recent claims being those of DeLamater[12, 13], etc., but the validity

flagella which arise in closely-knit bunches from single granules[16], and may thus be regarded as intermediate in this respect between other bacteria and flagellate protista. Thus it is reasonable to conclude that the polar-flagellate, spiral water bacteria bear the closest resemblance to the ancestral type; and in confirmation of this conclusion, it has been observed that very many rod-shaped bacteria are, in fact, slightly spiral[34]. This general hypothesis concerning the morphology of the ancestral bacterial type was first proposed by the present writer eight years ago[3], and I understand, although I have not yet seen it, that the forthcoming edition of Bergey's *Manual* has now arrived independently at the same conclusion!

From the spirilla, the vibrios, pseudomonads and thence the typical, peritrichously flagellate bacteria may readily be derived in an evolutionary series, and it is notable that this hypothetical process involves, as in other groups of living creatures, a progressive adaptation from an aquatic to a terrestrial existence, culminating in such an organism as *Proteus*, which possesses hundreds of flagella, peritrichously arranged, whereby it is enabled to move on moist surfaces or in viscid media, but to swim much less well than does, for example, *Vibrio*, with a single polar flagellum.

This description applies only to the origins and relationships of the Gram-negative bacteria, most of which are unicellular, and relatively simple in form (Plate 2, fig. 10); the more complex, septate, multicellular Gram-positives (Plate 1, figs. 2, 3, 4) may well prove to be descended similarly from the spirilla, since many of the latter are also septate, and are not clearly definable by Gram's stain, but the line of descent must be assumed to be independent. It has been suggested that the Gram-positives are derived, by a process of degeneration, from the elaborate, fungus-like *Streptomyces*, but although, as will be explained in a later section, this may be true of some, closely related types, it cannot be held to be true of those groups which have flagellated representatives. These, beyond any doubt must have had flagellated, which is also to say, aquatic ancestors, whereas the *Streptomyces* are an outstanding example of successful adaptation to a terrestrial environment. In addition, the theory of descent from a fungus-like ancestor implies that the *Streptomyces* are indeed fungi, whereas they are typical Gram-positive bacteria in respect of their cytology and their chemical constitution, and must be considered to have converged in superficial form with the moulds, in the process of adopting a similar mode of life.

There appears thus to be a good *prima facie* case for regarding all the bacteria as derived from flagellated aquatic ancestors. These ancestors formed a group which had representatives capable of a photosynthetic, chemosynthetic, and saprophytic mode of existence, and thus had much in common with the smaller flagellate protista. Accordingly it is not unlikely that the bacteria arose independently from the flagellate protista,

of this evidence has been harshly criticized[4, 39] and the application of such techniques as electron microscopy of ultra-thin sections[2, 35] or phase-contrast microscopy of dividing nuclei in the living condition[27, 45] has given no encouragement whatever to the concept of mitosis in bacteria. Unfortunately, it is also true that many interpretations of nuclear configurations in bacteria have been made without due consideration of the possibility that more than one complete cell might be concerned. If such an organism as the coccus shown in Plate 1, fig. 4 is stained so as to demonstrate the nuclei, but not the cell walls, then a complex pattern might well be seen; and because it is much less obvious to investigate the cell walls than the nuclei of such bacteria, considerable errors of interpretation have been made by workers unaware of the cellular complexity of their material.

The manner in which the nuclei of bacteria divide (Plate 1, fig. 9) is in effect the simplest and most straightforward method for ensuring division of genetic material in a very small cell, tending to the production of short filaments, and it might thus be expected to occur in blue-green-algae of comparable morphology. The genes must be arranged in a longitudinally divisible rod, irrespective of whether this is a chromosome or an entire nucleus, and the resemblance between the two groups may thus equally well be indicative of a primitive condition or of biological convergence. Light can be thrown on the problem as thus conceived by an investigation of the nuclear condition in the smaller apochlorotic flagellates, about which, at present, very little seems to be known.

3. *The Interrelationships of Bacteria*

Some idea of the relationships of the various groups of bacteria one with another is implicit in the argument developed in the preceding sections with reference to the nature of bacteria and their relationships with other groups of living creatures. The two main lines of development correspond to the Gram-positive and Gram-negative groups, and between them there are numerous fundamental differences. In this respect the spirilla, whether autotrophic or heterotrophic, from which both of these groups are presumed, on the present hypothesis, to have arisen, form a third group.

The differences between the cell walls of Gram-positive and Gram-negative bacteria come under the heading rather of cytology than of systematics, and are discussed by the author in a monograph devoted to the cytology of bacteria which has already been quoted on the subject of cellular structure[4]. In general, Gram-negative bacteria are unicellular, their cell walls are more rigid, although apparently thinner, and possess a higher lipid fraction, associated with this rigidity, which enables them to dispense with the cross-walls which Gram-positives produce. The amino-acid content of the cell-walls of Gram-negatives shows a much fuller range, and this may

explain the fact that they are more satisfactory antigens than are the Gram-positives. The spirilla are irregularly and occasionally septate, and their cell walls show a flexibility unlike that of either of the other groups, so that in this respect, as well as in the arrangement of their flagella they are intermediate between other bacteria and flagellates. The cell wall of spirilla is also distinct, in that it has an unusual macromolecular structure, at least in some cases.

The evolutionary development of the Gram-negative bacteria has not led to a high degree of morphological specialization. A progressive adaptation to terrestrial life is shown in the gradual reduction of degree of spiral, and in the increase in number of flagella, eventually resulting in peritrichous arrangement. The most primitive representatives of the series are presumably the vibrios, which are unicellular, but spiral, with a few polar flagella, whereby they swim actively. From these the less spiral pseudomonads, with more numerous polar flagella and capable of a wide range of habitats, are readily derivable. The typical "coliform" bacteria are similar to pseudomonads but with a relatively small number of peritrichous flagella. They are seldom aquatic, but often live in viscous materials. The most highly evolved Gram-negative bacteria have adopted a completely terrestrial habitat, and may either, like *Proteus*, be capable of mobility on damp surfaces, by virtue of an enormous number of peritrichous flagella, or may have lost their flagella completely, like *Aerobacter*. Some vibrio-like bacteria have become specialized sessile aquatic forms with mobile distributive stages, such as *Caulobacter* (Plate 2, fig. 15) which is attached to the substrate by a stalk, continuous with the cell wall. More complex sessile bacteria, such as the colonial *Rhodomicrobium* (Plate 2, fig. 14) represent the furthest evolutionary development in this direction, so far as Gram-negative bacteria are concerned.

Gram-positive bacteria show much greater morphological variation. Almost all are multicellular, and in some cases the individual cells are extraordinarily minute (Plate 1, figs. 3, 4). Flagella are found in representatives of all the main groups, except the complex, branched mycelium formers, but are invariably peritrichous and seldom numerous. The existence of these flagellate forms, possessing typical, unifibrillar bacterial flagella, is of itself a powerful argument against the otherwise attractive theory that the Gram-positive bacteria have a separate origin from the Gram-negatives, in some fungus-like (and fungus-derived) *Streptomyces*. It is excessively unlikely that such unusual flagella could have been evolved twice over.

The most highly evolved members of the Gram-positive group also appear to have become adapted to life in a terrestrial environment but they have achieved this adaptation in a variety of ways, and have gone one stage farther than the Gram-negative forms, in that they have contrived to

make use of the air for their distribution. As already described, the *Streptomyces* resemble small moulds, with a feeding mycelium and aerial hyphae bearing chains of spores. The *Bacillaceae*, which possess the very characteristic endospore, are much more typically bacterial; some species have retained their flagella and may be capable, like *Proteus*, of moving over damp surfaces. The endospore has been the subject of considerable speculation, prompted almost entirely by its unique powers of resistance to heat and antiseptics. There is, however, little doubt that this property is a biological accident, due to the partial dehydration of the spore proteins. This dehydration has, after much controversy, been proved conclusively by refractive index studies[40]. Since high temperatures and concentrations of injurious chemicals are most unlikely to be encountered under natural conditions, it is reasonable to suppose that dehydration is a device to reduce the weight of the spore and render it more efficient as an agent of aerial dispersal and that the resultant resistant properties are an accident, not so much fortunate for the bacilli as unfortunate for man, under certain circumstances[3, 5].

The cocci, which have abandoned bilateral for radial symmetry, have representatives with both flagella and spores, and they are probably quite closely related to the sporing bacilli. However, some spore-less non-flagellate cocci are very small and light and exhibit an almost spore-like resistance to inimical agencies, so that they may be presumed to have adopted a simpler and more straightforward solution of the same problem. Both cocci and sporing bacilli have secondarily Gram-negative representatives which, however, are quite recognizable when examined by appropriate cytological methods. For example, the nitrogen-fixing bacteria *Azotobacter* and *Rhizobium*, which are normally Gram-negative but which some believe to be rather specialized members of the sporing bacilli, strongly resemble the latter in their reactions to plasmolytic agents[17].

These nitrogen-fixers are of especial importance in the present argument, because they share with the spirilla a reproductive mechanism of considerable interest, of which only traces are found in most other bacterial groups. This is the production of tiny, motile swarmers or gonidia. It is rather curious that although the ability of certain bacteria to reproduce in this manner has been known for the last thirty years at least in *Azotobacter*[26] and *Rhizobium*[42], the knowledge has had no effect upon the accepted definitions of bacteria, as dividing solely by "simple fission." The same process in spirilla has been many times reported, and is clearly illustrated by Pease[33]. Other members of the sporing bacilli, in addition to these specialized forms, may adopt the same method of reproduction, although it is best known in the nitrogen-fixers, and this apparent connection between these advanced Gram-positive bacteria and the spirilla is of value in establishing the theory of a single origin for the bacteria. It is also of interest to recall that spirilla

and vibrios have from time to time been credited with the capacity for producing endospore-like structures[30], although these have been very little studied.

Recent observations[6] have led the present writer to the conclusion that although the Gram-positive bacteria in general may not be descended from the *Streptomyces*, some of the other sporogenous actinomycetes probably are, including the true *Actinomyces*.

In a botanical context, it may be advisable to insist that priority in the generic name *Actinomyces* belongs quite unequivocally to the oral parasites and pathogens of mammals, of which *A. bovis*, the agent of actinomycosis in cattle, is the best known. The morphology of these parasites is complex, but quite distinct from that of the *Streptomyces* which were for long, and until quite recently, referred to as *Actinomyces*. Spores are produced singly on branched coenocytic filaments[28], not in chains on an aerial mycelium, and the saprophytic genus most closely resembling *Actinomyces* is *Micromonospora*[8]. However, *Streptomyces* are capable of producing bizarre growth forms simulating any of these genera, and may well be ancestral to all of them[6]. A similar ancestry, but a different line of descent, may be postulated for *Leptotrichia*, another oral parasite[1] (Diagram 2). In this case the production of thin branches from the normally thick filaments of the *Leptotrichia* suggests an affiliation with *Streptomyces* growth forms in which the thick, secondary mycelium, usually in fluid culture, germinates with the production of such slender filaments instead of proceeding to typical sporulation[32]. *Leptotrichia* species may also retain the power of sporulation, but both from this genus and from *Actinomyces* it is easy to conceive the origin of more completely degenerate parasitic bacteria, such short filaments, asporogenous and sparingly branched, often anaerobic, as have been variously assigned to *Corynebacterium*, *Fusiformis*, *Nocardia*, *Lactobacillus bifidus*, etc., as well as to species of *Actinomyces* and *Leptotrichia* themselves. These classifications are often dubious since some of these genera have flagellated representatives which must be regarded as primitive, at least by comparison with the *Streptomyces* and their putative descendants. Accordingly, as indicated in Diagram 2, among the non-sporing, filamentous parasites there can be found those which have degenerated from more complex ancestors and those which are relatively little altered from the primitive condition. The occurrence of flagella in, for example, *Corynebacterium* and *Nocardia* is well attested[20, 31], although it must be borne in mind that these genera are themselves typical of the condition just described in that they are almost certainly convergent rather than natural groups.

One of the biggest puzzles in the relationship of bacteria both to one another and to other natural groups is presented by the myxobacteria. These are micropredators, having a life-cycle exactly resembling that of the *Acrasiae*,

except that the units of the vegetative swarm are not amoebae but bacteria. However, although similar to other bacteria in size and nuclear behaviour they are unique in that they have no rigid cell wall, and are motile without flagella. They appear to crawl by contractions of the flexible cell envelope, and can only move when in contact with a solid surface. In this respect they resemble certain members of the blue-green algae, but there is not, at

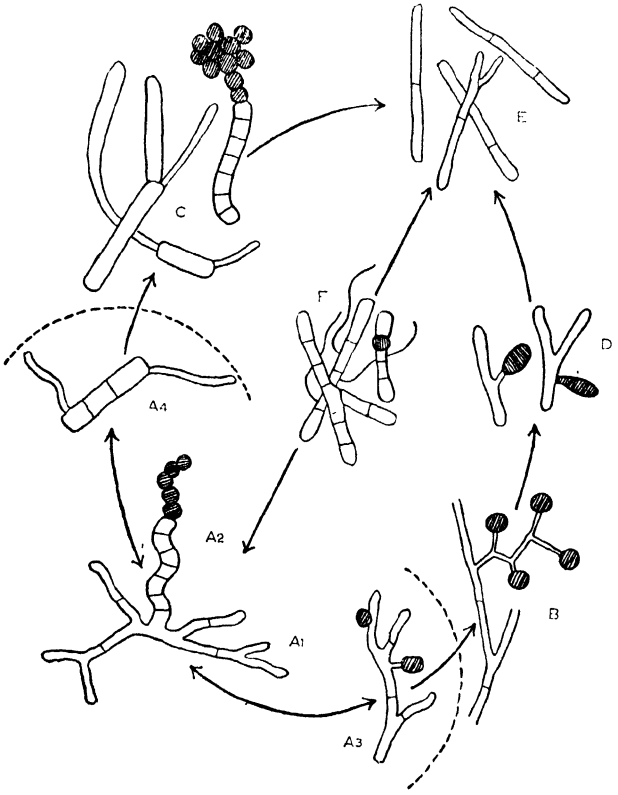


Diagram 2. Suggested scheme of evolution of filamentous bacteria. The *Streptomyces* (A) may be regarded as ancestral to many superficially simpler forms. In the vegetative mycelium (A_1) are found aberrant forms (A_3) resembling *Micromonospora* (B), from which the parasitic *Actinomyces* (D) appears to be derived. The sporogenous, aerial mycelium (A_2) especially in fluid culture, may fragment and produce slender branches (A_4) in a manner resembling the parasitic *Leptotrichia* (C). Both from *Actinomyces* and *Leptotrichia* can be derived sparingly-branched asporogenous parasites of various genera (E).

The greater diameter of the sporogenous mycelium and of the forms derived from it, by comparison with the vegetative mycelium and its derivatives, is in accordance with observed facts.

The primitive branched bacteria (F), some of which are sporogenous and some motile, are assignable to various genera, and are presumably ancestral to the *Streptomyces*, and thus, indirectly, to the other genera. At the same time, the parasitic representatives may be indistinguishable from the degenerate forms (E), so that these genera are almost certainly of dual origin (e.g. *Corynebacterium*).

present, any available evidence tending to show whether this condition is primitive or secondary. If the former, then the myxobacteria cannot truly be regarded as bacteria at all; if the latter, then they are among the most highly evolved. They are, in any event, decidedly a terrestrial group.

4. *The Reproduction of Bacteria*

The preceding sections of this paper should already have given the reader to understand that the concept that bacteria reproduce solely by simple, binary fission has not gone unchallenged. Not only is it quite certain that bacteria reproduce by a variety of methods to which the term simple fission cannot conceivably be applied, but it is distinctly dubious whether they do indeed reproduce by simple fission at all! If reproduction by means of spores of various types is for the moment disregarded, and the question of vegetative reproduction alone considered, it must first be remembered that many bacteria are very far indeed from unicellular, so that an important distinction exists between fission of the entire micro-organism and cell division. All too often the two terms tend to be used as if they were synonymous, whereas this is, in fact, true only of the unicellular Gram-negative bacteria; but even these divide in a manner which cannot correctly be regarded as simple fission, but rather as a process of longitudinal budding[4, 8, 18] (Diagram 3, A). The mother-cell and the bud can be shown to differ in several respects; the cell walls and cytoplasm are in different conditions, indicative of different physiological ages, and the flagella of the bud are usually absent or much less well developed than in the mother-cell.

Fission in multicellular rods, such as *Corynebacterium* (Plate 1, fig. 3; Diagram 3, B) is not synchronized with cell-division. The usual course of events is that the smaller, central cells of the filament proliferate (Diagram 3, B *a* and *b*), after which the filament divides centrally and the terminal cells of the newly divided poles increase in size (*c* and *d*[4]).

Vegetative reproduction by means of flagellated swarm cells of various types is commonly found in bacteria. The simplest type is found in the little-known genus *Polysepta*[41], which is very exceptional among bacteria in that it is capable of lateral, as well as transverse fission (Diagram 3, C). The long, slender, flagellate filaments are divided into numerous cells by septa running both parallel and at right angles to the main axis. Some of the lateral cells bud off as small, spherical, motile swarm cells, each with one, two or more cells and a similar number of flagella. By contrast, the nitrogen-fixing bacteria *Rhizobium* and *Azotobacter* produce similar swarmers from within enlarged mother-cells (Diagram 3, D[4]), and these may even be capable of passing through anti-bacterial filters before reverting to the larger, typical form[23].

In the case of the stalked, aquatic *Caulobacter* (Plate 2, fig. 15) the bud or

daughter-cell is provided with a flagellum, and swims away freely when fission takes place. It then settles down on a solid surface (or upon another organism, even including larger bacteria) and grows a stalk at the flagellate pole. The flagellum is then discarded (Diagram 3, E). The sheathed

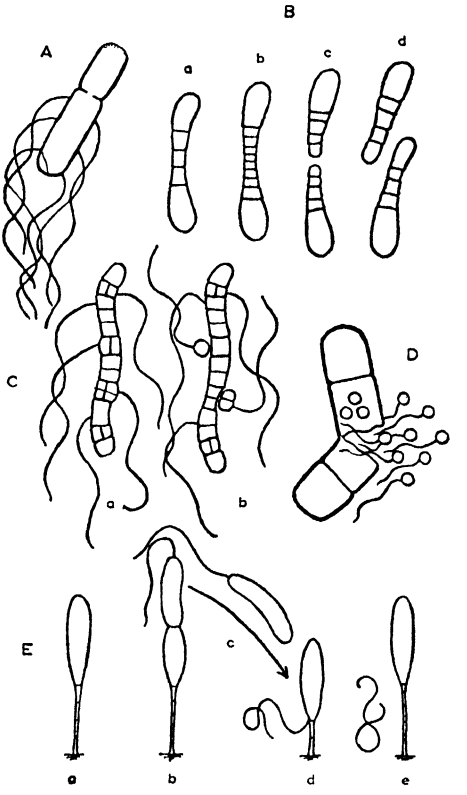


Diagram 3. *Reproduction in Bacteria*

A. Unicellular, Gram-negative bacterium. In bacteria of this type, the process which is usually regarded as simple fission actually consists in the production of a bud at one end of the cell. Growth is from a growing point at the tip (shown stippled) and the new bud may be devoid of flagella at first.

B. *Corynebacterium.* These bacteria have numerous small cells divided by septa (compare Pl. 1, fig. 3). The terminal cells are usually enlarged, and fission is preceded by proliferation of the smaller, central cells (*a*, *b*). After fission, the new terminal cells commence to enlarge (*c*, *d*), and the new central cells to proliferate.

C. *Polysepta.* Cell division occurs in both senses, as in most cocci (Pl. 1, fig. 4), and motile swarm cells are budded off laterally from the septate filament, (*a*, *b*).

D. *Rhizobium.* By contrast with the preceding, the swarm cells of the nitrogen-fixing bacteria *Rhizobium* and *Azotobacter*, and of some other bacteria, including spirilla, are released from special, enlarged mother-cells.

E. *Caulobacter.* This stalked bacterium produces a bud or daughter-cell with a polar flagellum (*a*, *b*), and on division the motile bud swims away until it encounters a suitable surface, to which it becomes attached, growing a stalk and discarding its flagellum.

Chlamydobacteria have a similar life-cycle, with alternation between sessile filaments and flagellated swarmers.

Like most other protista, the bacteria vary asexual, vegetative reproduction with occasional sexual conjugation or syngamy, the latter being especially common in the processes of maturation of the spores and resting cells[4]. An excellent example of such a process is found in the formation of the "initial cell" of the secondary, sporogenous mycelium in *Streptomyces*[14, 21]. Two elements of the primary mycelium fuse, and at the point of junction a spore-like body arises, which germinates to produce the secondary mycelium.

Sexual conjugation between individuals has been proved to occur in the small unicellular, Gram-negative bacteria[25, 46]. The two cells fuse over a narrow area and nuclear material passes between them. This occurs relatively seldom in nature, but artificially induced mutants may show a high degree of coupling between compatible strains. A similar but more complex process is found quite commonly in plant-pathogenic bacteria, for example *Phytomonas tumefaciens*; these conjugate not in pairs, but in stellate groups, joined at the poles of the bacilli[9, 19].

GENERAL

It is obvious that this general account of the bacteria is written only from one, rather limited point of view out of very many which might equally well have been chosen. Not long ago, the vast majority of bacteriologists were medical men; nowadays these are almost certainly outnumbered by microbiological chemists. Biologists have always been and probably always will be in a very small minority in this field. None the less, the progress which has been made in the study of purely biological problems in bacteriology has been very considerable of recent years, and indicates that there exists a great deal of interest in these matters. In addition, as is well known, bacteria have become increasingly important, for example, to geneticists, biological physicists, etc. A description of any of these applications would require a separate paper, to take no account of the biochemical studies which have accumulated at an enormous rate since the invention of the new chemotherapeutic agents and the discovery of antibiotics.

These researches are not usually designed to contribute to our knowledge of the biology of bacteria, but, as might be anticipated, they nevertheless do so upon occasion. For example, the observations of Newton[29] upon the action of fluorescent derivatives of the antibiotic polymyxin against sporing bacilli provided an exceptionally clear illustration of the complex subdivisions of the cell membrane; and the biochemical analysis of the bacterial cell wall (e.g. Cummins and Harris[11]) has proved to be a most valuable tool for taxonomic purposes. Innumerable other examples could, of course, be quoted, but because of the practical background of the majority

of such projects they have not often provided information concerning such groups of bacteria, of very great interest to the biologist, as the caulobacteria or myxobacteria, of the very existence of which many people who work with bacteria are only vaguely aware, even today.

By comparison with the older biological disciplines, bacteriology has much leeway to make up, but although there is no room for complacency, there are signs of an improved awareness of this fact. It is axiomatic that nobody can hope properly to understand one aspect of a science in the absence of a working knowledge of the whole field, and if this continues to be understood we may not be too sanguine in hoping that the problems, the existence of which has been indicated in this paper, may be investigated and if possible solved, as a contribution to this all-round knowledge.

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PHYCOLOGY IN RETROSPECT AND ANTICIPATION

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THE whole of phycology, the development of which I am asked to review, is a very great field in which I have a definitely restricted experience, and an obviously unequal interest in its various aspects. Consequently, the best I can do is simply to note some features of the progress achieved in phycology and indicate what seem promising opportunities for research in this branch of botany. With very little time for preparation I cannot try to treat all topics with proportioned weight.

We are dealing with a very large plant group, much more widespread and adaptable than vascular plants or bryophytes, much greater in their morphological diversity. It will be hard for most botanists to appreciate this. Perhaps one botanist has studied algae to a hundred who have worked with vascular plants, so we phycologists find ourselves in a curious position. Great parts of the world have never been explored for our plants, thousands of new kinds doubtless remain to be described, many even from near the centres of scientific enquiry, and yet very advanced biochemical and hydrobiological researches on algae are going on at the same time. In effect the ages of exploration and of technology are for us in a remarkable degree overlapping.

Early or pre-Linnean scientific references to algae are neither voluminous nor common. Interest in the sea and the lakes was practical; they were sources of fish and avenues for transporation. Scientists noted things brought to them; they did not greatly search the waters of the world for new plants. Consequently Linnaeus[65], who was himself a land botanist, was limited to the recognition of five genera of plants which we still accept as algae, and included about seventy algal species in them. He also included liverworts, lichens, sponges, and a few other things as algae, and in other works misplaced a few more algae among corals and in other groups. Linnaeus's discretion, however, is shown by the fact that most of his species are recognizable, and for many of the larger ones confirmatory specimens remain in his herbarium in the rooms of the Linnean Society at Burlington House. Linnaeus, as other botanists of his time, lacked the knowledge requisite to enable him to prepare adequate descriptions, failed to supplement his phrases with good figures, yet made a clear start in cataloguing these plants.

Good illustrations were, however, not long delayed, notably those of Gmelin[31].

In fact, standards of discrimination and description have only slowly developed; it is not surprising that the next group of observers, coming about 50 years after Linnaeus, made effective use of illustration. We have, as examples, Dillwyn[18], Turner[104], and Sowerby[93]. In fact the history of algal exploration and description has been marked by the frequent appearance of notably illustrated works, culminating in such as Ruprecht's[83] splendid figures of Pacific rockweeds and kelps, the exquisite polychrome plates of *Batrachospermum* in Siridot's monograph[88] and the very famous analytical plates published by Bornet and Thuret in their *Études Phycologiques*[8]. It is, indeed, fortunate that high standards were set early, for in such groups as desmids and diatoms the utmost precision is needed in illustration, since words fail to convey concisely the essential distinctions.

This phase of scattered description of new forms began to close when the first district floras were prepared (Greville[33]), and when C. A. Agardh[1] first attempted a general encyclopedia of species. Preparation of district floras continues to be important as we add to our knowledge of algae and their distribution, but the accumulation has now so far surpassed financially feasible encyclopedic coverage that J. G. Agardh's *Species Genera et Ordines Algarum*[2] and J. de Toni's *Sylloge Algarum*[17] may well be the last encyclopedic collections of descriptions attempted. Henceforth we may have to rely on compendia of particular groups.

One will note that descriptive phycology relied entirely on superficial characters in the early years, but by J. G. Agardh's time a very considerable understanding of structure and reproductive organs was evident. In the early decades of this century this sort of knowledge was extensively applied in untangling the complicated life histories of the various groups, and now physiological and biochemical studies begin to play a major role.

II

Let us consider how far the exploratory census of the algae of the world has developed and been brought into the compass of regional manuals. Algae at first shared place in various botanical manuals and later stood alone. For Britain we had early notable examples of the first type in Lightfoot's *Flora Scotica*[64] and of the second in Greville's *Algae Britannicae*[33] and Harvey's *Manual of the British Algae*[38] culminating in his *Phycologia Britannica*[39]. These serious works were followed by a remarkable number of inexpensive handbooks such as those of Gifford, Cocks, Hibberd, and most particularly Landsborough[61], and of albums of specimens interspersed with sentimental verse, often anonymous, all calculated to make these plants very familiar to amateurs of the 19th century. More recently we have

had Newton's *Handbook*[67], but this should be superseded by a more technical volume incorporating the latest researches. It is extraordinary that other Western European nations have failed to complete modern regional floras. European scientists have the great advantage that early collections and type specimens are relatively accessible to them, and they do not have far to travel to carry on the necessary field work. Germany has the volumes of Hauck[43] and Migula[66], and Holland that of Van Goor[105], but they are far out of date. France has a partial manual (Hamel[35]), so does Denmark (Rosenvinge and Lund[82]), as does Italy (Preda[78]), and Russia (Zinova[114]) but for the most part one must rely on rather local floras, such as Funk's excellent *Marine Algae of the Gulf of Naples*[28], or Feldmann's *Algues marines de la côte des Albères*[22]. We must look for a comprehensive flora of Greenland and the northern islands eastward from it, one of Norway, another of the Baltic, completion of the French and Danish floras, a general Mediterranean and Adriatic flora, and so forth—for no other part of the world have we equal reason to expect so detailed a coverage.

Marine studies in East and West Africa have yet to become well established, but a flora of the South African area is in hand, though only preliminary notes have appeared (Papenfuss[73]). India is in but a little better case, with hardly more than the studies of Børgesen[6] to build on. A vast amount of field work must be done on the tropical African coasts and in India before floras can be assembled, but these would be very rewarding enterprises. Early travellers noted the great beauty of the "red seaweeds" from Australia, Tasmania, and New Zealand. They figured in Harvey's *Nereis Australis*[40] and in the first case more particularly in *Phycologia Australica*[42], as in many minor publications since, but though provincial floras have been attempted for Australia there is a no modern one for the whole continent in prospect. For New Zealand a beginning has been made by Chapman[12]. Algae of the Malayan and Indonesian areas are sketched but not exhaustively treated in the *Siboga Expeditié* (Weber-van Bosse[106]), but much remains to be done. The coast east and northward from Malaya is only represented by preliminary notes, but with strong interest and trained men now in China the situation may be expected to alter. The Philippines are as yet almost unknown, but the writer has received for study extensive collections, and some preliminary notes by his students have appeared. Japan is quite another case. Many preliminary studies have appeared, there are several beautifully illustrated handbooks for the non-specialist (Okada[69], Segawa[85]) and the technical papers culminate in Okamura's *Icones of Japanese Algae*[70] and his manual[71], but these ar econstantly being supplemented by excellent local studies. Melanesia and Micronesia likewise demand exploration; the writer's *Plants of Bikini*[102] outlines the state of our knowledge. Hawaii

stands isolated; a good deal is known of the flora, but no completely satisfactory manual exists. The American continents have very unsatisfactory coverage. Scattered reports must represent South and Central America; the Magellan area (Taylor[99]), Chile and Peru (Taylor[101], Howe[46]), Ecuador and the Galapagos Islands and shores to the northward (Taylor[100]) are all in a pioneer state of exploration without much more to be expected soon. Mexico, on the other hand, has been a good deal studied (Setchell and Gardner[87], Taylor[100], Dawson[16]). The coast from California to Alaska has been quite well explored for algae and the excellent local flora of G. M. Smith[91] for the Monterey area supplements the incompleted general work of Setchell and Gardner[86], which lacks the Rhodophycease, but which we may expect to see finished by other hands.

The east coast of the Americas is in a similar state. Nothing is known of the Argentine algae; little of those of Uruguay (Taylor[99]), rather more of those of Brazil and the countries and islands northward, for which greater area the writer has a manual in an advanced stage of preparation. This volume when it comes out will cover the tropical and subtropical regions north to Bermuda and the Carolinas.

America north of Mexico has long been the best studied of western Atlantic shores. The first major work appeared in Harvey's monumental *Nereis Boreali Americana*[41] which, however, was based on so little field work that it does not do justice to either east or west coast. Farlow[21] published what was a much less pretentious but more adequate manual of New England algae, and this served all the northeast until the writer's manual appeared[98].

It is clear that the major exploration of South and Central American coasts is yet to come, that distribution of the marine algae in the West Indies is imperfectly known, and that of the Gulf of Mexico even less well. Otherwise on the mainland our knowledge is in about the same state of advance as in western Europe, until we approach the Arctic. Here our studies have fallen far short, and much remains to be done, although a student under the writer has made large collections and has a general sketch of conditions in press (Wilce[108]).

We have been dealing with the larger littoral and sublittoral algae; the economic importance of the marine plankton is greater, but the number of species involved is less and their distribution broad. In general works on marine life the phytoplankton has received due quantitative but minimal qualitative attention. No works specifically on these plants exceed in value the volumes of Lebour[62, 63] on diatoms and Dinophyceae of northern seas. We very badly need comparable compendia for the South Atlantic, Indian, and Pacific Oceans.

In summary respecting marine algae, one may venture that a very small

part of the shores of the world has been well explored, a considerably greater part—but less than half—has been given brief visits at isolated spots, while the rest is virgin territory for the adventurous botanist, with the excitement of discovering new plants as sure for him tomorrow as it was for Hooker in the Himalaya or Spruce on the Amazon a century ago.

One cannot go into equal detail respecting freshwater algae, and, indeed, there is no need to do so. Marine algae are fairly restricted in range (although less so than land plants), and the floras will therefore cover relatively small regions, but most freshwater algae range very widely, their chief limitations being local ones of the chemistry of the substrate and the climate.

Because microscopes are needed for their identification early advance in our knowledge of them was slow, but the later part of the 19th century, during which various clubs for the pursuit of microscopy flourished, saw much amateur interest in freshwater algae, and the beginnings of comprehensive studies, especially in Great Britain. Very notable were the volume on diatoms by W. Smith[92] and that by Ralfs[81] on which our desmid nomenclature depends. Some other countries followed, with general works of greater or lesser accuracy, like Migula's *Kryptogamenflora Deutschlands*[66] and Wolle's volumes on the freshwater algae, diatoms and desmids of the United States[109, 110, 111].

With the 20th century new standards appeared and very excellent works adequate for the northern hemisphere exist, such as West, West and Carter's *British Desmidiaceae*[107], Pascher's *Süsswasserflora Deutschlands u.s.w.*[72], the appropriate parts of the revised *Kryptogamenflora Deutschlands*, particularly Geitler's volume on Myxophyceae[29] and Krieger's regrettably incomplete volumes on desmids[57], G. M. Smith's *Phytoplankton of the Wisconsin Lakes*[90], Prescott's *Algae of the Western Great Lakes Region*[79] and others, and the exhaustive volumes on plankton algae by Huber-Pestalozzi[47]. Superb monographs on special groups and regions abound, such as those mentioned for desmids and Myxophyceae, or of Skuja on Swedish lakes[89]. We can count on continuing interest in these organisms; it is a misfortune that they lend themselves to observation by inexpert people, and a multitude of published lists with unconfirmable determinations confuse the records of distribution of these algae, not the least in the United States.

Unfortunately other parts of the world have not fared as well as Europe, Canada, and the United States, and though scattered papers abound, comprehensive floras are lacking for all other major areas. However, there is evident in the publications of Hirano[45] on Japanese desmids, and of other writers, a belated but very strong development there, and in China under the direction of C.-C. Jao[51] extensive studies are in progress and many papers are appearing.

III

That phycology is still productively in the exploratory phase was brought out early in this review, but it has proven exceptionally adaptable to other approaches. The extraordinary range of habitats, for instance, has made descriptive ecological studies most attractive. In the sea biological oceanography is greatly concerned with the initial productiveness of the plant component of the plankton and here quantitative researches on sources of nutrients and energy and on the biological yield have been manifold (Sverdrup *et al.*[95]) and not limited to the North Atlantic, although far more complete there than elsewhere because of British and Scandinavian studies and the work of the Woods Hole Oceanographic Institute. In the Pacific the chief centre of activity continues to be the Scripps Institution of Oceanography.

The development of oceanographic stations around the world, as in Texas, Brazil, Japan, and elsewhere suggest that more and well connected studies will come, but the great cost of vessels and their operation hampers most of the projects. Fortunately, the results of oceanographers in observations on currents, in detection of large submerged objects and schools of fish, and in determining the nature of the bottom deposits have attracted military interest, and through the economic implications the fisheries and geological bureaus of maritime countries. Indirectly, therefore, support may be expected for botanical as well as physical and chemical studies of the sea.

Studies on the ecology of larger littoral and sublittoral algae are still unsatisfactorily in the descriptive rather than in the quantitative stage because the violence of the waves makes instrumentation difficult, and until studies can be set up, staffed, and financed adequately to cope with this, no very exact information respecting conditions on the open shore can be recorded. This is a great misfortune.

However, very attractive opportunities lie in studies of embayments with narrow passages to the sea, particularly if these receive freshwater increments from the land by small streams and springs. The instrumentation and chemical analyses can now be adapted from those used at sea; wind-driven waves are an ecological factor but not an instrumental hazard; there are currents, however, a shifting salinity gradient, and a maze of most interesting problems such as were attacked for a Massachusetts embayment for plankton and its environment by Hulburt[48, 49, 50] and for attached algae by Conover[18] when with my students a few years ago. Such studies should be widely prosecuted.

More accessible to many people are rivers and streams, and these also are easily subjected to organized study. Many papers have appeared and have been summarized by Blum[4] but few are of major scope or cover the

characters of the environment completely. With the increasing and often critical dependence of communities on water supplies, studies of whole river systems are needed. A few have been made, but most, like the classic one on the Illinois River by Kofoid[53] cover only part of the problem. For the individual student local studies such as that of Blum[5] on a part of the Saline River in Michigan are practical and valuable, providing the instrumentation and analyses are adequate. Particularly needed are studies of small, fast-flowing mountain streams, and of all flowing waters in the tropics.

The availability which has made freshwater algae a favourite subject for petty and unsubstantiated listing of species has made their occurrence, seasonality, and more obvious environmental conditions in ponds and small lakes the subject of ineffectual attempts at ecological studies. The vast number of such small water bodies, all differing in some degree, has produced hundreds of papers of which many are so imperfectly provided with exact limnological data as to be almost useless. Many others are excellent, well coordinated studies, such as those centring on the Freshwater Biological Association station on Lake Windermere in England, those directed by Birge on the lakes in Wisconsin, those on Lake Balaton[97] in Hungary and on lakes in Denmark, Norway, Sweden, and Switzerland[68, 44, 24, 14].

For small ponds and lakes the simplest boats and hand-operated sampling gear are sufficient, while for very large lakes ships capable of remaining away from shore for several days and handling gear equal to that of moderate-depth marine studies become necessary. The methods for estimation of the phytoplankton and the limnological analysis of chemical and physical factors parallel those for marine work. Studies on ponds and lakes are, then, greatly to be desired, providing the analyses of conditions are comprehensive and carried on for a long enough time, at least one or two annual cycles, to be meaningful.

Less common than the more ordinary lakes are those with very high concentration of one salt or another. Such would be the brine lakes like Great Salt Lake in the United States, soda lakes (Kol[54], Gessner[30]) and the like. They show quite different though limited floras, but call for just as comprehensive studies, rather than the merely descriptive ecological treatment they have usually received.

Winter conditions in ponds and lakes require modified field technique, but do not show a particularly specialized flora. Far otherwise is the situation on land when ice and snow persist throughout the year. For these enduring frigid matrices there have evolved special floras. The plants lying within and on the snow and ice give it characteristic colours, of which the well-known "red snow" of alpine snowfields is an example. Studies of these plants have

been made in Alaska, Scandinavia and the Alps, as well as elsewhere and particularly by Kol[55] whose work continues. One would like it to be extended to the farther Arctic, the Himalayas, the Andes, and the Antarctic, as major potential cryobiont areas which are as yet unexplored. The hitherto descriptive studies need now to be supplemented by full chemical and physical analyses of growth conditions.

Conversely, there are algal developments under conditions of quite high temperatures, such as are found about hot springs. Studies have been made in Alaska, the western United States, Europe, and Japan (Emoto[19], Petersen[76]) but they have mostly been descriptive and superficial. The high hydrogen sulphide and carbonate content of the water and the deposits about the shores, involving the algae, render classification difficult. More long-continued studies with full instrumentation and analyses are needed, designed to show the actual temperatures and concentrations of solutes about the algae themselves.

Algae obviously are dependent on light, and only very few are known to have become saprophytic in nutrition, but many can get along with very little light. We have studies, then, on the algae of the dim entrance chambers of caves as well as of very deep freshwater lakes and the oceans, but more remarkable are the algae of soils. Extensive studies of many soil types have been made (Petersen[74, 75]), both in very northern countries and nearer the population centres.

These studies show many algal types specialized for life one or many centimetres below the surface. As this flora is part of the general soil biology, and from the economic standpoint is concerned in its fertility, it should be studied in all regions more thoroughly, particularly in the tropics, and with suitable instrumentation.

Another terrestrial habitat which demands much more careful analysis than it has received is the subaerial one. In temperate regions the subaerial flora is limited to damp ground and rocks, and merges with that of rivulets where slight water dripping occurs, but in particularly humid and especially in tropical areas algal growth (indeed, that of bryophytes as well) invades the foliage of vascular plants, and we know essentially nothing of the exact ecological conditions for these situations, so that a large field for research is opened here.

Under somewhat similar environmental conditions a few genera have become endophytic (*Anabaena*), or partly parasitic (*Phycopeltis*, *Cephaleuros*) and even of considerable economic importance as damaging agents in agriculture. It is even uncertain what species distinctions exist in some cases, and much taxonomic work needs to be done preliminary to studies on their specialized physiology.

IV

Lack of adequate knowledge of the physiology of the algae is the main hindrance to advance in fully interpreting ecological situations, to experimentation involving maintenance of colonies for long periods, and to complete life history studies. It was found possible over 30 years ago to isolate and grow many Chlorophyceae, some Myxophyceae, diatoms, and flagellates in unialgal, even bacteria free, cultures. There have been too few people willing to devote themselves to algal physiology to take full advantage of this. Except for species of *Chlorella* and *Chlamydomonas*, few genera have been extensively employed, and even in these cases it has often been assumed that the identity of the organism did not matter, as if all species in any algal genus would necessarily react the same under all conditions. The work, nevertheless, has been fruitful. It has developed, as might have been expected, that microscopic algae with their large surface-to-volume ratio and rapid reduplication were very efficient tools in the study of the production and conversion of numerous physiologically active substances. They are particularly suited for the study of photosynthetic pigments[113] associated with these, both in chemical respects and their functions in the plants, and work has been active in these respects. What is now needed and can be seen beginning is the comparative physiological study of numerous species from various taxonomic groups. Thanks to the pioneer work of Kufferath[59] and Pringsheim[80] culture methods suited to a wide range of freshwater algae have been tested, and Pringsheim established a culture collection of excellent scope at Cambridge. This has led to the formation of subsidiary or of independent collections at several places, as in Bloomington, Indiana, originally based on the Cambridge collection, in Paris and elsewhere, so that well-known clones may, if desired, be secured readily. Researches based on these alone are not enough. The clones may after a time suffer physiological changes in some respects. New stocks must be established and many additional species characteristic of special environments must be brought in from the wild, identified, isolated, and studied.

These advances have passed the marine algae by. It is indeed curious that here, where we have direct harvesting for economic ends, there should be no macroscopic species which man has become able to maintain in artificial culture indefinitely. The reasons lie in the very complex ecological requirements for the plants, involving tidal and light conditions and the slow maturation of the plants (several years in *Ascophyllum*), persisting through changes in salt and temperature requirements with the seasons.

Nevertheless, these problems simply parallel what the physiologist dealing with land plants takes as a matter of course; why one should expect anything different in the sea is hard to explain. For land plants the physiologist has the knowledge of field culture methods established by farmers over

thousands of years and the refinements in analyses of growth requirements worked out at Rothamsted and hundreds of other agricultural experiment stations during the last several decades. For marine plants this experience does not exist. It will require thorough study of the physiology of individual species before much better laboratory or field culture methods can be evolved, but it would be of value should this be done. Field cultivation of *Gelidium* for its high gel yield of agar would be most advantageous, for instance. *Porphyra*, of great economic value in Asia, is cultivated successfully on the shores of Japan and China on an empirical basis, but it is alone in this respect, and does not seem amenable to controlled laboratory culture.

Without waiting for culture methods to produce the material for analysis a great deal of advance has been made in our knowledge of the biochemistry of the algal wall constituents. The industrial use of the gels from *Chondrus crispus* and other plants has necessitated accurate knowledge of the chemical structure of these substances; at least one firm (Seaplant Chemical Corporation) in the United States maintains a chemical research as well as a testing laboratory, and doubtless some others do likewise. Very notable studies on the rockweeds and kelps have come from the former Institute of Seaweed Research laboratory at Inveresk as to the mechanics of harvesting, the seasonal changes in composition and the biochemistry of the extractives. With controls such as these the utilization of gels from both rhodophycean and phaeophycean sources is spreading widely from the old traditional and simple uses as food adjuvants or sizing for cloths, to a wide range of industrial applications.

A different type of utilization has recently come into rather premature prominence: that is, the exploitation of mass culture techniques to freshwater algae[11]. Roughly, these projects fall into three classes. First, the direct utilization of natural plankton. The impracticability of this shows first in the disproportionate power costs for separating and drying it, and second in the questionable uniformity and utility of the product. The second uses algae in partially purified sewage to facilitate part of the conversion process, and there is a chance that by controlling the flora a useful concentration could be achieved. However, adjustment of the chemical composition of the medium would be necessary, for it would not otherwise be uniform, and at present it does not seem that there would be a demand for the product. Most precise are the projects based on pure cultures of *Chlorella* or similar organisms. This has been done on a generous pilot plant scale and its practicability assured, but again the power costs are very high and the product, while quite usable as an ingredient in feeds for domestic animals, seems to offer no commensurate advantages. There seem few data demonstrating that algal concentrates are efficiently utilized as food by the human body. Those who have tested such products as human food

take a dim view of their acceptability. Suggestions that freshwater algal culture is adaptable to the needs of depressed areas with inadequate food production fail to recognize that to be successful at all heavy capital outlay, abundant cheap power, and careful technical control are all necessary, and all conspicuously absent from such areas. Unless species are found which in mass culture yield particular substances of special value these projects seem for the present to be unprofitable.

Culture of algae offers much more opportunities for fundamental experimental research. Mention has been made of the adaptability of continuing cultures in biochemical and physiological work. Much can, however, be done with short-term culture methods applied to larger algae. Experiments based on *Nitella* and *Chara* have long been commonplace. These plants have recently been found suitable for studies on the submicroscopic structure of the cellulose cell wall.

There are many more marine species which would be suitable provided their cultural requirements were met by the physiologists. An example of notable successes are the experimental studies of Hämmerling[36] and his associates on *Acetabularia* and its relatives, which he keeps successfully in culture. These are important in their bearing on nuclear and cytoplasmic functioning. The same workers have found *Acetabularia* suitable for cytological studies as well as experimental ones. Many more things could be studied, however, even in this family. They show, for instance, neatly progressive calcification along the axis in *Neomeris* and *Cymopolia*, and in the latter the details of the process could be analysed far better than in a diffusely calcified plant like *Chara* or *Corallina*.

While *Cymopolia* offers advantages for one kind of study *Chara* allows studies of diffuse carbonate deposition from fresh water to be made, while the lithothamnia pose a situation where calcification is completed very abruptly beneath the very thin surface zone of one or but few uncalcified layers of cells. Equally ill analyzed are the instances (of which there are many) where algae can penetrate firmly calcified structures, plant or animal; the exact chemistry of the process and the rates of penetration, for instance, need study.

V

Morphology as used by the phycologist is observed in more exacting detail and the details applied more comprehensively in systematic work than in other plant groups. Macro-morphology, histology, embryology, and of course cytological features are all applied and at all levels from *phylum* to *forma*. Consequently, the phycologist must be a meticulous microscopist. Long ago diatomists were recognized as leading other botanists in their skill with lenses and the rigorously careful observations they made. These

skills are still in full demand in most phases of algal study. Superficial morphological observations served Linnaeus and Gmelin; little more use was made of microscopy on marine forms by Greville or Harvey, but by the middle of the 19th century, as we see in the works of Kützing and J. Agardh on marine algae, Smith and Ralfs on freshwater species, microscopic surface details and histology yielded recognized taxonomic criteria.

A new phase appeared when the old classes of algae began to be broken up into more natural categories. Perhaps this can be signalized for the "green" algae when Blackman and Tansley[3] separated the Heterokontae, Stephanokontae, and Akontae from the bulk of the "green" algae or Isokontae. Readjustments have been made; these groups no longer are used as first proposed but the ideas persist and have been elaborated on morphological grounds by Pascher[72] and many others, so that five or six Classes have received portions of the original Chlorophyceae and vaguely defined flagellate groups (Fritsch[27]). A vast deal of systematic work still needs to be done to organize these groups; an example of what may be accomplished is the review of the Chrysophyceae by Bourrelly[9].

Sauvageau[84] stirred up interest in the "brown" algae with his demonstration of alternating microscopic gametophytes in *Laminaria* and related genera; widespread dimorphic alternation in the "brown" algae could have been suspected on the basis of the *Cutleria-Aglaozonia* observations made years before (Falkenberg[20]). The Laminariaceae is the only family in which enough genera and species have been studied—and the papers (good and bad) are very numerous—so that we may feel reasonably sure that the characteristics are stable throughout.

Many of the "brown" algal genera in various families have been studied and our ideas of their life cycles have been greatly modified; the distinctions between microscopic gametophytes and filamentous protonemal stages are often not clear, but the sampling is so scant that the data from one or few species have been accepted as characteristic of whole families, even orders. In view of the short cuts eliminating certain stages, or modifying the function of the reproductive bodies from the several types of reproductive organs, as as seen in *Ectocarpus*, suggesting that in less well-studied genera only parts of the cycle have been recognized, we may be sure that reappraisals of many of the new groupings will come in time and there is room for many researchers here.

The reorganization of the "red" algae came earlier when the details of the carpogonium, the nutritive and auxiliary cells, with the connecting filaments, and the gonimoblasts, became worked out. It soon became clear that the cystocarp should be regarded as the culmination of a carposporangial generation beginning at zygosis. The marvellous diversity of these organs has yielded excellent criteria for classification ranging from the very simple

forms shown in *Porphyra* or *Acrochaetium* to the highly complex but well displayed apparatus of *Platoma* or *Dudresnaya* (Kuckuck[58], Bornet and Thuret[7, 8], Taylor[103]) to the complex and compact in *Polysiphonia* (Yamanouchi[112]) and those simplified by condensation in the corallines (Suneson[94]). Kylin has summed up the whole situation regarding "red" algal vegetative morphology and reproduction[60] and it is easy now to see what groups most need more study.

These studies may follow classical lines and complete the evidences for the types of mechanisms in the various families, perhaps moving many genera hitherto but superficially known, or may seek evidence along a new line which has just been opening up of recent years affecting both "green" and "red" algae. Many years ago Howe suggested that in some Galaxauras the sexual plants were smooth and the tetrasporic plants densely hairy: hitherto these generations had been considered alike throughout the "red" algae. It now begins to appear that differences between the generations may in some instances have been so diverse as quite to escape recognition: *Trailiella* as tetrasporophyte and *Asparagopsis* as gametophyte for instance in the "red" algae (Feldmann[23], Harder[37]), and perhaps *Codiolum* a zoöspore forming stage of *Urospora*, which can reproduce sexually (Jorde[52]). It is probable that thorough studies in culture of algae for which one independent stage was supposedly unknown will show that it was a morphologically different thing altogether, calling for revised descriptions and nomenclatural treatment. Even if this is not the case it may show, as in *Porphyra*, different and unsuspected developmental stages.

Respecting embryology of algae the situation is curious. There is really a great deal of information on the developmental stages of a great many species already in the literature. These observations have generally been incidental to studies of reproduction or of the adult morphology. In few cases have several species in a genus been studied (*Sargassum* being an exception), and there has been no comprehensive organization of this material. We need an organized treatment, such as we have for animals, and we need to have studies made in the scores of genera about which we know nothing in this regard.

VI

Cytology in the sense of algal cell studies with the optical microscope has lagged sadly behind other groups. The early discovery that nuclear studies were only a little easier with algae than fungi discouraged most good workers, and the numerous very poor papers, notably on *Spirogyra* and Myxophyceae, have given this field a bad name. This is undeserved, for there are excellent opportunities provided the investigator is a really skilled

and devoted technician. Years ago the beautiful centrosomes and asters of *Stypocaulon* were figured by Swingle[96] and while they have been seen in *Cladostephus* and other genera no comprehensive study of them throughout the family has appeared. These structures are too rare in plants to deserve such neglect.

Respecting nuclei and the chromosomes in division the greatest opportunities exist. Godward[32] has shown that *Spirogyra* in some species has by no means the great number of nondescript chromosomes assumed characteristic for the family, but quite small numbers and of distinctive shapes. It is to be hoped that these studies can be carried throughout the Zygnematales and extended to the Desmidiales, not only with care as to cytological observations but likewise to identity of the plants studied. Particularly in the Zygnematales this is only to be trusted to a highly trained specialist. As other orders of "green" algae have hardly been studied at all the opportunities are manifold. They are valuable precursors to genetical experiments among algae, which have hardly begun.

With traditional cytology of the protoplasts poorly developed, it is most interesting to see that electron microscopy has been applied with spectacular success to formed wall structures, flagella, etc. Algae are especially suited for studies of the fundamental structure of the cellulose wall[15]. Notable are the splendid photographs and interpretations of siliceous diatom walls by Kolbe[56], showing accurately the types of structure resolved with such difficulty and disputed so vehemently by the very skilled diatomaniacs of the turn of the century, and on the frame of these a whole new and far smaller category of structures and markings which doubtless are taxonomically significant, and will have to be searched for and described through the thousands of known species.

Diatoms have led the way, but other groups are now being studied and the development of this field is likely to be rapid for some time. The Coccolithophoridae, important in marine plankton, have been studied by Braarud[10] and Halldal[34] and good wall characters shown to be present. *Synura* has been known to possess minute surface projections: these Petersen[77] and Fott[26] have shown to possess very characteristic structures, as do the scales of *Mallomonas* (Fott[25]), these being structures beyond the practicable range for study by optical, even ultra-violet, microscopy. It is not only the "hard" structures of the wall which can be studied by this means. For some years by older techniques we have been learning much about the structure of flagella and have come to know that they are not all simple smooth homogeneous rods, but these observations are now being extended by the electron microscope to show various types of surface, smooth to elaborately brush-like, and a considerable complexity of internal structure. Here, too, the work is just beginning.

VII

I have tried to indicate, subject by subject, the situation respecting each facet of algal study as this account was developed, since it seemed more useful to suggest the possibilities for advance in each part in direct relation to what has already been done. Consequently I will here give only a very brief summation.

Studies of algal distribution and systematics are still in the very actively growing phase, with great areas of the world almost completely unsurveyed. A very great deal of field and laboratory work, enough to occupy the probable corps of investigators for many decades, still needs to be done and until it is done designation of local races and forms is premature. Practical manuals are needed first of all, of such areas as South America for an example.

Ecological studies of bottom-growing algae, marine and freshwater, have hardly passed the superficial descriptive phase. Plankton ecology has gone further and there are numerous good examples, quantitative as to conditions and productivity, in the literature, but of course many more are needed. Studies of equal precision bearing on bottom algae, especially the marine species which are macroscopic and physically comparable to land plants, are almost lacking and should be carried out. Observations on the marine algae of deeper waters are fragmentary and reports misleading; many extensive dredge surveys at depths of 50–200 m are needed and will show a much more varied flora than one would assume from the general literature. Systematic and ecological studies on algae of special habitats, such as snow and ice, brine and soda lakes, hot springs, sulphur water springs, and the soil itself will all be profitable; only enough work has been done to show the need and the nature of the results to be expected.

Algal physiology and biochemistry has suffered from the fact that the studies have usually been made to use algal material to elucidate some point in a broader problem, rather than to make a comprehensive study of the comparative physiology of related algal types. For many isolated problems the algae, as aquatic organisms showing among them various capacities respecting the salt content of the medium, offer unique advantages among plants. More studies are needed on practically all phases of algal physiology, and particularly the processes in the marine species. Studies on the biochemistry of substances formed by algal cells have far to go before they are comparable in completeness to those on land plants.

Morphological studies on the algae are so essential to basic classification and even immediate recognition of individual species that this field has not been as neglected as some others. However, the approach has been one of sampling rather than of comprehensive studies of defined groups, and it has too often been assumed that individual observations yielded information characteristic of a group of many genera. There is ample room for much

significant research and past work has set good standards. Cytological studies have been rather simple in the past, and very much more needs to be done not only at the pedestrian level of chromosome counting but of all parts of the cell in all growth relations, and with the most exacting techniques. Electron microscope studies, which so far have been rather limited to studies of firm wall structures and flagella, but which have been remarkably informative, should be applied to all practicable structures.

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FUNGI

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I. THE EARLIER HISTORY OF MYCOLOGY

FROM the earliest times the larger fungi must have excited Man's interest, and it is not, therefore, surprising to find many references to them in the writings of the Greeks and Romans. The Ancients were concerned with fungi mainly as delicacies such as truffles and *Amanita caesarea* (described in a vivid word-picture by Pliny under the name "boletus"). They were also aware of the poisonous nature of some kinds such as *Amanita muscaria*. Further, the medicinal use of *Polyporus officinalis* ("agaricum" of Pliny) was widespread and the dry flesh of *Fomes formentarius*, or of touchwood heavily loaded with the mycelium of this or similar species, was used as tinder. The earliest known illustration of a toadstool is found amongst the frescoes of Pompeii, overwhelmed in A.D. 79. Cereal rusts attacked the crops of the Ancients as they do our own fields today, but the rust was not, of course, recognized as a fungus and the only method of control lay in propitiating the god Robigus.

The herbalists of the Renaissance period paid little attention to fungi. Caesalpinus in *De Plantis* (1583) refers to them in these terms: "Some plants have no seed; these are the most imperfect, and spring from decaying substances; and they therefore have to feed themselves and grow, and are unable to produce their like." This view that fungi were simply products of decay ("excrementa terrae" according to John Bauhin's *Historia*, 1620) was the dominant one and was to persist in many quarters well into the 19th century. One herbalist, Porta, writing in his *Phytonomonica* (1588) took a more enlightened view. He said: "From fungi I have succeeded in collecting seed, very small and black, lying hidden in oblong chambers or furrows extending from the stalk to its circumference."

In fungi most of the significant structure is microscopic so that no adequate understanding of their anatomy and reproduction was really possible until after the invention of the compound microscope. Robert Hooke, the most distinguished of the early microscopists, excited by his new toy, examined a great variety of things including some microscopic fungi on a wide range of decaying substances. In his *Micrographia* (1665) he exclaims with astonishment: "The Blue and White and several kinds of hairy mouldy spots which are observable upon divers kinds of putrified bodies . . . are all of them nothing

else but several kinds of small and variously figur'd Mushroms. . . ." Hooke also saw and figured the teleutospores of the rust *Phragmidium* on rose and thought they might be "seed-cods."

Only a few years later Leeuwenhoek, in a letter (1680) to the Royal Society, recorded his examination, using his superb simple lenses, of beer undergoing fermentation. It contained minute objects "some of these seemed to be quite round, others were irregular and some exceeded the others in size and seemed to consist of two, three or four of the aforesaid particles joined together." However, it was not until 1837 that Schwann rediscovered the yeast cell and regarded it as a fungus (Zucherpilz).

The first major work on mycology was that of Micheli published in his *Nova Plantarum Genera* in 1729. His success lay in the fact that his approach to the fungi was not only microscopic but also experimental. To him we owe the establishment of the "seed theory" as against the "spontaneous generation theory" of fungus development, although his views were not to be generally accepted for over a century after the publication of his great work.

It is to be noted that in Micheli's time the distinction between seeds and spores had not yet been made. Indeed, the term spore (spora) was coined by Hedwig in 1793 and only much later did the essential differences, apart from size, between seeds and spores become apparent.

Micheli figured "puffing" in a cup-fungus and observed asci with their contained "seeds" in a lichen. He noted the "seeds" on the surface of the gills in toadstools and in one species drew their arrangement in fours. He studied the catapult mechanism of *Sphaerobolus*. Most important of all, he carried out cultural experiments. By dusting spores from one kind of mould on freshly cut surfaces of fruit such as melon, he showed that the same species subsequently appeared covering the surface on which the "seed" had been sown.

Many contributions were made to the study of the fungi during the next hundred years or so, but it was Anton de Bary (1831–1888) who really laid the foundations of modern mycology. Not primarily a systematist, his contribution was essentially to the study of development and life histories in fungi. His great text-book *Vergleichende Morphologie und Physiologie der Pilze, Mycetozoen und Bacterien* was published in 1866 with a second edition eighteen years later which was translated into English (1887). This book is still to be read with great profit by all mycologists, for it deals with fungi as living, dynamic organisms. It is a great pity that those who in this century have written text-books on fungi did not study to a greater extent the outstanding example set by de Bary. Amongst his chief contributions were the discovery of the full life-cycle in rusts and particularly the demonstration of heteroecism in the black stem-rust of wheat (*Puccinia*

graminis), the proof of the pathogenic nature of *Phytophthora infestans* on potato which laid the foundation of the germ-theory of disease, and the investigation of sex and development in Ascomycetes and Phycomycetes.

De Bary began his work in the middle of last century when there was a general stirring of interest in the fungi. Persoon (1761–1836) in his *Synopsis Methodica Fungorum* (1801), the starting point for nomenclature or rusts, smuts and Gasteromycetes, had laid the foundation for modern fungal taxonomy. Elias Fries (1794–1878), the Linnaeus of mycology, had published his *Systema Mycologicum* between 1821 and 1832. Except for the groups which start from Persoon's *Synopsis*, fungal nomenclature stems from the *Systema*. Fries was a great naturalist and systematist, but he was not much concerned with fungi as living developing organisms and all his work was done without the aid of a compound microscope. The Tulasne brothers (Louis 1815–1885 and Charles 1816–1884) were working in Paris and published their *Selecta Fungorum Carpologia* between 1861 and 1865, which contributed so much to the morphology of Ascomycetes. The brothers especially stressed pleomorphism in fungi, that is the existence of more than one spore-type in the life-cycle. The work was particularly noteworthy on account of the beautiful illustrations of microscopic details drawn by Charles Tulasne which have never been surpassed and have only, perhaps, been equalled by those of Brefeld, Thaxter, Buller and, more recently, Corner. Again, in our own country, Rev. M. J. Berkeley (1803–1884), the father of British mycology, was making monumental contributions to systematic mycology. In 1938 he had discovered the true nature of the hymenium in toadstools with the basidiospores borne, usually in fours, externally on basidia—a discovery which had been made independently a year earlier (1837) by Léveillé. Berkeley realized the immense importance of the fungi in agriculture and horticulture, and contributed an important series of articles on "Vegetable Pathology" (1854–1857) to the *Gardeners' Chronicle*.

In the fifties of last century the main outlines of modern mycology had been sketched. It would be a difficult and tedious matter to trace the development of the science during the last hundred years. It is proposed, therefore, to consider individual aspects of the subject and to outline their course, their present position and sometimes their possible future. But here again there is difficulty, for no single topic can be isolated from others. The course of evolution of the subject is not like a branching tree but, appropriately enough, like the mycelium of a higher fungus, with anastomoses frequently occurring between neighbouring branches.

In concluding this section it should be mentioned that the fungus lore of the Ancients has been considered in some detail by Buller[30], Ramsbottom[126] has given a scholarly account of the expanding knowledge of

mycology since the time of Linnaeus, and the history of fungi in relation to plant pathology has been told by Large[109].

II. SEX AND INHERITANCE IN FUNGI

Sexuality in fungi was first recorded in 1818 by Ehrenberg who described and figured conjugation in the mucoraceous mould *Syzites megalocarpus* (= *Sporodinia grandis*). In the next forty years or so the sexual organs in Oomycetes and a number of Ascomycetes were described by de Bary, Pringsheim, Cornu, and others, whilst the Tulasne brothers had figured conjugation of the primary conidia of *Tilletia*. These earlier studies in sexuality were made on living material and before the special significance of the nucleus was recognized. In the seventies of last century, however, botanists became alive to the importance of the nucleus in the cell due to the researches of Strasburger, Flemming, and others. Karyogamy became recognized as the really essential feature of sexuality and the attention of mycologists was turned towards the recognition of this phenomenon in fungi. For example, in the eighteen-nineties, Trow[145] demonstrated nuclear fusion in oospore formation in *Saprolegnia*, Dangeard[48] described nuclear fusion in the ascus-initial cell in *Peziza* and Wager[146] in the young basidium. It was realized that in certain fungi, notably rusts and smuts, a very remarkable phenomenon occurred with a prolonged interval between nuclear association (at the time of union of the sexual organs) and nuclear fusion, with conjugate division of paired nuclei occurring between times.

During the first half of this century controversy raged over the life-cycle in the higher Ascomycetes with special reference to the minute discomycete *Pyronema confluens*. Harper[76] reported two fusions in the life-cycle: the first following union of the sexual organs when the contents of the antheridium entered the ascogonium (oogonium), and the second in the ascus initial cell. According to this view the single nucleus in the young ascus was tetraploid. This idea was strongly supported by Gwynne-Vaughan (née Fraser) and her school. She further gave evidence of two reductions in the ascus: the first ordinary meiosis involving two divisions of the nucleus with the production of four diploid nuclei, and the third, a shortened meiosis (brachymeiosis), reducing the chromosomes in each of the final eight nuclei of the ascus to the haploid number (Fraser[60]). The controversy stimulated a great deal of valuable work on sex and cytology in fungi, but now there are very few mycologists who are convinced that brachymeiosis occurs, and all the genetical evidence, now of considerable volume, is completely inconsistent with its occurrence.

One of the most significant advances came in 1904 with Blakeslee's discovery of heterothallism in Mucorales[17]. This was followed by the demonstration by Edgerton[53] in 1914 of the same phenomenon in the ascomycete

Glomerella. In most heterothallic Ascomycetes, however, it soon became apparent that the difference between the two strains (+ and −) could not be accounted for on the basis of sex, since both produced male and female organs. Self-incompatability was involved. The next big advance was the discovery by Bensaude[10] and Kniep[106] independently of heterothallism in larger Basidiomycetes involving vegetative fusion between compatible monokaryotic primary mycelia to give a secondary dikaryotic mycelium with clamp-connections on which a fruit-body could develop. Further, Craigie[47] showed that heterothallism also obtained in rusts, with insects acting in Nature as agents in crossing + and − strains by the transfer of pycnidial nectar. Another considerable contribution concerned sexuality in the yeasts. Winge[160] in 1935 showed that *Saccharomyces* is normally diploid, the ascospores being haploid. Lindegren[112] and others have shown that in some strains heterothallism occurs. A single ascospore buds to give a haplophase colony of small cells. Mixing of + and − haplophase results in pair-wise fusion, the diploid zygotes budding at once to give the diplophase. *Saccharomyces* is unusual in having an extended diploid stage. In most fungi it is replaced by a dikaryophase, as represented by the secondary mycelium of the higher Basidiomycetes and the ascogenous hyphae of Ascomycetes, but an interesting parallel occurs in the beautiful phycomycete *Allomyces* (investigated by a series of workers of conspicuous quality: Butler[33], Kniep[107], and Emerson[54]) in most species of which an alternation of generations occurs between haploid gametophyte and diploid sporophyte of essentially similar vegetative morphology.

An outstanding advance in the study of sexuality in fungi was made by J. R. Raper[127]. Certain species of the water mould *Achlya* are heterothallic. Male and female strains were found to remain asexual and indistinguishable one from the other when grown alone. When grown together each stimulated the other to produce its characteristic sexual apparatus. Raper made the important discovery that the development of the sexual organs and the course of the whole sexual process was co-ordinated by a series of hormones successively produced (fig. 1). None of these has, however, yet been identified chemically. Very recent work by Bistis[13] from Raper's laboratory suggests that hormones may also be involved in the sexual process of the ascomycete, *Ascobolus*. Clearly this is a field of research in which interesting developments may be confidently expected in the coming years.

The discovery of heterothallism opened the field for genetical experimentation on fungi. The initiation of this work was due largely to the great American mycologist B. O. Dodge who used *Neurospora*. From the point of view of the geneticist such an organism had great advantages: the generation time was short; the mycelium being haploid, the phenotype directly reflected the genotype; but above all the products of a single meiosis were

neatly wrapped up in orderly arrangement within the uniseriate ascus. Further, the production of mutants by standard genetical procedure was a simple matter. Fungi have now become some of the favourite tools of the geneticist. Pyrenomycetes are by no means the only fungi involved. There is a considerable literature on the genetics of yeast, inheritance in rusts and

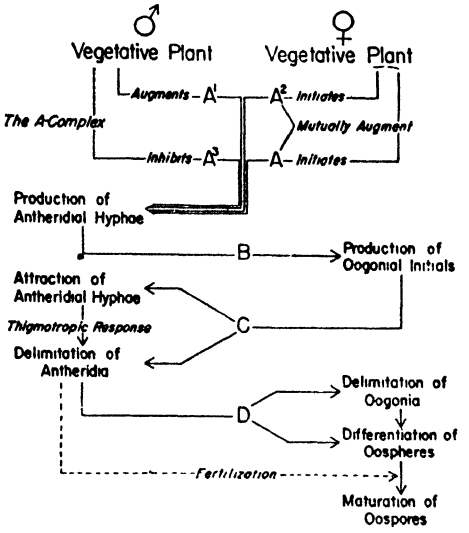


Fig. 1. The hormonal mechanism which co-ordinates the sexual reaction between male and female plants in a heterothallic *Achlya*. Each line designated by a letter indicates a specific hormone, its origin, and its specific activity. (After J. R. Raper.)

smuts has been much studied, and now agarics such as *Coprinus* and *Schizophyllum* are being extensively employed.

In Mucorales and Ascomycetes in each heterothallic species there are + and − strains. In most agarics, however, four strains of primary mycelium occur making two compatible pairs. This is due apparently to compatibility being determined by genes at two separate loci (not one as in Ascomycetes). Thus from a fruit-body the strains might be a^1b^1, a^2b^2, a^1b^2 and a^2b^1, the first and second, and the third and fourth being compatible. The basic principle is that any strain will mate with any other which has no common allele. Further it has been found, starting with the work of Kniep[106] and Hanna[71], that each locus has a series of multiple allelmorphs (e.g. a^1, a^2, a^3, a^4 . . .) with, in most fully investigated species, a large number in each series. Thus any strain derived from a single basidiospore from one fruit-body is likely to be compatible with all four strains from another fruit-body a few hundred yards away. A rather efficient outbreeding mechanism is involved.

Although there have been staggering advances in fungal genetics in the past fifteen years, the association of genetical behaviour with that of the

chromosomes has been slow to develop. The result is that cyto-genetics and particularly cyto-taxonomy of the fungi are subjects largely for the future. This is due to the fact that most fungal nuclei are so terribly small. Indeed, in some groups the position is quite exasperating. Thus in Mucorales the nuclei are so minute that karyogamy in the zygospore and subsequent meiosis have not been established on really satisfactory cytological evidence. However, here and there, cytological work of the kind that may ultimately

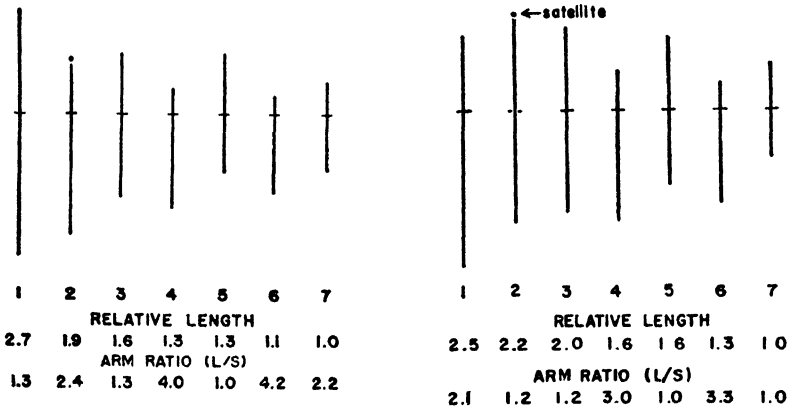


Fig. 2. Relative lengths, centromere positions and the ratio of long-short arm of the mitotic metaphase chromosome complement of *Neurospora crassa* left (after Singleton, 1952) and of *Sordaria fimicola* right (after Carr and Olive, 1958).

help in cyto-taxonomy has been started. Thus, Wilson[158] has made a beginning with *Allomyces* and several workers have obtained clear cytological pictures of chromosome morphology in Pyrenomycetes. Particularly interesting has been the work of McClintock[114] on *Neurospora crassa* confirmed and extended by Singleton[133]. These workers give clear pictures of the morphology of each of the seven chromosomes constituting the haploid set. It is most interesting that Carr and Olive[38] have recently shown that the 7 chromosomes of *Sordaria fimicola* show a very close similarity to the *Neurospora* set (fig. 2). It would seem that there is a promising field of cytotaxonomic work in higher Ascomycetes. The position is very different in the lower Ascomycetes, particularly the yeasts. Although so much is known about yeast genetics, the nuclear picture is as obscure as ever. There is no agreement about the basic structure of the nucleus, nor about the interpretation of division figures in terms of chromosomes.

A feature of higher fungi with septate mycelia which, in recent years, has come to be regarded as of great significance, is the existence of a pore in each cross-wall through which not only cytoplasm but also nuclei can pass. There is strong evidence to suggest that when compatible monokaryotic mycelia of a toadstool meet and vegetative anastomoses occur, the nuclei

of one strain can pass into the other and quickly and completely dikaryotize it. This phenomenon was originally recognized on the basis of indirect evidence. However, in recent years due to the use of the technique of phase-contrast microscopy, it has been possible to follow directly the invasion of one mycelium by nuclei from another. Dowding[50], who has been a pioneer in this work, has shown that in *Gelasinospora tetrasperma* the invading nuclei may travel from cell to cell through the mycelium at the extraordinary rate of 40 mm/hr.

A most important advance in the genetical study of fungi was the demonstration by Hansen[72] of the heterokaryotic condition in septate fungi in the asexual conidial condition. It has been shown further by Jinks[99] that external conditions (e.g. nutrition) can affect the relative numbers of the two kinds of nuclei present in the heterokaryotic mycelium.

The most extraordinary sexual phenomenon to be found in conidial fungi is the parasexual cycle discovered and investigated by Pontecorvo[125] and his associates particularly in *Aspergillus nidulans*. This fungus, as well as reproducing by asexual conidia, has a normal sexual cycle. However, an asexual heterokaryotic mycelium may be formed following vegetative union of two genetically different mycelia. Since the conidia are uninucleate, the two genotypes of the heterokaryon separate at conidium formation. Occasionally nuclear fusion occurs within the mycelium with the production of diploid heterozygotic nuclei which may pass into conidia. In the asexual diploid strains developing from these, mitotic crossing over followed by gradual reduction (haploidization) in some of the nuclei may lead to new haploid conidia, borne on the predominantly diploid mycelium, combining characters originally present in the two different mycelia which joined to form the original heterokaryon. The implications of parasexuality in mycology generally have yet to be explored.

A further most important aspect of the genetics of fungi has been the study, with which the names of Beadle and Tatum[8] are especially associated, of biochemical mutants particularly in *Neurospora*. By the ordinary procedures of the geneticist a large number of mutant strains were produced, each heterotrophic for some complex organic growth factor which the "wild type" could synthesize. By studying a series of different mutants all heterotrophic for the same substance, but with the reaction blocked at different stages in the synthesis, the steps in the *in vivo* reaction could sometimes be deduced assuming the "one gene, one enzyme" hypothesis. Beadle and Tatum's work laid the foundations of a new branch of study—biochemical genetics. This new technique has become a most important tool in the study of certain purely biochemical problems.

Thus in the course of little more than a century the study of sex and inheritance in fungi has developed to a surprising degree and some of the

lines of research have passed beyond the range of most mycologists. Still they cannot ignore the results of this rather esoteric work which throws light on the factors influencing variability in fungi, a subject all too familiar to every student of fungi whether in the field or in the laboratory.

III. PHYSIOLOGY OF FUNGI

The foundations of the physiological study of fungi are to be seen in de Bary's work. Division III of his great text-book treats of the "Mode of Life of the Fungi"[7]. However, de Bary's approach was primarily biological rather than physiological. The development of fungal physiology really depended on pure cultures of individual species derived from single spores. This vitally important technique was introduced to mycology by Brefeld in 1869.

Fungal physiology as a subject came much to the fore after the Second World War and within a year or two of one another three important text-books were published: Foster[58], Hawker[80], and Lilly and Barnett[111].

Using pure culture methods many mycologists investigated the nutritional requirements of saprophytic fungi and facultative parasites, for the obligate parasites defied study of this kind since they could not be grown apart from their hosts.

Carbon sources available to fungi were studied. It became clear that nearly all species could use glucose, but that the ability to use other carbohydrates varied considerably. Thus the yeast (*Saccharomyces cereviseae*) cannot utilize starch. Many of the higher fungi can attack cellulose but, apart from chytrids, most Phycomycetes cannot. Some fungi, especially certain chytrids, can utilize the complex polysaccharide chitin.

Again the nitrogen requirements of fungi were investigated. It was found that some could grow only with an organic source (amino-acid, peptide, or protein) but others could use either an organic or an inorganic one such as an ammonium salt or a nitrate. It has been suggested that a very few species can fix atmospheric nitrogen but the evidence in this connection is weak.

Then again the mineral requirements of fungi were studied and were found to be much like those of higher plants. Phosphorus, potassium, magnesium, sulphur, and iron were shown to be essential for fungal growth, but the evidence suggested that calcium was not needed by most species.

The method used in most nutritional studies of the fungi in the first few decades of this century was to grow the organisms on agar in which the nutrients were incorporated. Growth was then measured by the rate of spread of the colony. The use of agar had certain grave disadvantages. Not only did it contain appreciable and unspecified quantities of mineral substances, but it also might have a certain amount of utilizable organic nitrogen and other substances affecting growth. Further, diameter of colony was a

most unsatisfactory measure since no account was taken of the denseness of the growth. All the critical work on fungal nutrition has of necessity been carried out in liquid culture on chemically defined media and growth has been determined by increase in dry weight.

Using refined methods Steinberg[139, 140, 141] from 1919 onwards published an important series of papers on the inorganic nutrition of *Aspergillus niger*. He showed that, in addition to other inorganic substances, minute traces of zinc, manganese, copper, molybdenum, and gallium were all necessary for growth of this mould.

Careful nutritional work indicated that traces of certain organic substances as well as traces of inorganic ions were necessary for the growth of some fungi. The study of growth substances, or accessory growth-factors, or vitamins has occupied the attention of experimental mycologists considerably during the past twenty years. The work really started with Wildier's[157] (1901) demonstration in yeast of an unknown growth-promoting substance which he called "bios." Later investigation found that bios was not a simple substance but a complex including several vitamins.

A landmark in fungal physiology was the demonstration by Schopfer[131] (1931–1934) that *Phycomyces* required thiamin (vitamin B_1) for growth. Indeed, at very low concentrations (less than 20μg/l) growth is directly proportional to the concentration of thiamin in the medium, and so *Phycomyces* can be used in the biological assay of this vitamin, measuring amounts far below those that could be detected chemically. This technique of biological assay has developed into an important tool for biochemists and physiologists (see Barton-Wright[5]).

As the result of the considerable work of the past twenty years on the vitamin and amino-acid requirements of fungi, it has become apparent that there is a great variation amongst different species. It is now clear that these growth-substances are necessary for fungi generally, the question is whether a particular species can synthesize its own supplies or not. Thus *Phycomyces* needs an external source of thiamin, but some Mucoraceae are autotrophic in this respect. In *Neurospora*, although the "wild type" is autotrophic for thiamin, mutants can be obtained which are heterotrophic for it. Further, some of these can perform part of the thiamin synthesis, but not the whole. Thus one mutant can synthesize the thiazole part of the molecule and another the pyrimidine part. Neither by itself can grow on a medium without thiamin, but the heterokaryon, formed following hyphal fusion of the two mutant strains, can grow freely.

Nutrition affects not only the amount of growth but also its nature. Reproduction, referred to loosely in fungi as "fruiting," is often greatly influenced by nutritional factors. Further, fungi frequently produce more than one type of reproductive body and the kind of reproduction may itself

be influenced by the nutritional status of the medium or by other external conditions. The effect of nutrition on reproduction was first studied by Klebs in a series of classic researches at the very end of the last century[105]. In more recent years attention has been given to vitamins in relation to reproduction. The pyrenomycete *Sordaria* has been particularly studied (Hawker[77, 78, 79], Lilly and Barnett[110], and Bretzloff[21]). Few generalizations can be made concerning the fruiting of fungi, but it seems that one is fully justified, namely that the conditions necessary for sporulation are more exacting than those for vegetative growth. A further point is that fruiting is often to be considered as a multiple-stage process with the possibility of special requirements at the different stages.

There has accumulated a great amount of empirical information concerning the influence of nutrition, pH, temperature, and light on growth and fruiting in fungi, but it is now realized that the type of question that really needs an answer is how does a particular condition exert its effects, and it is generally realized that the answer is likely to be a biochemical one. In this connection the recent work of Cantino[36] and his associates during the past few years is of special interest. He has worked with a minute aquatic phycomycete, *Blastocladiella emersonii*. The thallus of this is of limited growth and a pure culture consists not of a single mycelium, but of a collection of millions of individual plants. It reproduces by zoospores. A particular zoospore may give rise either to a microscopic plant bearing a single thin-walled zoosporangium or to a similar plant with a resting spore having a thick brown wall. The course of development can be determined by bicarbonate. With this in the media the individuals bear resting spores; without, zoosporangia. Cantino's team have attempted to find evidence for the metabolic shunts responsible for this difference—shunts towards increased chitin and fat production, and *de novo* synthesis of melanin to produce the wall material necessary for the brown resting spore. Although it is not always easy for the non-biochemical mycologist to follow Cantino's arguments in detail, it nevertheless seems that the future lies in developing work of this kind. Indeed, the biologist, however reluctantly, is coming to realize that most biological problems eventually lead him into biochemistry.

Cantino's work is an attempt to grapple with the problem of morphogenesis in a very simple fungus. Another remarkable field of work in morphogenesis centres around the study of certain members of the Acrasieae, especially *Dictyostelium*. Outstanding contributions to this problem have been made by K. C. Raper[128], Bonner[18], and Sussman[142]. However, it may well be doubted if the Acrasieae can possibly be included in fungi unless we define fungi as "organisms studied by mycologists." In the higher fungi (toadstools) the physiology of morphogenesis has been studied by

Plunkett[124]. There is no doubt that further work on the underlying causes of structure in fungi is much to be desired.

In connection with nutrition, mention must be made of the by-products which accumulate in fungal cultures. These have been known for a long time and, since they often lead to retardation and finally cessation of growth, are referred to as staling products. These, however, came to have a great significance following the discovery of penicillin as a by-product of *Penicillium notatum*. This bacteriostatic antibiotic was first studied by Fleming[57] in 1929, but its full importance in medicine came only during the Second World War. The study of antibiotics has had a profound effect on the study of fungi. From being a rather obscure subject, apart from phytopathology, mycology suddenly found itself in the limelight, and in the intense search for more and better antibiotics a great deal of important mycological work has been accomplished. However, in general, antibiotics themselves appear to be of little interest to students of fungal physiology, for they do not seem to have much significance for the life of fungi themselves. One conspicuous exception is gliotoxin produced by the very common soil fungus *Trichoderma viride*. In a series of important papers Weindling and his associates[154, 155, 156] have shown that this antibiotic is intimately concerned in the poisoning mechanism by which *Trichoderma viride* attacks other soil fungi such as *Rhizoctonia solani*.

Increase in dry weight and in colony diameter have been studied in relation to the general question of nutrition, but other aspects of growth have also been considered. Further, differential localized growth produced as a result of external stimuli and leading to tropistic movement has been the subject of much investigation. In this connection the beautiful sporangiophores of the mucoraceous mould *Phycomyces* have proved especially valuable as experimental material. Blaauw[14, 15] (1914–1915) studied the rhythmic changes in growth rate following brief illumination and Castle[40, 41, 42] in a long series of brilliant papers has contributed greatly to the story of growth and phototropic curvature in this fungus. In the study of phototropism another mucoraceous mould, *Pilobolus*, has been extensively used. The action spectrum of the process in these fungi shows a maximum in the shorter (blue) visible rays in the region round about 450$\mu\mu$ (Castle[41] and Bunning[31, 32]) and this is also the region of maximum light absorption by the carotinoid pigments present in *Phycomyces* and *Pilobolus*. However, there is a danger in assuming that these pigments are, indeed, concerned with the photo-reception, because, besides carotinoid pigments, flavins, very generally present in fungal cells, have closely similar absorption spectra. In the fungi generally when light exerts an effect as in phototropism, stimulation of spore discharge (Ingold and Dring[98], and Ingold[95]), or in carotinoid pigment production, it is the blue rays which are effective. It is to be hoped that future research

will settle the point of the photo-receptor and pass on to a consideration of how the light brings about the observed effects. Again the answer is in all probability a biochemical one.

The rapid enlargement of mushrooms and toadstools has often attracted attention and most mycologists have assumed that the sudden expansion of the fruit-body from the "button" stage is due to rapid absorption of water, accompanied by little inflow of solid material. However, recent work by Bonner[19] has shown that during the rapid expansion of a mushroom, the proportion of water in the tissues does not increase. Water and solid matter must enter the fruit-body together. The question of growth in the aerial structures of higher fungi involves translocation about which very little critical information is available. An exacting experimental approach to the problem of translocation both of water and of organic food in fungi is greatly to be desired.

Another outstanding matter much in need of investigation is the question of hormone control of growth. In higher green plants auxin (indole-acetic acid) has been shown to be of essential importance in controlling and co-ordinating growth. However, available evidence suggests that it plays no comparable part in the fungi. Auxins seem to exert their effects principally on the cellulose cell-wall, but with the vast majority of fungi a chitinous rather than a cellulosic one is involved. It seems possible that griseofulvin, a by-product of certain species of *Penicillium* discovered by Brian[22, 23] which in very low concentration (0·1 mg/l) causes spiral growth (curling) in fungi, may be a fungal auxin. Banbury[3] has shown that when griseofulvin is incorporated in lanoline and applied unilaterally to the growing region of a *Phycomyces* sporangiophore, localized increased growth causes curvature. This is a most promising line of study. A real understanding of tropistic response in fungi would constitute a considerable advance in fungal physiology.

Another important aspect of growth in fungi is spore germination. The first major contribution to this study came from Hoffman[86] in 1860 and the large literature on the subject since then has been reviewed by Gottlieb[67]. The germination of fungal spores presents many problems. Some spores can germinate at once, some only after a period of rest, others, especially those of coprophilous species, require special stimulation before germination can occur. Many basidiospores germinate with difficulty and in particular in the Phallales (stink-horns and their allies) germination has never been satisfactorily demonstrated. A systematic attempt to germinate these spores might throw interesting light on the biology of these fungi.

Since the first stage in the attack of a parasitic fungus on a host plant is usually the germination of spores on the leaf-surface, this matter is of great interest to the phytopathologist. Usually for a successful germination the

spore must find itself in sufficiently persistent "infection drops" provided by a recent shower or dew, but with certain powdery mildews the oidia can germinate in the absence of free water and at extraordinarily low humidities (Yarwood[161] and Brodie and Neufeld[26]). The physiology of this unusual but well-attested phenomenon is difficult to understand and would repay critical study.

The behaviour of the spore in the infection drop represents the point of departure of a most important study by Brown[27, 28] on the physiology of parasitism of the unspecialized parasite *Botrytis cinerea* which can attack the soft aerial tissues of a wide range of host plants. As so often, this work stems from that of de Bary[6] who in 1886 contributed a classical paper on the mode of attack of *Sclerotinia libertiana* on broad bean, carrot, and other fleshy tissues. As a result of Brown's researches it has been established that there is a pre-penetration stage in the infection drop when spore germination may be stimulated by outward diffusion of dissolved substances into the drop from the tissue below. The cuticle is unaffected by enzymes produced by the germinating spore, but an appressorium, formed from the tip of the germ tube, grips the surface while its centre grows and punctures the cuticle mechanically. Then the post-penetration phase begins. An enzyme (pectinase), produced by the hyphal tips, diffuses in advance, killing and partially disintegrating the tissue. The fungus then flourishes on the dead cells. Conditions favouring the production of this enzyme may determine whether or not a particular tissue is parasitized by the fungus. Not all fungi enter and attack their hosts after the manner of *Botrytis*, and the story of parasitism is certainly quite different in the obligate parasites. However, the work of Brown and his students is a model, and is undoubtedly the greatest single contribution to this fundamental problem. The whole question of the physiology of parasitism has been summarized rather fully by Gaümann[64] in a somewhat controversial volume.

The fundamental problems of physiology concern metabolism, the transformation of substances involving energy release and interchange within the fungal cell. On the whole these problems have largely been studied by plant physiologists rather than by mycologists and cannot be considered to any extent here. However, it is interesting to note that fungi often provide most useful experimental material for the physiologist. In this connection yeast has been particularly prominent and an understanding of the process of alcoholic fermentation has largely contributed to knowledge of the whole process of plant respiration. The all-important part played by phosphorus was first established by the work of Harden and Young[73] on yeast in 1905.

Moulds have also been much to the fore as experimental organisms in the study of organic acid metabolism. Twenty years ago mycologists

confidently stated that the fundamental difference between green plants and fungi was that the former could assimilate carbon dioxide whilst the latter could not. Now, arising particularly out of the work of Foster and Davis[58], it is known that carbon dioxide may be absorbed and incorporated into organic acids. Further, for some fungi at least, carbon dioxide appears to be an essential nutrient (see Foster[58]). It is true that this assimilation of carbon dioxide bears no relation to photosynthesis. However, recently Cantino and Horenstein[37] have shown that in *Blastocladiella*, although assimilation of carbon dioxide goes on in the dark, it proceeds at a much greater rate in the light. This brief mention of the subject of carbon dioxide assimilation in fungi serves to remind us that major generalizations often fail to stand the test of time.

IV. LIBERATION AND DISPERSAL OF SPORES

In fungi the feeding part is usually hidden away as a branched and often perennial mycelium in the nutrient substratum. The fruit-body that the field mycologist collects is, however, usually an ephemeral structure concerned with spore production and liberation, processes with which much of the beauty of form and structure in fungi are intimately associated. It is usually necessary to distinguish between spore liberation and subsequent dispersal and the study of these two processes has developed rather independently, although they are so intimately connected. It will, therefore, be simpler to consider them separately.

Micheli (1729) seeking for "seeds" in fungi, made important contributions to the study of spore liberation by observing "puffing" in *Peziza* and by describing the catapult mechanism of the minute gasteromycete, *Sphaerobolus*. Nearly a century and a half later de Bary's text-book (1887) included a chapter on "Development and scattering of spores." This gives an excellent account of spore liberation particularly in Ascomycetes, but at that time little was known about basidiospore escape in toadstools.

Certainly the greatest contribution to the subject of spore liberation was the work of Buller reported in his seven magnificent volumes of "Researches on Fungi," published between 1909 and 1950[29]. In particular he studied the liberation of basidiospores from fruit-bodies. He found that the spores are discharged in succession from the basidium to a distance of 0·1–0·2 mm. He showed how in Hymenomycetes the structure of the sporophore is intimately related to its function, the arrangement of vertical or downward facing hymenial surfaces on gills (in Agaricaceae), lining pores (in Polyporaceae), covering teeth (in Hydnaceae), or on erect branches (Clavariaceae) being associated with violent discharge of spores to a very short distance. He also made interesting observations on form and function

in Asomycetes and emphasized the importance of phototropism of the asci during spore discharge in Discomycetes.

In more recent years spore discharge in Pyrenomycetes has been considered by Ingold[92, 95, 97] especially in *Daldinia* and *Sordaria* and he has also reviewed the general field of dispersal in fungi[93]. Brodie[25], developing a line of research initiated by Buller in the last years of his life, has made a careful study of the beautiful splash-cup mechanisms of peridiolum discharge in *Cyathus* and *Crucibulum*, and Gregory[69], using the technique of high-speed cinematography, has shown how the puff-ball *Lycoperdon* is operated as a natural bellows by falling raindrops. Gregory and his co-workers have studied the important question of splash-dispersal of slime-spore fungi, but their findings have not yet been fully published.

In connection with violent spore liberation one noteworthy point remains obscure. It is quite clear how an ascus works. It is essentially a turgid cell which bursts, scattering its contained spores. However, it is not at all clear how basidiospores are discharged from the basidium. The visible events associated with discharge are well-known, thanks to Buller's researches. The spore is poised asymmetrically on a fine sterigma. Near its junction with the sterigma the spore has a minute projection (hilum). Just before discharge a drop of liquid appears at the hilum, grows to a certain definite size and then spore and drop are shot away. The four spores normally present on the basidium are discharged in succession. The theories[94] concerning discharge need not be enumerated here. None is really satisfactory, but it is greatly to be hoped that the problem of the mechanism will soon be solved. Perhaps high-speed cinematography might provide the essential clue.

Aside from questions of violent spore discharge, it has become increasingly clear that even with the commonest fungi and with pathogenes of economic importance, exact information concerning the take-off of spores is often sadly lacking. Critical experimental studies in this field would be most valuable.

Turning to the question of the actual dispersal of liberated spores a fundamental point—the omnipresence of fungal spores—was made very early (1765–1779) by Spallanzani. As the result of careful experimental work on the growth of moulds, he concluded that spores "may be disseminated in such abundance as to enter into the composition of all animal and vegetable substance . . . it is the readiest method of accounting for the extraordinary abundance and universal existence of mould. . . ." However, it was not until the researches of Louis Pasteur (1861) a century later that the "aerial spora," as P. H. Gregory has called it, was fully demonstrated. Pasteur drew air through a tube stuffed with gun-cotton. Later he dissolved the nitrocellulose and examined the catch microscopically finding the spores of moulds and cells of yeasts. This was the first step in what has become known

as aerobiology. A few years later, catching spores on a greased slide exposed in an "aeroscope," Cunningham (*circa* 1873) investigated the spores in the air in the grounds of an Indian jail recording his results in a beautifully illustrated monograph. Since that time much work on the air spora has been accomplished partly by those interested in inhalent allergy and partly by plant pathologists concerned with studying the epidemic spread of fungal diseases. In Britain, from the point of view of allergy, the work of Hyde

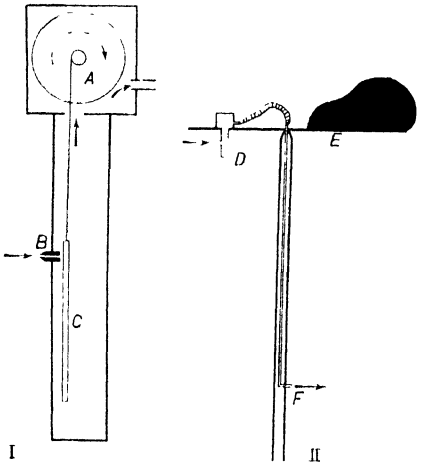


Fig. 3. Hirst spore-trap. I. Impactor unit about half natural size shown, very diagrammatically, in vertical section. Air is drawn through the unit by a suction pump entering through slit (B) flowing as shown by arrows. Spores are impacted on sticky slide (C) which is moved upwards at 2 mm per hour by clock A.

II. Diagram showing mounting of impactor unit (D) on wind vane (E) so that the inflow slit always faces into the wind. The tube F is connected to the suction pump.

and Williams is particularly outstanding[89]. In addition to their study of pollen in the air, these workers have given much attention to the prevalence of *Alternaria* spores, although the evidence suggests that they are not important allergens.

In plant pathology the work of Stakman in America is especially significant in relation to the epidemiology[136]. In an early series of experiments Stakman and his co-workers[137] exposed sticky slides from an aeroplane and caught spores of *Alternaria*, uredospores of rusts and conidia of *Helminthosporium* in a viable condition at heights up to 11,000 ft. This type of work appealed to mycologists of a somewhat adventurous nature and the air, particularly in America, was combed for fungal spores, without adding greatly to the earlier knowledge.

The more recent developments in the study of aeromycology centre round the work of P. H. Gregory. In 1945 he published a long paper on

dispersion of air-borne spores, giving a mathematical treatment of the fundamental meteorological problems involved[68]. Since then, using slit-sampler impactors which give a quantitative measure of numbers present in unit volume of air, he has studied dispersal both under the controlled conditions of a wind tunnel and in the field[70]. Further, Hirst[84] has devised a slit-sampler which can be used to obtain a continuous record of the spore content of the air over a 24-hour period (fig. 3). With this accurate method the outbreak of disease caused by air-borne pathogens with recognizable spores can be studied in relation not only to predisposing weather conditions but also in relation to the actual spore load in the air. Hirst and his co-workers[85] have used this method with great success in studying the outbreaks of apple scab (*Venturia inaequalis*) in orchards. With the general employment of sound quantitative methods in the study of epidemiology considerable progress in this field may be expected in the coming years.

V. FUNGI OF SPECIAL HABITATS

In this section it will not be possible to deal with the very large subject of the ecology of fungi in all its aspects, but two biological groups will be discussed, selected for their special importance or interest and the others will be little more than listed.

Soil Fungi

Because of the economic significance of the soil its fungal flora has received much attention. The first major contribution came from Oudemans and Konnig[123]. A conspicuous figure in this work has been Waksman[148–150] who from 1916 onwards has contributed important studies on soil fungi. He demonstrated that the soil contains a world-wide and fairly characteristic mycoflora in which species of *Mucor*, *Penicillium*, *Trichoderma*, and *Aspergillus* predominate. In half a century an immense literature on the subject has accumulated.

The problem of studying fungi in soil presents great difficulties. The method of plate counts from soil dilutions is applicable to bacteria since each cell is usually a separate reproductive unit, but the position is quite different in such a highly differentiated structure as a fungus. Many have, however, used this method (e.g. Brierley[24]), but although it gives objective results their interpretation is not easy, especially when it is also borne in mind that the results are greatly affected by the medium used and by the different rates of growth of the various species. An attempt to gain a picture of the true mycelial distribution in soil was made by Rossi[129] and Cholodny[44]. This method (Rossi-Cholodny slides) consists of pressing a clean glass slide against a fresh soil surface and, after brief incubation, fixing the mycelium on its surface for microscopic examination. This method has now been

developed as a quantitative one, but it has its obvious disadvantages. An extreme example of an attempt to gain a picture of the *in situ* occurrence of soil fungi is the work of Alexander and Jackson[2] who, by impregnating soil with a suitable resin, converted it into a rock-like mass which could be sectioned by petrological procedure. In the "rock-sections" mycelia and even conidiophores could be seen in their true relationship to the soil particles. This would seem, however, to be too tedious a method for routine use.

A considerable advance in the study of soil fungi has resulted from the work of Warcup[151, 152, 153] using his simple "soil-plate" method. In this a few milligrams of soil are mixed in a petri dish with a suitable agar just before it sets. Warcup has reported on the distribution of fungi in a number of soil profiles, and it is a measure of the value of his method that he has been successful in isolating Hymenomycetes on his plates. He has shown that in a volume of soil occupied by the mycelium of such a species as *Marasmius oreades*, the occurrence of other soil fungi is considerably reduced. Chesters[43], in a review of the whole subject, emphasizes the fact that the fungi grow on organic matter in the soil and stresses the need for studying not only the fungi in the soil proper, but also those on the dead and dying vegetation on the surface which is contributing organic matter, and also probably donating part of its mycoflora to the soil itself. Gilman[65] has helped the study of the subject by collecting information on the systematics of soil fungi in a single volume.

Soil is heterogeneous and in a profile there is a general decrease in fungal numbers with depth no doubt associated with decreasing organic matter. Also a special environment for micro-organisms occurs around roots. Hiltner[83] in 1904 first drew attention to this "rhizosphere," and its mycological study has been pursued by a number of workers, particularly Starkey[138].

Fungi in soil are not simply saprophytes breaking down organic matter and, perhaps, also binding soil particles into suitable crumbs; they may also be parasites of varying degrees of specialization. We owe to Garrett[63] an ecological grouping of soil fungi into (1) soil-inhabiting fungi including obligate soil saprophytes and unspecialized parasites and (2) root-inhabiting fungi including specialized parasites and mycorrhizal fungi.

It is appropriate, perhaps, to make brief mention here of the subject of mycorrhiza. This association between fungi and higher plants was first described by Frank[59] in 1885, and in the past three-quarters of a century a great amount of work has centred around this problem. Two fairly clearly separate types of mycorrhiza occur. In the ectotrophic type, associated with our forest trees, the fungal hyphae form a compact mantle around the growing roots with some hyphae passing outwards into the soil and others inwards to constitute the "Hartig net" between the cortical root cells. Here the

fungi concerned are species of such genera as *Boletus, Russula, Lactarius, Amanita* amongst Hymenomycetes, and *Scleroderma* and *Rhizopogon* in Gasteromycetes. In the endotrophic type, found particularly in Orchidaceae, Ericaceae, and Cistaceae, the fungus develops no root mantle, although scattered hyphae grow out into the soil. The mycelium occurs in the intercellular spaces and also grows into the host cells. The relationship is one of "balanced parasitism." In the inner cortical region the fungus is kept in check and prevented from being an aggressive parasite by actual digestion within the root cells. The fungi concerned are a very mixed lot including species of *Rhizoctonia* and *Endogone* and even *Armillaria mellea.* So far as orchids are concerned, seedling infection seems necessary, in Nature, for successful development of many species with minute seeds. The whole subject of endophytic mycorrhiza has been rather fully summarized by Harley[74].

In recent years interest has centred mainly around ectotrophic mycorrhiza with special reference to the nature of the relationship between fungus and tree. There is no doubt that healthy trees have well-developed mycorrhiza whilst in unhealthy ones it is poorly developed, but whether the fungus is a cause or merely a symptom of health has remained undecided. However, although full proof may not be forthcoming, there is now general agreement that the fungus is very important, if not normally essential, for the life of the tree. Much of our exact knowledge comes from the work of Melin[119] in Sweden and of his able pupils, especially Björkman and Hatch. Melin, working on conifers and using techniques involving pure cultures of both seedling tree and fungus, has demonstrated that a large number of toadstools are capable of forming mycorrhiza. He has, further, studied the nutritional requirements of the fungi concerned and demonstrated that most make rather exacting demands needing simple carbohydrates (principally sugars) together with certain vitamins and amino-acids. Simple carbohydrates have a very ephemeral existence in soil and it is only within living roots that these fungi can satisfy their carbohydrate needs. On the other hand many other toadstools growing on leaf-litter and dead wood have the enzyme equipment for dealing with cellulose and lignin.

In the ectotrophic mycorrhizal relationship it seems quite clear that the fungus gets its organic food from the tree. The difficult question is: what benefit does the tree derive from the fungal partner? It is now generally suggested that the answer lies in the supply of inorganic salts. Melin[120], using phosphate containing radioactive phosphorus, has shown in pure culture experiments that the hyphae passing out from mycorrhizal roots of pine seedlings can transfer phosphorus to the roots, and also in due course the labelled element appears in the leaves.

Considerable advances have come from the researches of Harley and his

associates at Oxford (Harley[75]). Working with mycorrhiza of beech, salt absorption has been carefully considered. In particular, by elegant dissection, the fungal sheath has been separated from the rest of the root and phosphate accumulation in both has been studied. As compared with an uninfected one, a mycorrhizal root accumulates phosphorus much more rapidly, but the accumulation is mainly in the fungal mantle. The manner in which the salt may later be transferred to the beech tissue is still obscure. Much remains to be discovered in this field, but it is only by exacting experimental study, such as that of Harley's School, that progress can be expected.

Another important problem in connection with true mycorrhiza is whether prolonged saprophytic survival in the soil of the fungi concerned is possible. Ecological work by Dimbleby[49] on certain *Calluna* moors suggests that the fungi (probably *Boletus scaber* and *Amanita muscaria*) forming mycorrhiza with birch, can survive for many years in old, dead stumps and re-establish the mycorrhizal relationship when birch is re-introduced.

Water Fungi

Fungi are characteristically land organisms and probably less than 2 per cent are aquatic, but the water fungi are often of considerable interest since they include forms with zoospores, probably to be regarded as primitive aquatics, and also Ascomycetes and Hyphomycetes, the ancestors of which may well have been terrestrial. There are no known submerged aquatic Basidiomycetes.

The primitive aquatic fungi have attracted the attention of many workers, but it would be too long a story to trace historically. The general field was ably summarized by Sparrow[135] and only more recent developments will be considered here.

There has been much interest in Chytridiales (chytrids) by far the largest order of aquatic Phycomycetes. During the past dozen years they have been extensively studied in Britain by Hilda Lund (née Canter[34, 35]). In particular she has concentrated on those species which parasitize planktonic algae and has shown, with the algalogical aid of her husband (J. W. G. Lund), how they may be responsible for severe epidemics in lakes, leading frequently to a disturbance of the normal pattern of algal periodicity. Workers both in America and Britain have succeeded in growing more and more chytrids in pure culture and a better knowledge of their nutrition is now in sight.

In other groups of Phycomycetes important contributions have been made such as the study by Thomas-Perrott[144] of British Monoblepharides; the survey of the genus *Achlya* by Johnson[102]; the demonstration by Johns and Benjamin[100] of a primitive form of oogamy in *Gonapodya*, and Emerson's[54] cultural work on *Allomyces* and *Blastocladia*. In particular

Emerson discovered the remarkable fact that in *Blastocladia* resting-spore formation is induced by very high concentrations of carbon dioxide, conditions which the fungus must encounter when, as so often, it is overgrown with a slime of bacteria.

From the point of view of detailed morphology, investigators using the electron-microscope have made an especially valuable contribution to an understanding of zoospore structure. Manton and her co-workers[115, 116, 117] have studied the motile cells of *Saprolegina* and *Olpidium* confirming the distinction between tinsel and whip-lash flagella and discovering the fact that, as with other plant zoids, each flagellum is an eleven-strand structure. It has also been shown that the coat of the encysted zoospore of *Saprolegina*, during its brief rest between the two phases of diplanetism, is beset with beautiful ultra-microscopic anchor-like hooks.

During the past fifteen years a flora of aquatic Hyphomycetes growing on submerged decaying leaves of deciduous trees has been recognized and described (Ingold[90, 91, 96]). This flora seems to be world-wide and many of the species involved are extremely common and can be found with ease in any not-too-sluggish stream. Their whole life story, the production, liberation, and dispersal of the spores, takes place below water. Their most curious feature is that in most species the spore consists of four long filamentous arms diverging from a common point (fig. 4). A study of ontogeny shows that the four-armed spore develops in many different ways. Clearly a beautiful example of parallel evolution is involved suggesting that this type of spore has a definite biological value in the aquatic habitat. Due to the experimental work of Webster, not yet published, it seems clear that the value lies in the ability of such a spore to anchor itself on a suitable substratum. For a spore in a stream this may be a very real problem in the dispersal story.

These are not the only Hyphomycetes which grow on submerged leaves of trees and shrubs. There are also the aero-aquatic fungi studied in recent years by van Beverwijk[11] and by Glen-Bott[66]. These fungi, mostly with beautiful helicoid spores, grow on submerged leaves, often under almost anaerobic conditions, but produce their conidia only when the leaves are brought to the surface. No spore production occurs below water.

Attention has also been given to aquatic Ascomycetes which occur abundantly in lakes on submerged, dead stalks of reed-swamp plants or on submerged twigs and branches. These include both Discomycetes and Pyrenomycetes and much work remains to be done on their systematics and ecology.

In recent years considerable attention has also been given to marine fungi. As with the freshwater species, there are primitive Phycomycetes and also Ascomycetes, although the latter all appear to belong to the Pyrenomycetes

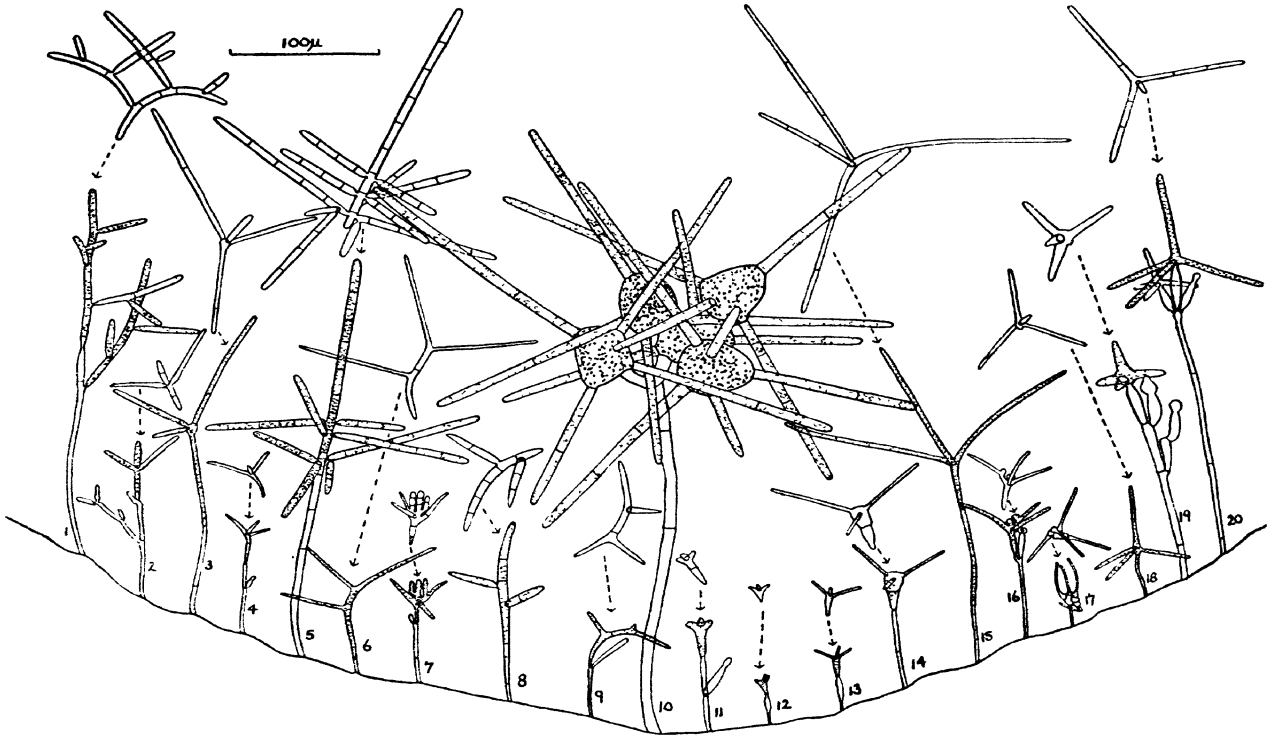


Fig. 4. Freshwater aquatic Hyphomycetes. Substratum of decaying leaf-tissue shown diagrammatically. For each species a conidiophore with at least one mature spore (shown stippled) is figured with one liberated spore (except in the case of *Actinospora*) nearby.

1. *Varicosporium elodeae*
2. *Articulospora tetracladia*
3. *A. inflata*
4. *Alatospora acuminata*
5. *Dendrospora erecta*
6. *Tricladium gracile*
7. *Tetracladium setigerum*
8. *Tricladium splendens*
9. *T. angulatum*
10. *Actinospora megalospora*
11. *Heliscus lugdunensis*
12. *H. stellatus*
13. *H. longibrachiatus*
14. *Clavariopsis aquatica*
15. *Tetrachaetum elegans*
16. *Tetracladium marchalianum*
17. *Campylospora chaetocladia*
18. *Triscelophorus monosporus*
19. *Lemonniera brachycladia*
20. *L. aquatica.*

All drawn to same scale.

which are to be found as parasites of the larger brown seaweeds and as saprophytes of wood submerged in the sea. Early work in this field was by Cotton[46] and Sutherland[143] but the outstanding recent contributions have been from Barghoorn and Linder[4], Wilson[159], and Johnson[108] who has also produced an exhaustive review of the literature on halophilous fungi[104].

A very interesting feature of the ascospores in many of the marine Ascomycetes is that they invite comparison with the conidia of the freshwater aquatic Hyphomycetes, for they usually have mucilaginous appendages which seem to be concerned with anchoring the spores to the substratum in a medium in continuous and often violent motion.

Little study has been made in recent years of the minute primitive fungi which attack planktonic algae, especially diatoms, in the sea. It is to be hoped that in the future workers will be attracted to their study to see if epidemics occur in the sea comparable with those which affect *Asterionella* in the lakes of the English Lake District. Indeed, generally marine fungi would without doubt repay further detailed investigation.

Two ecological groups have been given brief consideration, but so far as the others are concerned it is possible to give them only passing attention. There are the large and economically important wood-rot fungi responsible for spoilage and decay of standing trees, stored timber, and woodwork in buildings and boats. This subject has been ably considered by Cartwright and Findlay[39]. Then again there are the so-called predaceous fungi which capture and consume amoebae and nematodes. These have been exhaustively studied in America by Drechsler in a long series of beautifully illustrated papers. They have also been found in Britain and the literature dealing with them has recently been reviewed (Duddington[52]). The entomogenous fungi which attack living insects form an ecological group with a remarkable range of systematic types: Entomophthorales, *Cordyceps*, Laboulbeniales, *Septobasidium*. The Laboulbeniales were so elegantly and so thoroughly treated by Thaxter that later mycologists have tended to feel that there is little left to be done. It is, therefore, pleasing to observe a renewed interest in the recent work of Shanor[132]. So far as Britain is concerned this is an open field and it is much to be hoped that some mycologist, who also knows his insects, may devote himself to the study of these fascinating fungi.

The exceptionally interesting and beautiful coprophilous fungi growing in such abundance of genera and species on the dung of herbivorous animals represent another distinct flora. Over the past hundred years and more mycologists have been attracted to the study of these fungi. Many of the outstanding genera such as *Pilobolus*, *Ascobolus*, *Sordaria*, and *Coprinus* have figured prominently in physiological and biological studies. However,

there is room for further work and an experimental ecological approach to the problem of succession on the dung might be well worth while.

Again the hypogeal fungi, forming subterranean macroscopic fruit-bodies, represent a biological group embracing Phycomycetes, Ascomycetes, and Basidiomycetes. These interesting fungi have recently been monographed in this country by Hawker[81].

The ecology of the larger fungi in woods and in grassland is still in its infancy in spite of the pleasing autumnal habit of mycologists of "foraying amongst the funguses." This study is still essentially at the descriptive stage. However, there is here a big field for experimentation and one which will certainly be explored in the future.

VI. FUNGI AND PLANT DISEASE

The causes of disease in plants, apart from insect pests, are numerous. There are physiological upsets, mineral deficiencies, virus attacks, and also some important diseases caused by bacteria. However, it is the fungi which provide the chief plant pathogens.

The great science of phytopathology developed largely from the work of such pioneers as de Bary and Berkeley. The history of the subject has been written by Large in his *Advance of the Fungi* (1940), a most readable book for anyone at whatever stage he may be in his study of fungi. It is, moreover, a scholarly contribution to mycological literature.

Since the primary aim of mycological phytopathology is to prevent, or at least control, fungus diseases in plants, it is perhaps reasonable to consider this huge subject from the point of view of the major methods of control. Certain specific diseases will be given prominence, partly because of their outstanding economic importance and partly because of their historical significance in the development of the subject.

Where foliage is attacked by air-borne spores the application of a fungicidal spray is a common method of control. With the introduction of copper spraying (1885) the name of Millardet is particularly associated, although Prévost had shown as early as 1807 that copper sulphate, at a dilution of four parts per million, prevented germination of the bunt spores, a method of treatment that was soon adopted by English farmers. Millardet's discovery is described in the following manner by Horsfall[87] "the French peasants . . . wanted a . . . poisonous-looking mess to daub on to ripening grapes to prevent pilfering . . . Alexis Millardet, hiking along the highway in 1882 observed that the anti-thief plaster was also an anti-mildew plaster." This "plaster" was to become famous as Bordeaux mixture, a concoction of copper sulphate and lime giving a fine suspension of cuprous hydroxide which could be sprayed on the foliage. It was soon recognized that this spray effective for *Peronospora viticola* on vine was usable against the related

Phytophthora infestans which had appeared some forty years earlier as a deadly murrain of the potato crop whenever the weather in August was warm and muggy. In spite of the enormous volume of research devoted to fungicides during the past 75 years, Bordeaux mixture is the spray most used for the control of potato blight.

The difficulty about spraying is that it is fairly costly and only the foliage actually covered, both above and below, is protected. New leaves produced after spraying are vulnerable and so are those from which the spray has been eroded by the mechanical action of heavy rain. Thus proper timing is essential and in more recent years plant pathologists concerned with the potato crop have tried to define exactly the concatenation of weather conditions likely in late summer to lead to the development of blight, so that warnings can be issued to farmers to spray. Thus van Everdinger[56] suggested specific weather conditions which must normally obtain before outbreaks of blight: dew for at least four hours during the night with a minimum temperature not below 10°C, combined with rainfall in the day immediately following of at least 0·1 mm, the mean cloudiness exceeding 0·8. On this basis a spray-warning service has been organized with considerable success in Holland. For British conditions Beaumont[9] has proposed simpler but essentially similar rules, and Bourke[20] has used in Ireland a basis for spray-warning differing slightly from that in use in Britain. Another element in further developing a warning service may be the determination of the actual presence of spores in the air in a quantitative manner. This type of information now becomes possible with the wide use of the Hirst spore-trap by phytopathologists. There is now a strong tendency for plant pathologists to take an increasing interest in meteorology with special reference to infection, production of sporophores, liberation of spores, their actual dispersal, and final deposition. In the future the life history of a fungal pathogen must be considered very incomplete if its relationship to meteorology and to the microclimate is not fully considered.

There is a widespread feeling amongst mycologists that spraying is a messy method of disease control and that the development of resistant varieties of the host is much cleaner and in a way more "scientific."

Work of this nature began with the classic research of Biffen[12] who showed in 1907 that resistance of wheat varieties to yellow rust (*Puccinia glumarum*) was inherited according to Mendelian laws. The story of this kind of control may be best illustrated by a consideration of the history of black rust of wheat due to *Puccinia graminis*, one of the greatest menaces to the world food supply. Enormous efforts have been devoted to its study during the last hundred years. De Bary in 1866 discovered the heteroecious nature of the parasite, demonstrating that the aecidial and pycnidial stages are on barberry, and the others (the uredospore and teleutospore stages) on

wheat or other members of Gramineae. In the final decade of last century Eriksson[55] showed that there are some six "formae speciales" each limited in the dikaryotic (uredial) stage to a single genus, or group of genera, e.g. *Puccinia graminis secalis* on rye and barley, *P.g. tritici* on wheat, *P.g. avenae* on oat and certain grasses, and so on. He thought that they were morphologically indistinguishable. Actually they can be separated by spore size, if a sufficient number of uredospores of each "forma" are measured, and are now regarded as distinct varieties. However, the work of American phytopathologists, particularly Stakman and his associates, has shown that within each variety are a large number of races distinguishable by their reaction on differential host varieties. Thus in *P.g. tritici* there are over 200 of these identified by the type of reaction on twelve pure-breeding varieties of wheat grown under standard conditions. Each physiologic race is given a number and extensive surveys show which particular race is prevalent. Thus from 1919–1924 races 17 and 29 were common in North America, but for some five years after 1925 races 3, 18, and 36 predominated. Rust control largely consists in developing resistant host varieties for the particular physiologic race of the fungus which is becoming prevalent. It is thus an unending battle, for new races of rust are apt to make their appearance either by mutation or by hybridization followed by genetical recombination, for as Johnson and Newton[101] have shown rusts can be crossed and all varieties and physiologic races of *P. graminis* can infect barberry which thus becomes not only a springboard for early infection of the wheat each year, but also a meeting ground where hybridization can occur.

The existence of physiologic races of specialized parasitic fungi has now been established as a general phenomenon which must be taken into account in phytopathological work. Especially interesting are some recent genetical studies of the relationship which may exist between the genes of a host plant conferring resistance to a particular parasite and the genes of the fungus concerned with its pathogenicity. The work of Black[16] on potato and *Phytophthora infestans* may be cited. Resistance of potato foliage to blight is due to hypersensitivity to the fungus. This resistance is determined by four unlinked, dominant genes: R_1, R_2, R_3, and R_4. On the basis of these, sixteen strains of potato are possible ranging from $R_1R_1R_2R_2R_3R_3R_4R_4$ to $r_1r_1r_2r_2r_3r_3r_4r_4$, the former being resistant to all strains of the fungus and the latter susceptible to all. There are a number of strains of the fungus with different powers of infection. Strain A attacks only potatoes without any of the four R genes; strain B^1 only those without R_2, R_3 and R_4; strain D only those without R_1, R_2 and R_3, and so on. Apparently each gene for resistance in the host is capable of being matched by one for virulence in the parasite. One of the most interesting questions for the future is how general is this picture of "matching genes."

Crop rotation is a control method of general use in connection with those fungi which attack their host from the soil (e.g. *Ophiobolus graminis*. Take-all and White heads of wheat; *Phymatotrichum omnivorum*, Texas Root-rot; *Plasmodiophora brassicae*, Club Root). The biology of these fungi has recently been considered in masterly fashion by Garrett[63]. For control of disease by crop rotation the central problem is the determination of the minimum period between crops of the same type for reduction of the infection potential in the soil to a relatively safe level. Garrett points out that, except for the obligate parasites which simply continue to exist in the soil as resting spores, the question of survival as a saprophytic mycelium is essentially an ecological one in which the other soil organisms are involved as competitors for organic food or as antagonists producing antibiotics. Garrett's philosophy is that the study of disease in all its aspects is essentially an ecological one.

In the present century seed-borne fungal diseases have received much attention and the list of these is now a very long one. Two aspects of their control have become especially important: first the inspection of seed samples to determine the extent to which pathogens are present, and secondly fungicidal seed treatment. The study of seed-borne fungi and the development of seed inspection methods has been undertaken in a number of laboratories especially in Belfast, Northern Ireland (Muskett[121]), and at Wageningen in Holland (Doyer[51]). From the point of view of seed treatment most pathogens are superficial and few penetrate deeply into the seed. Thus most seed-borne fungi can be controlled by treating the seed with a fungicide, usually an organo-mercury compound, provided that the seed sample is not too heavily contaminated by the fungal pathogen.

This brief mention of plant pathology from the disease control viewpoint can give only a one-sided picture of this vast subject and it would be quite unfair to leave the impression that the phytopathologist is not also, and indeed primarily, concerned with the fundamental problems of parasitism namely: entry, colonization of the host tissue, production of the reproductive units, and the dispersal of spores.

VII. TAXONOMY OF FUNGI

Taxonomy still remains one of the major activities of mycologists and probably the majority of papers published on fungi are essentially taxonomic. New species are still being described in great numbers every year. Mycologists owe a lasting debt for the great systematic compilation inspired by P. A. Saccardo[130] (1845–1920). In the twenty-five volumes of the *Sylloge Fungorum* (1882–1931) most of the genera and species described up to 1920 are listed. The essential part of this labour has been continued at the Commonwealth Mycological Institute since 1940 by the periodic issue of lists of

new species, the gap between the Sylloge and these lists being covered by a compilation of Petrak.

One fundamental taxonomic question which has increasingly been raised in recent years is: "Are fungi plants?" and probably a growing number of students of the group would give a negative answer. Indeed, many would envisage four kingdoms of living organisms: Plant, Animal, Fungal, and Bacterial.

Within the Kingdom of Fungi, from which most would exclude the Mycetozoa, the four divisions Phycomycetes, Ascomycetes, Basidiomycetes, and Fungi Imperfecti are generally accepted. The fourth is a dust-bin group, but so far as the others are concerned, fungal systematists have been searching within each for a natural classification.

The term "natural classification" is, of course, difficult to define, but at the back of the mind is the concept of phylogenetic relationship. Most botanists view phylogeny, except within a small and restricted taxon where cytogenetical and experimental evidence is available, with a jaundiced eye, and phylogenetic concepts are particularly shaky in the fungi. Nevertheless, the pursuit of more natural classification continues and, in general, considerable advances have been made, although it may be difficult to show by logical argument that the new systems are any more "natural" than those they replace. In discussing this matter each major group will be considered in turn.

There is no reason to believe that Phycomycetes is a natural assemblage, and, further the old division into Archimycetes, Zygomycetes, and Oomycetes has little justification. The following scheme, developed in its essentials by Sparrow[135] on the suggestion of W. H. Weston, gives the impression of being much less unnatural.

Chytridiales Blastocladiales Monoblepharidales	zoospore uniflagellate with posterior whip-lash flagellum
Hyphochytriales	zoospore uniflagellate with anterior tinsel flagellum
Plasmodiophorales	zoospore with two unequal flagella
Saprolegniales Leptomitales Lagenidiales Peronosporales	zoospore with two flagella one whip-lash, the other tinsel
Mucorales Entomophthorales Zoopagales	no motile stage

The major characters used are the motility or non-motility of the asexual spore and, where it is motile, the type of flagellation is considered basic. The use of this last character parallels its employment in the classification of Algae, the central theory being that the structure of the motile cells reflects a flagellate ancestry. Thus we may recognize a number of orders in Phyco-

mycetes. Some of these do seem as if they might be inter-related, for example the three orders in which the zoospore has a single posterior flagellum of the whip-lash type, but for the most part there seems little basis for phylogenetic speculation. The older mycologists were prepared to construct phylogenetic trees indicating possible (or even, to them, probable) connections, but few nowadays would be bold enough to construct such trees which are rightly regarded as the most noxious of all weeds. Perhaps the

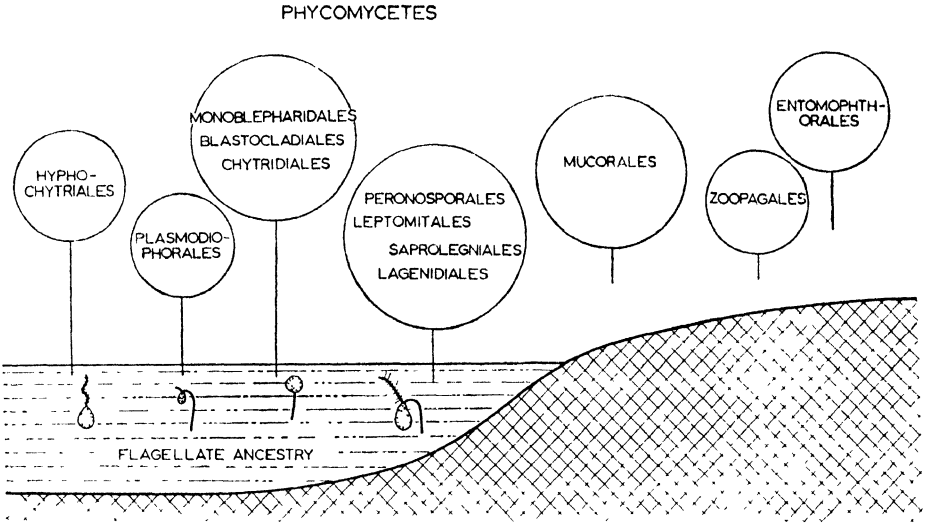


Fig. 5. A possible phylogenetic picture of Phycomycetes.

Phycomycetes might be pictured as a kind of phylogenetic balloon barrage with some balloons anchored in the water, but with others with unknown attachments merely drifting around in the neighbourhood of the anchored ones (fig. 5).

The ascus seems to stamp Ascomycetes as a natural group, but fungal taxonomists have been seeking a more natural arrangement within the group, based primarily on the detailed structure of the ascus itself. Luttrell[113] in his valuable treatment of the "Taxonomy of Pyrenomycetes" says "the classification of the Ascomycetes contributes perhaps the most difficult taxonomic problem in mycology." An outstanding advance in this problem was made by Nannfeldt[122] who in 1932 divided the main body of Ascomycetes into Plectascales, Ascohymeniales, and Ascoloculares. The second group included Discomycetes and true Pyrenomycetes, leaving for the third the ascostromatic types. The unilocular ascostroma (such as occurs in *Sporormia*, *Pleospora*, and *Melanomma*) closely resembles a true perithecium and can only be surely distinguished by careful developmental studies. However, Luttrell has shown that associated with the difference between

Ascohymeniales and Ascoloculares there is also a striking difference in ascus structure, the ascus in the former group having a single-layered wall (unitunicate) whilst in the latter group it is bitunicate with an outer unstretchable wall and an inner one capable of considerable expansion. This feature can be determined with ease. Within the Discomycetes most students of the group accept Boudier's division on the basis of ascus dehiscence into an Operculate and an Inoperculate series. Again in the true Pyrenomycetes the Clavicipitales are characterized mainly by the curious ascus which is long and cylindrical with a thickened hemispherical cap pierced at maturity by a fine canal through which the thread-like spores escape one by one. It appears that more and more the microscopic features of the ascus will be used in the taxonomy of the group. So far as the ascospores are concerned their form has long been used. Thus the pyrenomycete family Diatrypaceae is characterized by the allantoid spore, and, in Operculate Discomycetes, Le Gal[62], in a beautiful study, has shown how important the details of spore ornamentation may be in fungal taxonomy.

In Basidiomycetes taxonomic interest has centred in recent years around the higher forms (Homobasidiomycetes). The classification of Hymenomycetes by Fries[61] (1874) into Agaricini (with gills), Polyporei (with pores), Hydnei (with teeth), Thelephorie (with smooth hymenium), and Clavariei (with the hymenium covering an upright axis or branched group of such axes) has, with change of suffix, been generally used, in spite of the fact that it is becoming increasingly clear that the classification is an artificial one. The characters used to separate the groups are gross ones related to the orientation of the hymenium in connection with spore discharge, characters which are likely to have selection value and, therefore, liable to develop independently along different lines of descent.

Recent workers especially in France have stressed the taxonomic importance of small microscopic characters such as sphaerocysts (nests of spherical cells) in the tissues, structure of cystidia, and details of spore shape and ornamentation. It has become apparent that *Boletus* spp. are very far removed from woody and leathery polypores; that *Paxillus* is much closer to *Boletus* than it is to other agarics; that *Russula* and *Lactarius*, with sphaerocysts, lactifers, and amyloid spores, should be separated entirely from other gill-bearing fungi; that in mycenoid fungi all stages exist between agarics (*Mycena*) and complete polypores (*Mycenoporella*) as indicated by Heim[82].

Again the technique of hyphal analysis, used to such good effect by Corner[45], is a valuable tool in suggesting more natural arrangements of higher Basidiomycetes particularly where the woody and leathery ones are involved. Thus Corner recognizes what appears to be a very natural assemblage, the Xanthochroic series, in which the uninflating hyphae are yellowish-brown, darkening with alkali, and without clamps. This series

includes forms which would be placed in four out of five (there are no agaric types) of the Friesian families. However, although it is quite clear that the old classification is unnatural, mycologists hesitate to abandon it until a new one is much more firmly established.

The state of affairs in Gasteromycetes is very similar. There is a growing feeling that, far from being primitive, the Gasteromycetes represent an odd

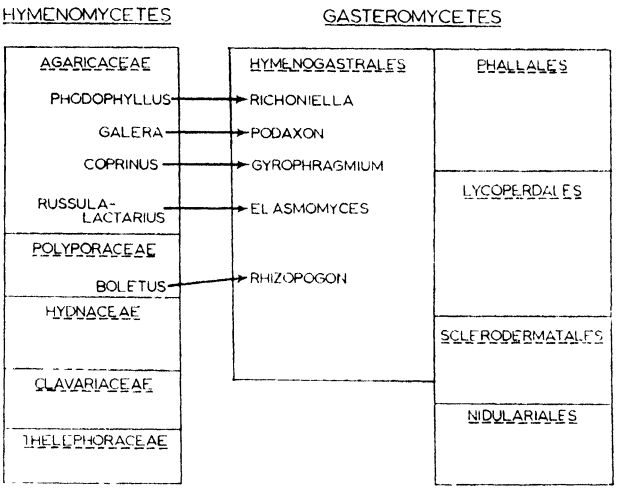


Fig. 6. Diagram of suggested links, based on small microscopic features (see Heim, 1948) between genera in Hymenomycetes and in Gasteromycetes.

assemblage of types, probably derived from hymenomycete ancestors, which, having lost the hymenomycete equipment of spore discharge, have been forced to develop diverse methods of spore dispersal along new and original lines. The continental workers have interested themselves in likely connections between Hymenomycetes and Gasteromycetes, and certain links are suggested based on the same sort of criteria used recently amongst Hymenomycetes. Some of these suggested connections are shown diagrammatically in fig. 6. It is to be observed that all are between Hymenomycetes and Hymenogastrales and, perhaps, as a first step towards a more natural classification, this order should be shunted from Gasteromycetes and coupled with Hymenomycetes as suggested by Lange[108].

The Fungi Imperfecti represent a dust-bin group in which no normal sexual fusion is known and in which neither asci, basidia, nor sporangia of the phycomycete type occur. Most, probably the great majority, would seem to be conidial stages of Ascomycetes where the "perfect" stage is unknown or has disappeared during the course of time. The mycologist is faced with a huge assemblage of these fungi and some classification of them is essential. However, the concept of a "natural" classification is here

especially difficult and for a long time mycologists have been content with Saccardo's purely artificial arrangement based on wall-pigmentation in the mycelium and spores, and on septation and shape of the conidia. The problem is further complicated by the fact that quite often a particular fungus has two quite distinct conidial stages each qualifying for separate generic rank. From the point of view of the practicing mycologist, because of the great economic importance of so many of these fungi, a workable classification is needed and, as in other groups of fungi, workers are tending to seek a more natural one.

Mycologists at the Commonwealth Mycological Institute have played a conspicuous part in this development. Mason[118] gave a valuable discussion of spore types and particularly emphasized the distinction between "dry" spores and conidia borne in a drop of liquid ("slime" spores). In the "List of British Hyphomycetes" (Wakefield & Bisby[147]) this character was used to separate these fungi into two major series: Xerosporae (with dry spores) and Gloiosporae (with slime spores). More recently Hughes (originally at C.M.I. and now at the Department of Agriculture in Canada) has rejected this classification on the grounds that the distinction between the two groups is "biological" rather than "natural" and widely separates two such genera as *Penicillium* and *Gliodadium* which in development are almost identical and differ only, and then not always consistently, in the biological feature of dry or slimy spore-heads. Hughes[88] emphasizes the necessity for stressing the nature of spore development in any classification of conidial fungi and has summed up his views in a valuable paper on "Condia, conidiophores, and classification." Extension of this kind of careful, detailed work to Fungi Imperfecti generally will be of great service to mycology.

Looking into the future, there will always be scope for the fungal taxonomist and particularly for the compilation of authoritative and well-illustrated literature for identifying the micro-fungi. It is still much easier for an experienced British mycologist to identify a flowering plant, moss, or seaweed than to identify a fungus, partly because in Britain the numbers of fungi are relatively enormous, but largely because the systematic literature is so incomplete and scattered.

VIII. CONCLUSION

In concluding this brief picture of the study of fungi its incompleteness must be stressed. For example nothing has been said about industrial mycology (Smith[134]) nor about the important medical aspects of the subject (Ainsworth[1]), nor has the study of lichens been considered. At the moment, indeed, lichenology is attracting more and more students, particularly amateurs, and a flourishing British Lichen Society has recently been formed.

"Beauty is in the eye of the beholder" and the vistas as seen by the writer of this chapter must inevitably be different from those seen by a fellow mycologist. Nor is it possible to foresee with any clarity the lines of future development nor to guess what mycology may be like in fifty years' time, but probably the views of the Tulasne brothers written nearly a hundred years ago are still true today: "Although the field of mycology has for long been deeply furrowed in every part by the tireless plough of the explorers, and has yielded an abundant harvest of knowledge, even now it hides in itself unexhausted treasures that challenge the wisdom of the eyes of the most skilful investigators."

"For there is no one who cannot easily understand that the hidden things which remain are plunged in far deeper darkness than those which up till now have gradually become known, none will wonder that as yet we have seen almost nothing beyond the surface of things."

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BRYOPHYTA

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INTRODUCTION

THE Bryophyta, or Bryopsida, traditionally divided into the two classes Muscineae (mosses) and Hepaticae (liverworts), are comparatively small plants, larger than the "micro-organisms," but smaller than the "higher plants." They belong to an intermediate "mesoscopic" realm which can often be explored better with the pocket lens than with the microscope or the unaided eye.

As well as being intermediate in size, the bryophytes occupy an intermediate evolutionary position with relationships on the one hand to the Chlorophyceae (green algae) and on the other to the higher Archegoniatae (ferns, lycopods, etc.). Though these relationships are unmistakable, they are supported by remarkably little fossil evidence and are certainly very distant; any common ancestry which may be inferred from them must be extremely remote. It would thus be generally agreed that the position of the bryophytes in plant classification is very isolated. The discovery of the extinct Psilophytales did something to narrow the gap between the bryophytes and pteridophytes, but no fossil plants have yet been found to link the bryophytes and algae. At least one supposed "algal" character of the bryophytes, the resemblance between the protonemal stage of the moss gametophyte to a filamentous green alga, has proved, when carefully studied, to be no more than a superficial similarity[77]; it is probably evidence of convergence rather than of close affinity. Even the individual orders of bryophytes are sharply isolated one from another and their real inter-relationships are largely a matter for speculation.

During the 19th century taxonomists such as Robert Brown, W. J. Hooker, W. Mitten, R. Spruce, W. P. Schimper, and many others made clear the main lines of bryophyte classification, while Hofmeister, Leitgeb, Goebel, and other morphologists built up a large body of knowledge about bryophyte structure and organography. Later, partly owing to the isolated position of the group and its lack of fossil representatives, which gave little scope for the kind of comparative morphology then in vogue, and partly because of its small economic importance, bryology came to be regarded mainly as a field for amateurs. Much fascinating detail might remain to be discovered, but the bryophytes were thought to have little to offer of great

interest or significance for biological science as a whole. Some very important contributions to other branches of bryology were made at that time, but in general the bryological work of the period was chiefly taxonomic and not always of the highest quality.

In the last twenty or thirty years the attitude has changed and bryology is beginning to acquire the status of an independent branch of botany. It has begun to be realized that the bryophytes, because of their peculiar life-history, have their own unique contribution to make to general biology. Thus for the geneticist they offer opportunities not normally provided by other organisms. In the higher plants and animals the expression of a gene or gene complex can generally be studied in the diploid phase alone, in many lower organisms only in the haploid phase, but in the mosses and liverworts, which have two generations similar in size and complexity but different in form, it can be studied in both phases, the gametophyte and the sporophyte each offering an abundance of morphological and physiological characters under genic control. The gametophytes of bryophytes, as some geneticist has said, are "personified gametes." Again, the remarkable differences in morphology between sporophyte and gametophyte, and between the juvenile (or protonemal) phase and the adult phase of the latter, is an intriguing and challenging problem in the search for the chain of connection between genes and their environment on the one hand and plant form on the other. The stimulating work of Burgeff[25] on the genetics of *Marchantia* shows the great possibilities of the bryophytes in problems of this kind.

Another aspect of bryology which has not yet been thoroughly explored, but which may prove to be of great general biological interest, depends on the fact that the bryophytes, like the Amphibia among animals, represent an early, and in a sense not completely successful, attempt at the evolution of a land plant. They are thus less independent of their environment than flowering plants, and more limited in ecological range; several environments, for instance deserts and the sea, to which the flowering plants have become successfully adapted, have not been occupied by bryophytes. Thus physiologically as well as in other respects they stand in an intermediate position between the algae and the higher land plants. There should, therefore, be much of interest to be learnt about their relations with their environment, especially about their water relations and some aspects of their mineral nutrition.

To stress the aspects of bryology of greatest general interest for biology is not to deny that bryophytes are worthy of study for their own sake. Though not as large nor as ecologically adaptable as the flowering plants, they play a modest but not unimportant part in the world's vegetation. For this as well as for their unique range of form they claim their own share of scientific attention.

The realization that the study of bryophytes has much to offer even to the non-specialist is one reason for the great increase in interest in bryology in recent years among both amateur and professional botanists. It is significant that though the word "bryology" was first used in 1863 (according to the *Shorter Oxford English Dictionary*) it has only come into common scientific use quite recently. The Paris Congress of 1954 was the first International Botanical Congress at which there was a separate bryological section, a fact which reflects the newly acquired status of bryology as a botanical discipline.

Like other plants bryophytes can be studied from a great many points of view and it would be impossible in a short chapter such as this to review even the work of the last few years in every field. All that will be attempted is to discuss briefly some branches of bryology which to the present writer seem significant at the present time, either in relation to biology as a whole or because of their promise of future development. With this in view it is proposed to renounce all pretensions to completeness and to deal first with taxonomy, then with the bryophyte life-cycle, the physiology of bryophytes in relation to their environment, and lastly with some current ideas on the origin and evolution of the group. A more comprehensive survey than is given here can be found in W. C. Steere's useful chapter on bryology in *A Century of Progress in the Natural Sciences*[91], which has a valuable bibliography.

TAXONOMY

Taxonomists dealing with bryophytes, like those working on plants of other groups, have two immediate aims: to discover and describe new taxa, and to add to our knowledge of the characters and distribution of those already known. Both aims contribute to the ultimate objective of bryophyte taxonomy, the perfecting of the system of classification as a whole. From time to time major systematic changes are suggested; these major taxonomic changes are, however, closely linked with ideas on evolution and bryophyte phylogeny and will be better dealt with later in that connection than in the present section which is mainly concerned with "minor" taxonomy.

Mosses and liverworts are easy to collect and preserve and during the 19th and early 20th centuries collections were made in practically every part of the world. There are now no large areas which can be said to be bryologically entirely unexplored. In the absence of an up-to-date index of either mosses or liverworts it is impossible to state the number of described species except in the roundest of figures. Steere[91] estimates, for the year 1951, 25,000 mosses, 350 sphagna, and 10,000 liverworts. To these figures new species are continually being added, but a not inconsiderable number are also subtracted as more precise methods, especially the rigorous use of the type system, relegate many supposed species to synonymy, especially those

created by uncritical 19th century taxonomists such as Carl Müller and F. Stephani.

Though, as has been said, no large regions are totally unexplored, even in areas such as the British Isles (which with parts of western, northern, and central Continental Europe may be regarded as bryologically the best known in the world) much floristic work remains to be done[81]. For example since the last published check list[83] (1950) at least seven species of mosses have been added to the British flora. Few if any of these could be regarded as "microspecies." One species discovered in 1950 (*Trochobryum carniolicum*) belonged to a genus not previous represented in Britain. At the other extreme are regions such as New Guinea and Borneo where even a comparatively casual collector has little difficulty in finding new species and even new genera.

Among the new taxa discovered in recent years in Europe or farther afield some of the liverworts especially are of great interest. Perhaps the most remarkable discovery of the 20th century is *Cryptothallus mirabilis*, a colourless saprophyte often living in the surface litter beneath *Molinia* or large mosses such as *Hylocomium splendens*[66, 67]. It is a thallose member of the Anacrogynae, apparently related to *Riccardia* (*Aneura*). First found in Sweden, it has proved to be fairly widespread in Europe and is now known from a number of British localities[107]. In being a total saprophyte *Cryptothallus* is unique among bryophytes, though some other liverworts appear to be partially saprophytic[59].

Two other outstanding discoveries of recent years are also among the thallose liverworts. One *Marchasta areolata* (*Neohodgsonia mirabilis*[27, 28, 78]) (fig. 1) is an apparently primitive member of the Marchantiales known from New Zealand and Tristan Da Cunha in which the female receptacle, instead of having the usual apparently radial construction, is a twice bifurcated branch system. The other is the very curious *Monocarpus sphaerocarpus*[29] (fig. 2) a minute almost spherical plant found on saline soils in south-eastern Australia. It also belongs to the Marchantiales and is the only known member of a new family, the Monocarpaceae.

Though there have been no discoveries among the Acrogynae quite as striking as those just mentioned, the recently described genera *Pachyglossa*[50] (with one species in New Zealand and one in Patagonia), *Chondrophyllum*[51] (Patagonia), and *Perssoniella*[52] (New Caledonia), all decribed by the veteran Th. Herzog, are of no little interest. The first two are remarkable among leafy liverworts for their almost succulent leaves, several cells thick.

In addition to the Monocarpaceae, three other new families of liverworts have been created in recent years, the Gyrothyraceae[87] and the Balantiopsidaceae[23]. A curious plant, *Takakia lepidozioides*[46, 46A], discovered in 1951 at high altitudes in Japan, and more recently in the Queen Charlotte

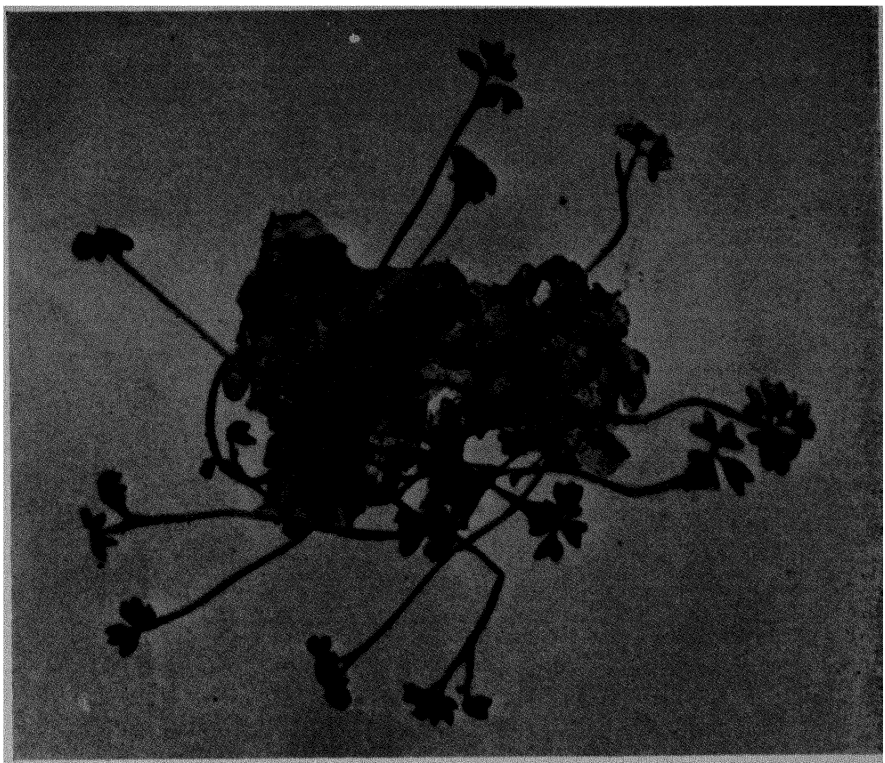


Fig. 1. *Marchasta areolata* E. O. Campbell. Dried specimen from New Zealand. Nat. size. (Phot. K. E. Samuelsson. From H. Persson, *Bot. Notiser*, 1954, Fig. a, p. 41.)

Islands (British Columbia), appears to belong to an entirely new order of Hepaticae, the Takakiales, though its systematic position cannot be finally decided until sporophytes are found. It has peculiar and possibly primitive features, the most remarkable being the cylindrical leaf-life outgrowths of the stem ("phyllids"). The "phyllotaxy" of these phyllids is irregular, though they tend to be paired and the pairs tend to be three-ranked.

Among the mosses numerous new species and genera have been described in recent years, but none of as great interest as the liverworts mentioned above.

Apart from the discovery of new taxa, recent advances in bryophyte

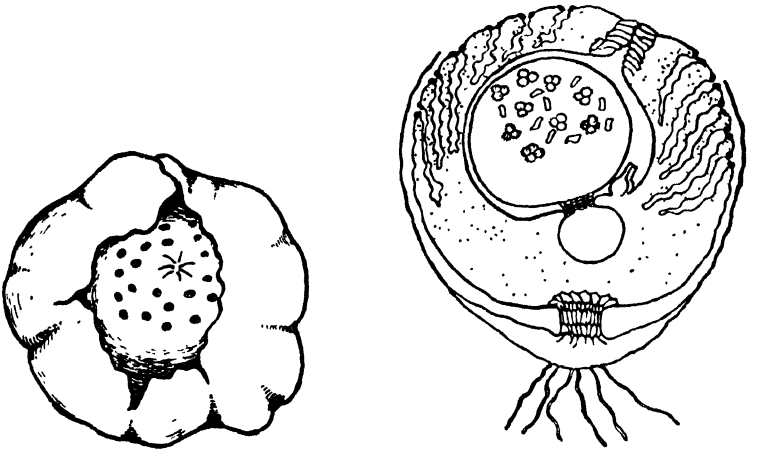


Fig. 2. *Monocarpus sphaerocarpus* D. J. Carr. A. Mature plant, × 40. B. Semi-diagrammatic median section of whole plant showing details of involucre and sporophyte. D. J. Carr, *Austr. J. Bot.*, vol. 4, 1956, figs. 1 and 2 (pp. 177 and 178).

taxonomy have depended partly on the use of characters not previously considered to be of taxonomic value, and partly on new techniques.

In the liverworts K. Müller[74, 75] has shown that a number of characters not used by previous systematists are of taxonomic value, including the form of the spermatozoids, the number of antheridia, the structure of their wall and stalk, the structure of the capsule and seta, the ratio of the number of spores to number of elaters, and the relative diameter of spores and elaters. Some of these characters, for instance the form of the spermatozoids, are of value mainly in establishing the relationships of the larger taxonomic divisions. For example, the spermatozoids of the Sphaerocarpales resemble those of the Marchantiales more than those of the Jungermaniales, supporting the conclusion, for which there is a good deal of other evidence, that the former is the group to which they are most nearly allied. The relative diameter of spores and elaters on the other hand sometimes differs significantly between species of the same genus; in *Bazzania trilobata* it is 1:1, in *B. tricrenata* 3:1.

Increasing use is also being made of such characters as the distribution and structure of the oil bodies.

Among the mosses there might seem to be little scope for using new characters, but there are some which may repay more careful examination. Thus the fine sculpturing of the spore wall, to which earlier taxonomists paid only perfunctory attention, has been shown by McClymont[64] in a study of the American species of *Bruchia* to be of considerable taxonomic value; what is true in *Bruchia* may prove to be equally true of other genera.

In bryophyte taxonomy, as in the taxonomy of other plants, new techniques are giving valuable results. Perhaps the most important of these are the use of biometric methods, culture methods, and the application of cytogenetic methods to taxonomic aims.

Some taxonomists of the inter-war years, for instance Walther[102] in his interesting study of geographical and other variation in *Polytrichum juniperinum* and its allies, and Malta[70] in his studies of the subspecies and varieties of the aggregate species *Zygodon viridissimus*, made occasional use of frequency curves for variable and conveniently measurable characters. More recently statistical methods have been used by Greig-Smith[42] to test the association of characters in various British taxa of *Lejeunea*. Statistical methods have also been effectively used by Lodge[61] in studies of *Drepanocladus*, by S. Agnew[1] in *Sphagnum*, section *Cuspidata*, and by Suzuki[93] in Japanese *Sphagna* of the section *Subsecunda*.

Culture methods are as valuable in bryophyte as in other taxonomy, but bryologists have been slow to adopt them, mainly because of their supposed difficulty[59, 82, 86]. Yet many bryophytes are easily grown on artificial media such as agar and silica gel and several methods are available for obtaining pure cultures free of algae and fungi (though perhaps not of bacteria). Such pure cultures are valuable for various purposes, including taxonomy, and have been used by Pringsheim[79] and others. Even simple culture methods stopping short of pure culture are often useful and have been effectively used by Buch[22] in his studies of *Scapania*, *Lophozia*, and *Calypogeia*. Following the time-honoured principle of growing plants of different origins in the same environment he was able to show that what had previously been regarded as distinct species were "modifications" of the same taxon, e.g. *Scapania undulata* and *S. dentata*. By the same method he showed that taxa differing by apparently insignificant characters, e.g. *Calypogeia neesiana* and *C. meylanii*, remain distinct and must, therefore, have a genetical basis. The converse method of growing clonal material in a variety of environments has also been applied to bryophytes and is valuable in giving a precise notion of the phenotypic plasticity of species which the field botanist can merely label "variable."

These experimental taxonomic methods are beginning to be applied to

mosses as well as to liverworts and will undoubtedly prove of great value in dealing with critical groups such as *Sphagnum*, *Drepanocladus*, and others which have proved resistant to the methods of "orthodox" taxonomy.

Cyto-genetical methods, in particular the study of chromosome numbers and morphology, have very recently begun to prove as valuable a tool in bryophyte taxonomy as they have long been in the taxonomy of flowering plants and ferns. The delay in applying these methods to the bryophytes is largely due to difficulties in devising satisfactory methods for fixing and staining their chromosomes. Liverworts, because their chromosomes tend to be larger and less numerous than those of mosses, have proved easier material for the cytologist to work with than mosses, consequently details of chromosome numbers and morphology are known for a relatively larger proportion of the species.

The chromosomes of mosses long had the reputation of being so small and difficult to deal with that reliable determinations of their number and structure were very difficult to obtain. As long ago as 1929 in a classic paper on heterochromatin in mosses Heitz[47] showed that the chromosomes of mosses present a number of very interesting problems for the cytologist, but it is only in the last few years that Vaarama in Finland, Lewis in England, and Steere and others in America seem to have been able to overcome the technical difficulties and, using squash methods, to demonstrate effectively that cyto-genetical studies are as valuable an aid to the taxonomy of mosses as to that of flowering plants. The latest catalogue by Wylie[108] (1957) lists the chromosome numbers of 364 species and this number is being added to almost daily.

In general it may be said that though the chromosomes of mosses have some peculiar features of great interest to the cytologist, the information of taxonomic interest they provide is similar in kind and extent to that derived from chromosome studies of the flowering plants. As Steere, Anderson, and Bryan[92] say in a paper on chromosome numbers of Californian mosses (which is the largest single contribution to the subject so far published) "Species of mosses, and of bryophytes in general, . . . present the same kind and degree of complexity as those of higher plants, and . . . speciation within natural populations of mosses is governed by the same patterns of cytological behaviour."

In bryophytes, as in higher plants, there are some genera or larger groups in which all, or nearly all, the species have the same chromosome number. Thus in *Polytrichum* all the species examined, with a few exceptions, have a chromosome number of 7 and processes not involving polyploidy or aneuploidy must have been mainly responsible for speciation. In *Sphagnum* all the species of which the chromosome number is known, except *S. palustre*, *S. inundatum*, and *S. robustum*, have $n = 19$ (with 2–6 "*m*"

chromosomes in addition[18]). Examples of polyploidy occur in *Mnium*, *Atrichum*, *Dumortiera* and many other genera.

It is of interest, especially bearing in mind the evidence found by Gemmell[38] that dioecious moss species tend to be more widespread (probably because they are ecologically more adaptable) than monoecious species, that there are numerous examples among bryophytes of pairs of nearly related species one of which is haploid and dioecious and the other polyploid and monoecious, e.g. among mosses *Mnium punctatum* ($n = 7$, $6 + x$, $6 + y$, dioecious) and *M. pseudopunctatum* ($n = 13, 12 + 1$, monoecious[48]), among liverworts *Metzgeria furcata* ($n = 8$, dioecious) and *M. conjugata* ($n = 17$, monoecious[73]).

The classical work of F. von Wettstein on experimentally produced polyploids showed that polyploidy in mosses is often accompanied by an increase of dimensions, in particular of cell size, so that the polyploids are readily recognized by their phenotypic characters. It is also true that pairs of species with a polyploid relationship sometimes show a corresponding difference of cell size, e.g. *Chiloscyphus polyanthus* ($n = 9$, leaf cells 20–25μ wide) and *C. pallescens* ($n = 18$, leaf cells 30–40μ wide[73]). There are, however, plenty of examples among bryophytes of races differing in chromosome number or structure, but not in any visible morphological character. Thus Vaarama[99] found that the very widely distributed *Funaria hygrometrica* includes races in which $n = 14$ as well as some in which $n = 28$. The two races do not seem to be phenotypically distinguishable in either generation and the race in which $n = 28$ differs in cell size and other features from Wettstein's artificially produced diploids. Races differing in chromosome number but not in appearance are also known in *Amblystegium serpens* and other species; in *Tortula muralis*[92, 100] races are known from Europe and North America with the numbers $n = 28$–30, 40 ± 2, 48, 50 ± 2, 55 ± 1, 60, and 66; "whether there is within *T. muralis* any correlation between morphological characteristics and chromosome number is still an open question," according to Vaarama. In some cases there are races differing in chromosome structure, but not in number or morphological characters. For instance, the European populations of the liverwort *Sphaerocarpus texanus* (*S. texanus* Aust. var. *europaeus* (Lorbeer) K. Müll.) differ from the American in the size and morphology of the X-chromosome, but do not seem to be distinguishable by any macroscopic character[62].

The last example illustrates the kind of difficulty, which is also found in flowering plants, which sometimes arises in applying the findings of cytogenetics to taxonomy. Lorbeer has proposed that the European *Sphaerocarpus texanus* shall be treated as a separate species, *S. europaeus*. Such a "species" in which there is a difference in the genome unaccompanied by differences in the phenotype is comparable to the so-called "cryptospecies"

in *Drosophila*, but the opinion of systematists does not readily accept the idea of "species" not recognizable by the normal procedures of taxonomy.

As far as the higher taxonomic units are concerned, cytological studies on the bryophytes have in general given results in harmony with the conclusions of taxonomy. Thus in the moss genus *Orthotrichum*[92] the species in which the stomata of the capsule wall are "immersed" (Section *Calyptoporus*) have a chromosome number of $n = 6$ in the gametophyte generation, while in those in which the stomata are "superficial" (Section *Gymnoporus*) $n = 11$–13. Bryan[20] has found that the number and gross morphology of the chromosomes, as well as the reactions of cytoplasm and chromosomes to fixing and staining reagents, supports the separation of the Ditrichaceae from the Dicranaceae (which were formerly united) and also the attribution of the morphologically reduced genera *Pleuridium* and *Bruchia* to the first and second of these families respectively.

It is of interest that as far as the evidence goes at present, bryophytes which have been regarded as primitive on the grounds of comparative morphology have low chromosome numbers, while advanced groups seem to have high numbers. Thus in *Anthoceros*[73, 80] the numbers so far found are 5 and 6, the lowest numbers known in the Hepaticae, while in the Tortulaceae, which because of their specialized peristome structure and for other reasons must be regarded as an advanced family of mosses, high chromosome numbers appear to be common. It may be noted also that the cleistocarpic mosses (*Phascum*, *Ephemerum*, *Nanomitrium*[19]) which are nowadays usually considered to be reduced rather than primitive, do not have low chromosome numbers, *Phascum cuspidatum* in fact has $n = 52$ (Finnish material[98]), which is one of the highest numbers known among bryophytes.

Hybridization is likely to play as important a part in the evolution of bryophytes as in that of most other organisms, but there is great uncertainty as to the frequency of interspecific hybrids in nature. There are many records of supposed hybrid mosses (i.e. gametophytes bearing sporophytes presumed to result from interspecific crosses) but the evidence that these are really hybrids is in most cases slender. One of the more plausible examples is the supposed hybrid between *Polytrichum aloides* and *P. nanum* which according to van der Wijk[106] is common and accounts for much of the reputed variability of these species. In various bryophytes the pattern of variability would agree well with the assumption that introgression from one species into another is occurring, but evidence that such phenomena in fact occur has not yet been produced. In the extraordinarily variable species *Hypnum cupressiforme*, Guillaumot[43] has suggested that much of the polymorphism is due to hybridization between a small number of related taxa. Though this is not at all unlikely, it remains an hypothesis for which there is no direct evidence.

It is probable that among bryophytes as among higher plants habitat selection leads to the formation of ecotypes. Preliminary work by the present writer on *Tortula ruralis* and *T. ruraliformis* suggests that the latter is perhaps to be regarded as a sand-dune ecotype of the former (perhaps best treated taxonomically as a subspecies). Unpublished work by P. Chamberlain suggests that many of the characters of the varieties of *Hypnum cupressiforme* are heritable; since several of these varieties (e.g. var. *tectorum*, var. *ericetorum*) have well-marked preferences for certain habitats and plant communities; these too are probably to be regarded as ecotypes.

In most groups of organisms—and bryophytes are no exception—in some families, genera or sections of genera, the species are sharply defined and show relatively little variability, while in others interspecific boundaries are hard to draw and variability is much greater. The former appear to have passed their period of active speciation and to be in a stagnant or senile phase of evolution, while groups of the latter class are still actively evolving. The stereotyped families and genera often show discontinuities in distribution and palaeoendemism, while among the actively evolving groups "wides" and neoendemics abound. Among the bryophytes, the Echinodiaceae, many genera of the Hookeriaceae, and the section *Planifoliae* of the genus *Scapania* may be mentioned as examples of taxa of the first type and the genus *Bryum* (in fact almost the whole family Bryaceae), the Hypnaceae (*sensu lato*) and to a lesser extent the Tortulaceae as examples of the second.

THE LIFE-CYCLE 1. THE ALTERNATION OF GENERATIONS

The bryophyte life-cycle has two outstanding features: the dissimilarity of the alternating gametophyte and sporophyte, and the abrupt morphological change from the usually filamentous juvenile phase of the gametophyte (the protonema), to the parenchymatous foliose or thallose adult phase. The former is a general feature of all bryophytes; the latter is shown best among the mosses of the order Bryales, other bryophytes tending to have a less prolonged protonemal phase and a less marked morphological contrast between the protonema and the adult plant. Both features present extremely interesting morphogenetic problems.

Though the sporophyte is always permanently attached to the gametophyte, never achieving independence as in ferns and other pteridophytes, its degree of nutritional dependence varies considerably and is related, as might be expected, to the degree to which its photosynthetic apparatus is developed and thus to the extent to which it is capable of providing for its own needs. Rink[84] has shown that even in *Anthoceros*,* a genus in which

* Most of Rink's work was done on a species of *Aspiromitus*, but *Aspiromitus* and *Anthoceros* are not now regarded as distinct genera.

the sporophyte is probably less dependent on the gametophyte than in any other bryophytes, the sporophyte cannot complete its normal development unless the gametophyte supplies a considerable proportion of its carbohydrate requirements. Though the alternation is partly obligate (in that the sporophyte can never give rise to other sporophytes like itself, as it can for example in many ferns), the gametophyte, in addition to reproducing sexually, can as a rule multiply by means varying from simple fragmentation to the production of specialized and sometimes highly complex gemmae (as the units of vegetative reproduction are termed). Successive gametophyte generations can thus follow one another indefinitely and there is a considerable number of bryophytes in which sporophytes are very rare (as in *Rhytidium rugosum* and several British species of *Campylopus*), or completely unknown (as in various British liverworts and in British, as distinct from American, populations of *Atrichum crispum*). Though in general the gametophyte generation is haploid and the sporophyte diploid, various exceptions and complications due to apogamy, apospory, and polyploidy are found either in nature or under experimental conditions.

Why does the spore normally develop into a gametophyte and the zygote into a sporophyte? Since both generations are stages in the development of the same organism and contain similar genes, two alternatives* are possible: either the morphological differences between the two generations are determined by their different chromosome numbers, i.e. by the number of sets of genes (genomes), or they may depend, not on the genes themselves, but on the environment of the developing spore and zygote respectively, that is, on phenotypic (or environmental) "influences" controlling the action of the genes during development. Though the first alternative can be definitely rejected, we are not yet in a position to define the "influences" affecting the developing spore and zygote and scarcely even to demonstrate clearly that they exist. The gametophyte is a free-living organism, growing as a rule on a substratum such as soil, rock, or wood, while the sporophyte remains attached to the gametophyte to the end of its life (and is actually enclosed within the archegonium during the earlier stages of its development); the inference is obvious that the "influences," whatever they are, must be conducted in some way from the cells of the gametophyte to those of the sporophyte.

The evidence that the morphological contrast between the two generations

* Since this chapter was written Mr. P. R. Bell in a paper to a Linnean Society symposium (to be published shortly) has suggested a third possibility, viz. that the development of the zygote into a plant of sporophyte form depends on a cytoplasmic change, which takes place when the egg is differentiated and is normally maintained until spore formation. This hypothesis, which deserves investigation, was originally advanced for ferns, but might apply equally well to bryophytes.

does not primarily depend on the number of genomes comes from polyploids (especially those experimentally produced) and from the apogamously produced sporophytes which are known in a few mosses.

There are various methods of inducing polyploidy in bryophytes, but that which is of most interest in the present context is by the "regeneration" of normal sporophytes (or portions of sporophytes) detached from the parent gametophyte. In many bryophytes whole sporophytes, or sufficiently large pieces, when cut off and placed on a suitable substratum, regenerate and develop, usually after a preliminary protonemal phase, into plants with the form of a gametophyte but with the ploidy of the sporophyte from which they were derived. If the sporophyte is a normal diploid, gametophytes obtained from it in this way are thus also diploid. Such plants often produce normally functioning sexual organs and can be crossed either with normal haploid gametophytes or with other polyploids. This technique was exploited extensively by F. von Wettstein[103, 104] in his classical researches on mosses and in this way he was able to build up artificial polyploid series (though, it may be noted in passing, he did not in most cases check the assumed ploidy, of the plants produced, by actual chromosome counts). Wettstein found that the polyploid gametophytes differed from the haploids chiefly in cell size and other dimensions; they did not show any morphological resemblance to sporophytes. As mentioned above in another connection (p. 394) polyploid gametophytes which are similar in cell size and are morphologically indistinguishable from haploids are found in nature in *Funaria hygrometrica* and some other species. From these and many similar facts we can have no hesitation in drawing the negative conclusion that the differing form of the two generations is not primarily determined by a difference in ploidy.

The only positive evidence suggesting a possible experimental approach to the second hypothesis (that the environment of the young embryo determines "sporophyte form" as opposed to "gametophyte form") comes from apogamously produced sporophytes which were first observed by Springer[90] on naturally occurring diploid gametophytes of *Phascum cuspidatum* and have since been found in *Tetraphis pellucida*[5] and a few other mosses.

Some diploid gametophytes of *Phascum cuspidatum* have a tendency to produce swellings at the end of the costa which forms the tip of the leaf (somewhat resembling the gemmiferous swellings at the apex of the leaf in such mosses as *Calymperes* spp. and *Ulota phyllantha*). These may eventually give rise to protonemal filaments from which further gametophytes (also diploid) may develop, or, under some conditions, to fairly normal sporogonia producing functional (haploid) spores (fig. 3). These sporogonia, since they arise from a gametophyte without an intervening sexual process, are apogamous.

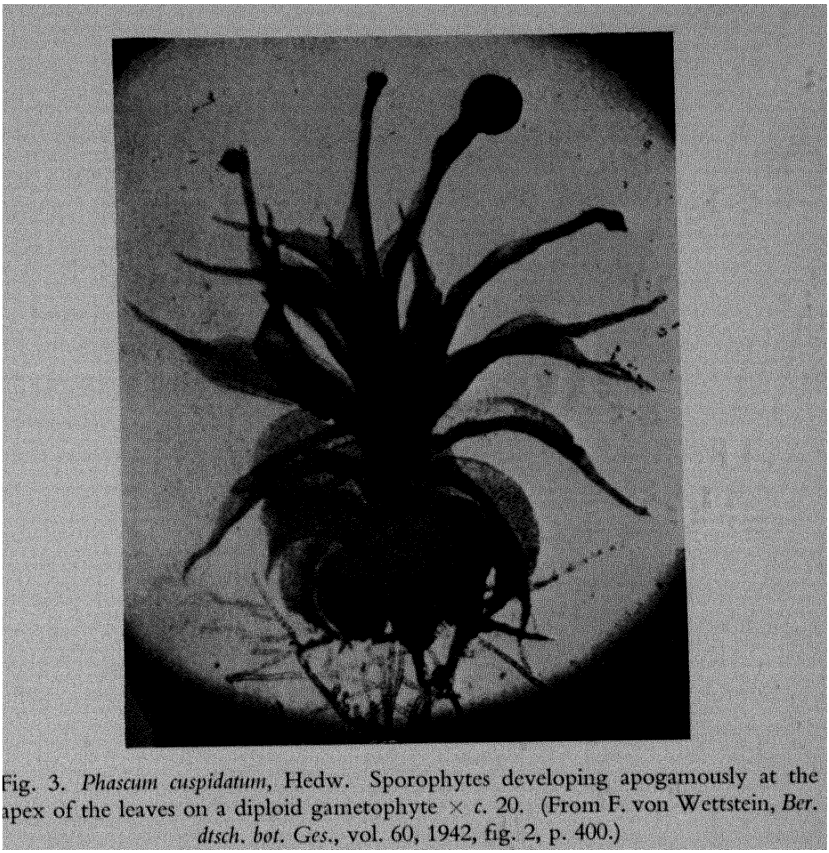


Fig. 3. *Phascum cuspidatum*, Hedw. Sporophytes developing apogamously at the apex of the leaves on a diploid gametophyte × *c.* 20. (From F. von Wettstein, *Ber. dtsch. bot. Ges.*, vol. 60, 1942, fig. 2, p. 400.)

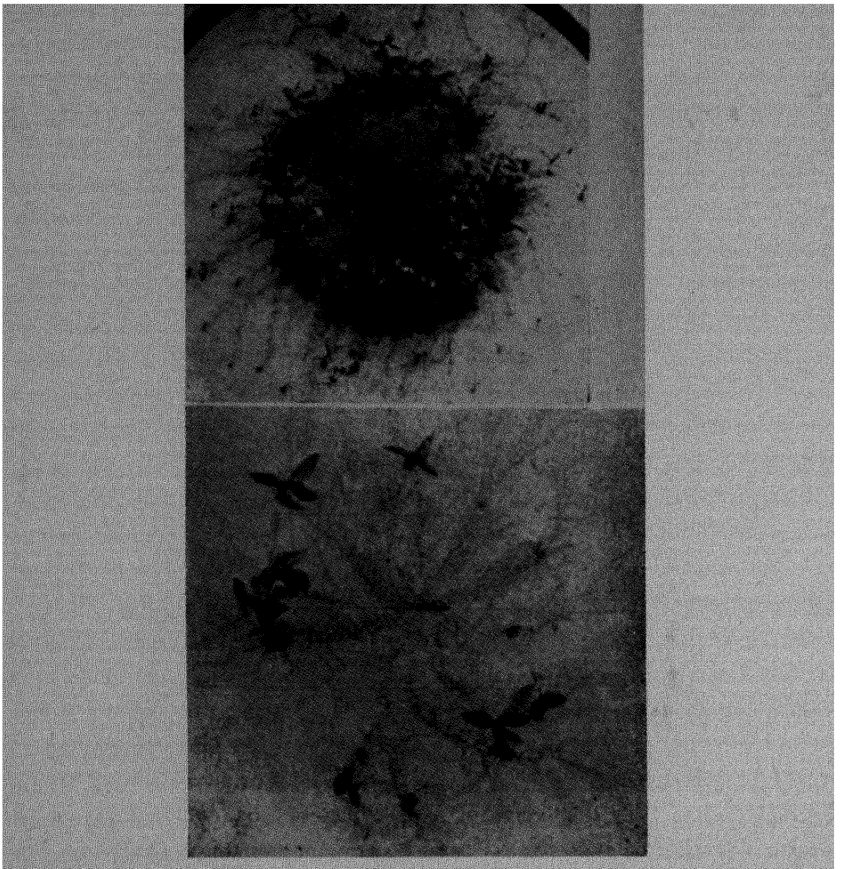


Fig. 4. *Funaria hygrometrica* Hedw. "Fairy ring" formation on protonema. A. Ring of young plants on protonema 35 days old, grown from a spore, × 1·5. B. Ring of young plants on protonema 20 days old grown from a detached leaf, × 3. (From M. Bopp, *Zschr. Bot.*, 1952, 40, figs. 1 and 4, p. 123.)

F. von Wettstein[105] showed that the two alternative paths of development of the swellings on the leaf tips of these diploid plants can be influenced by the environment: on dilute culture media in the presence of abundant water they tend to produce protonema and leafy shoots; under drier conditions and on more concentrated media they develop into sporogonia. By successive changes in the growing conditions a diploid plant originally of gametophyte form gave rise to sporogonia which produced leafy plants and these in turn more sporogonia. These experiments clearly show that the determination of a diploid plant can be altered by the environment, which can shift the balance, now in the direction of "gametophyte form," now in that of "sporophyte form," but the mechanisms involved have not yet been made clear.

The effect, doubtless indirect, of moisture conditions has also been demonstrated in Bauer's[6] experiments on the regeneration of detached sporophytes in *Physcomitrium pyriforme*. With increasing dryness of the environment the regenerating tissues give rise to new (secondary) sporophyte axes (or in extreme cases to callus-like growths), instead of to the usual protonemal filaments.*

Apogamous sporophytes such as those produced by diploid gametophytes of *Phascum* have never been observed on haploid gametophytes and we must assume that the principal role in the determination of the normal embryo towards "sporophyte form" is played, as already suggested, by "influences" (presumably growth-regulating substances) exerted by the gametophyte on the developing embryo. Evidence that such "influences" exist is provided by Bopp's[10, 13] observations on the effect of removing the calyptra from young moss sporogonia. In mosses the capsule develops at the apex of the sporogonium after the elongation of the seta. Until the capsule is nearly ripe, the tip of the growing sporogonium remains covered by a membranous cap or calyptra which is derived from the venter of the archegonium in which the sporogonium arose. The calyptra has generally been regarded as having simply a protective function, but several observers have shown that if the calyptra is removed prematurely the capsule and the upper part of the seta develop abnormally. Bopp has investigated these effects in some detail in a considerable number of species; he has shown that they are found in most mosses and are not confined to a few species, though some react more strongly than others. In the majority of the mosses investigated removal of the calyptra was followed after a few days by a more or less marked thickening of the seta. In some mosses, e.g. *Funaria hygrometrica*, the increase in diameter was due to both cell division and cell enlargement, in others, e.g. *Mnium hornum*, it was due to abnormal cell enlargement only.

* A similar "*télescopage*" has been reported in several species by Moutschen[72]; he does not refer to moisture conditions, but found that treatment with colchicine increased its frequency.

In all the Polytrichaceae studied there was little or no thickening of the seta, but both seta and capsule developed abnormally in various ways if the calyptra were removed. In many of the mosses studied the sporogonia became more strongly phototropic after removal of the calyptra; this did not seem to be due merely to the absence of the light-shielding effect of the calyptra. Bopp concluded from his observations that the calyptra (which is of course a gametophytic tissue) has a distinct growth-regulating action on the sporophyte. It seems probable that this may be brought about by controlling in some way the auxin level in the sporogonium; removal of the calyptra seems to disturb the balance between sporogonium and calyptra which results in normal growth in an intact plant.*

THE LIFE-CYCLE 2. THE PROTONEMAL PHASE

No less remarkable than the morphological contrast between the gametophyte and sporophyte is that between the juvenile phase or protonema and the adult phase of the gametophyte. This is best seen in the mosses of the sub-class Bryales, of which *Funaria hygrometrica* is a typical example.

In most Bryales the spore gives rise to a richly branched filamentous protonema, superficially resembling a green alga, on which after a longer or shorter period of growth numerous buds are produced. In each bud an apical cell is differentiated, the divisions of which build up the leafy shoot which constitutes the adult phase. Once the adult phase is established, the protonema usually gradually disappears, though there are many mosses in which it is persistent, and continues to grow and branch as a carpet beneath the leafy shoots, e.g. *Polytrichum aloides*, *Discelium nudum*. Sometimes a persistent protonema is associated with a morphologically reduced adult phase—as in the African *Nanobryum dummeri* and the curious epiphyllous moss *Ephemeropsis tjibodensis*. In some cases the protonema persists from year to year, giving rise to successive crops of short-lived leafy shoots, e.g. in *Ephemerum* and in at least some *Fissidens* spp. At the opposite extreme to the Bryales with a persistent protonema are those bryophytes in which the protonemal phase is abbreviated or apparently non-existent, as in the moss *Dicnemon* and some leafy liverworts such as *Frullania* and *Lepidolaena*. In liverworts the protonema is usually poorly developed and short-lived; often, though not always, each protonema (i.e. the product of one spore) gives rise to only one bud.

There is much variation in the form of the protonema among both mosses and liverworts. Fulford[37] recognizes ten different types among the leafy Hepaticae. Even among the Bryales, in which the morphology of the protonema was supposed to be fairly uniform, Allsopp and Mitra[2] have

* In a recent paper Bopp[15a] offers a different interpretation and considers that the effect of the calyptra is purely mechanical.

recently shown that there is much more variety than was previously suspected. In some bryophytes the protonema is not filamentous, but by divisions in more than one plane becomes a ribbon-like or disc-like structure; in *Sphagnum* it resembles a small thallose liverwort. The much branched filamentous type of protonema characteristic of the Bryales is regarded by Zimmermann[110] as an advanced rather than a primitive type.

Here we shall not discuss the comparative morphological, phylogenetic, or taxonomic aspects of the protonemal phase, but attempt to discuss (though only in a very summary manner) the stages in its development and the little that is known about the morphogenetic factors concerned in the change from the protonemal to the adult phase. Since nearly all the work which has been done on these problems has been done on mosses belonging to the Bryales (and most of it on the easily obtained and grown *Funaria hygrometrica*) it is to this group alone that the following discussion refers.

Though when the plant changes from a filamentous protonema to a leafy adult gametophyte its morphology changes abruptly, the adult phase still possesses some filamentous organs, notably the rhizoids which are morphologically similar to the rhizoidal branches of the protonema. Further, while the change from protonema to leafy shoot is irreversible after the earliest stages of bud-formation (an example of "*Dauerdetermination*," according to Bünning[24]), when the adult plant is injured or pieces are detached from it, the cells may "regenerate," giving rise to protonemal filaments (secondary protonema) which may later bear buds in precisely the same way as the primary protonema arising from the spore.

The primary protonema does not immediately give rise to buds; these are only formed after an interval, at a certain age or stage of maturity.

Bopp[15] found that when successive subcultures are made of *Funaria* protonema buds are not formed sooner on the later than on the earlier subcultures; the buds appeared when the individual protonema had reached a certain size (i.e. diameter), irrespective of the number of cell generations that had elapsed between spore germination and bud formation. When spores are sown on an artificial medium, such as nutrient agar, the protonema spreads out like a fungus mycelium from the point of inoculation, forming a green circular patch. In many species, e.g. *Funaria hygrometrica* and *Aulacomnium androgynum*, a "fairy ring" of buds often appears at a certain distance from the growing margin, later replaced by a ring of leafy shoots (fig. 4); in other mosses e.g. in *Polytrichum* and *Atrichum*, according to Bopp[8], buds appear at the centre of protonemata of much smaller diameter.

It has long been known that under ordinary conditions a certain minimum light intensity is necessary for bud formation. Keil[58] has, however, shown that the protonema of *Splachnum* when grown on a medium containing

2 per cent sucrose will form buds even in the dark, but most mosses on normal nutrient media form no buds below a certain light intensity. Servettaz[88] also found that in *Phascum* buds fail to form even at normal light intensity if the protonema is kept at low temperatures. These facts seem to suggest that for bud formation a certain threshold concentration of some "bud-forming substance" is required, or at least that the protonema has to undergo some physiological change in which light and temperature play an important part.

In 1947 Sironval[89] published an account of the development of the protonema in *Funaria hygrometrica* in which he claimed that it was not a gradual process leading from spore germination to bud formation as had hitherto been supposed, but consisted of two sharply marked stages, the chloronema and the caulonema. The chloronema is the protonema formed immediately after spore germination and differs from the later formed caulonema in being less branched, the main filaments having more or less transverse not oblique septa, colourless not brown cell walls, etc. After growing (under the conditions of Sironval's experiments) for about 20 days, the chloronema degenerates and the caulonema subsequently develops from the surviving branch apices. An important point is that buds which give rise to leafy shoots arise always on the caulonema, never on the chloronema. Sironval's description of the development of the protonema in *Funaria* differs in several important respects from what has been generally believed; before it can be accepted, and still more before it can be regarded as applicable to the Bryales generally, the work must be repeated and extended to a wider range of conditions as well as to other species. The later work of van Andel[3] on *Funaria* and of Allsopp and Mitra[2] on a large number of Bryales disagrees with Sironval's results on several points.

It may be noted that Sironval is not the first to claim that there are distinct morphological stages in the development of the moss protonema. Wallner[101], and later Bauer[5], found that in *Tetraphis pellucida* the first formed protonema consists of small parallel-sided cells about six times as long as broad, while the mature or "reproductive protonema" on which alone buds are formed, consists of larger cells with convex walls only 2–4 times as long as broad.

There seems little doubt that the structure and development of the moss protonema are in fact more complex than has generally been supposed. The main point in Sironval's account which seems questionable is whether there is really a sharp separation of two stages with an intervening phase of degeneration. It appears more likely, as Allsopp and Mitra suggest, that the characteristics which Sironval attributes to the "caulonema" are merely those of a mature protonema and that the development of a young into a mature protonema is normally a gradual process. The degeneration of the

chloronema which Sironval observed after about 20 days might have been due to unfavourable cultural conditions in his experiments.

It is of interest that Bopp found that when "caulonema" cells are isolated from the protonema to which they belonged, intercalary divisions take place and the number of chloroplasts increases, so that they become similar to "chloronema" cells.

If Sironval's interpretation is correct the problem as to the nature of the growth substances or the physiological change responsible for bud formation on the protonema merges in the slightly different problem of what brings about the change from chloronema to caulonema. Sironval himself considers that at least two growth substances (or complexes of substances) are required, both of which can be synthesized by the protonema when it is growing in normal daylight. He makes the further and surprising claim that one of these substances is formed only when the plant is growing in natural daylight and not under artificial (electric) light; it could, however, be replaced by a substance formed by a species of *Penicillium* which accidentally contaminated some of his cultures. Allsopp and Mitra, on the other hand, found that buds were formed under artificial light of 500 ft-candles as readily as in daylight, while in artificial light of 100 ft-candles they were eventually produced, though after some delay.

Other work by Hurel-Py[56] on *Funaria hygrometrica*, by Bopp on various species, and by Gorton and Eakin[41] on *Tortella caespitosa* has made interesting contributions to our knowledge of the conditions necessary for bud formation. Bopp[8] found evidence of a quantitative relationship between bud formation and carbon assimilation (which is also suggested by the dependence of the former on light). In secondary protonema formed from detached leaves placed on agar (which behaves in most respects like protonema grown from spores) buds were formed earlier on protonema derived from leaves which had been exposed to light for a long time than on that from leaves placed in the dark immediately after being detached from the plant. Further, sodium fluoride, which had been previously shown to be an inhibitor of carbon assimilation in mosses, inhibited bud formation in secondary protonema of *Funaria*. Both Hurel-Py[56] and Bopp[9] have shown that bud formation is affected by auxins; the latter found that heteroauxin in high concentrations (10^{-5} and 10^{-6} g/ml) diminished the number of buds formed, but in low concentrations (10^{-8}) it increased the number. Somewhat similar results were obtained by Gorton and Eakin with the protonema of *Tortella caespitosa*. These authors also found that adenine and certain derived compounds had a stimulating effect on the production of buds. What is perhaps of greater interest was that an unidentified substance which inhibited protonemal growth accumulated in the agar on which the protonema had been growing; this fact prompted Gorton and Eakin to

suggest that the onset of bud formation might be connected with cessation of elongation in the protonemal filaments. Since none of the treatments which increased the number of buds shortened the time between germination of the spore and budding Gorton and Eakin consider that the protonema must reach a state called "ripeness to bud" before buds are formed and they believe that the building up of at least two factors, a store of nutrients and a supply of certain growth substances, is involved. When the protonemal filaments cease to elongate, owing to the accumulation of inhibitor in the medium, the cells tend to become distended and spherical and divisions tend to take place parallel to the original direction of elongation, forming "pro-buds" of two cells side by side. The views of Gorton and Eakin are suggestive and should provide some useful working hypotheses for further studies.

The critical point in the development of buds on the protonema is the formation of a tetrahedral apical cell. Soon after this, but not immediately the cell is cut off, as Bopp[8] has shown, the change from protonema to leafy shoot becomes irreversible. An apical cell, once formed, seems to exert an influence, which appears to diminish with distance, on the formation of subsequent apical cells (or at least of secondary protonema); thus in *Funaria*, leaves taken from the base of the stem produce secondary protonema more readily than leaves from nearer the stem apex[12]. Sporogonia have an inhibiting effect on the production of buds from the secondary protonema arising from leaves detached from the gametophytes which bear them.

Bopp[14] also made a detailed study of the changes in the nuclei and plastids of cells in the older protonema of *Funaria* ("caulonema" of Sironval). He noticed several interesting and possibly significant features, for instance both nucleus and plastids tend to become ellipsoidal rather than spherical as the cells become older. No cytological change accompanying bud formation was observed however and no connection is apparent between the cytological changes observed and the transition from protonema to leafy plant.

Though the morphological change from the protonema to the leafy phase of the moss gametophyte has been stressed and discussed here at some length, it should not be forgotten that the first leafy shoots which grow from the buds do not represent the definitive form of the moss gametophyte. Meusel[71] in his illuminating analysis of the growth forms of mosses has shown that both "acrocarpous" and "pleurocarpous" mosses undergo a whole series of further changes of form before the sexually mature shoots are produced. In "acrocarpous" mosses such as *Bryum argenteum* a succession of shoots is formed, first by "*Erstärkungswachstum*" (strengthening growth) and subsequently by "*Erneuerungswachstum*" (renewal growth) (fig. 5). The first-formed shoots have distant leaves and bear little resemblance to the catkin-like shoots with densely imbricate leaves of the sexually mature plant. The production of new shoots by *Erneuerungswachstum* is

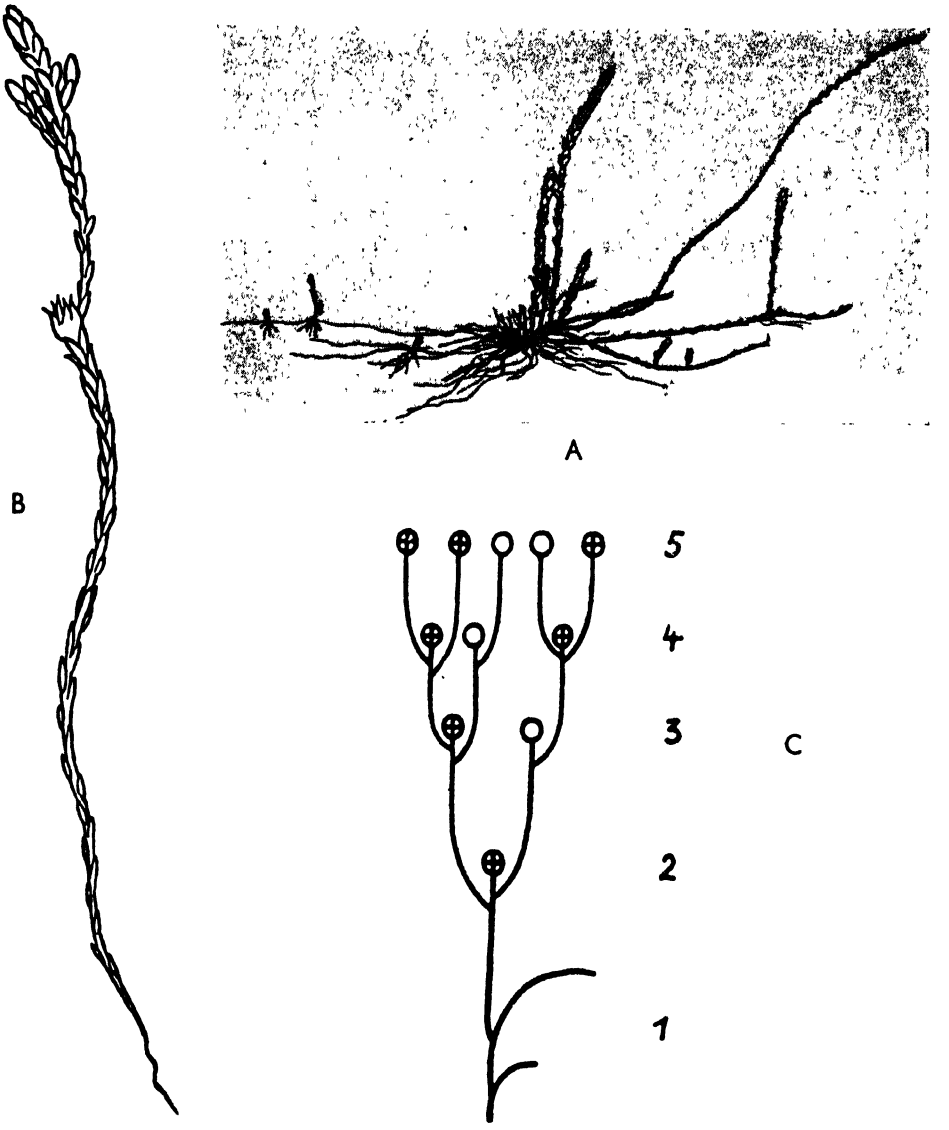


Fig. 5. *Bryum argenteum*, Hedw. Stages in the development of the gametophyte (much enlarged). A. "*Erstärkungswachstum*" (strengthening growth). The primary shoots formed from buds on the protonema have distant leaves and have fallen over. Further shoots have arisen from buds at the base and from lateral buds along these shoots; others from buds on the rhizoids. In this way a tuft of shoots is being built up. B. "*Erneuerungswachstum*" (renewal of growth). A mature male shoot with an "innovation" (branch) arising below a perigonium (male "flower"). C. Diagram of growth in *Bryum*. ⊕ perigynium or sporogonium, ○ perigonium. The figures indicate growth of successive years. (From H. Meusel, Wuchsformen und Wuchstypen der europäischen Laubmoose, *Nova Acta Leopoldina*, N.F., vol. 3, 1935.)

periodic and at least in mosses of temperate regions is closely related to their seasonal rhythms, which are discussed in the next section. Looked at in its proper perspective then, the change from protonema to leafy shoot which takes place at bud formation (or more accurately at apical cell formation) is the most striking of a series of metamorphoses of the gametophyte from spore germination to full maturity.

THE PHYSIOLOGY OF BRYOPHYTES IN RELATION TO THE ENVIRONMENT

Many physiologists have from time to time used bryophytes as experimental material in researches on the plant cell. In some cases they have been used simply because owing to their convenient size, their large cells, the lack (in the gametophyte) of a system of intercellular spaces and stomata, or for some other reason, they appeared to have advantages over the higher plants for the projected experiments. In other cases the object would seem to have been to find out how far results obtained for higher plants hold good for lower organisms. Examples, chosen more or less at random, of work coming into one or other of these categories include Harder's studies of carbon assimilation in *Fontinalis*, Stålfelt's and others on photosynthesis and respiration in mosses, Fitting's on the responses to light, gravity and other stimuli in various mosses and liverworts, and work on plasmolysis and permeability in which the exceptionally large and beautiful cells of *Hookeria lucens* have been used. There would be little purpose in attempting to review the results of these researches here—they belong to the field of general cell physiology rather than to bryology. There are, however, some aspects of the physiology of bryophytes, in particular their water relations, growth and mineral nutrition, which have a close relation to their ecology, and therefore to their status as simple land plants occupying an intermediate position between the higher plants and the algae; on these a few remarks may be made.

In the field of water relations in bryophytes the problems which have received most attention have been the conduction of water and solutes in the gametophyte and sporophyte of mosses and the remarkable resistance to drought shown by the spores and vegetative cells of many bryophytes.

Much of the older work on conduction in bryophytes suffered from faults in technique but many of the contradictions in earlier results have been cleared up by more recent studies, among which should be mentioned especially those of Mägdefrau[65], Buch[21], Zacherl[109], and a small but interesting recent contribution by Bopp and Stehle[16] dealing chiefly with the water supply to the sporophyte.

Buch's work is valuable, especially in focusing attention on the area of absorption, as well as the path of conduction of water in the gametophyte;

it also emphasizes the physiological differences with respect to water relations which exist among the bryophytes.

Observations made by Haberlandt and others in the last century seemed to indicate that, at least in a few mosses, there is an upward movement of water from the base of the stem to the leaves, comparable, at least in some respects, to the transpiration stream in a higher plant. Later, however, much controversy sprang up as to the relative importance of internal conduction through the stem and external conduction by way of the capillary channels between the leaves, paraphyllia, rhizoids, etc. In much of the discussion it has been generally assumed, in spite of a good deal of experimental evidence to the contrary, that all bryophytes are capable of absorbing (as well as losing) water over practically the entire surface of the leafy shoot or thallus. As Buch has pointed out, even when it has been demonstrated that there is a considerable external conduction of water up the stem, it still has to be determined how much of this water is absorbed into the leaf cells.

After discussing critically the work done up to the date of his paper (1945) and adding much evidence from his own experiments and field observations, Buch comes to the conclusion that bryophytes include two main physiological groups:

(1) Mosses in which the stem has a well developed conducting strand such as *Mnium undulatum*, *Bryum capillare*, *Polytrichum commune*, and *P. juniperinum*; in these water is taken up mainly by the rhizoids at the base and is conducted internally through the stem to the leaves. Such mosses, which Buch terms "endohydric," have a transpiration stream and, so long as the soil remains moist, are able to maintain turgidity in an atmosphere with a considerable saturation deficit, even when no external conduction of water can take place. The leaves in these mosses are relatively impermeable to water and appear to have a cuticle-like covering: in some of them, e.g. *Bartramia pomiformis*, the surface is actually unwettable. There is some evidence that the "cuticle" of endohydric mosses has thin spots through which water is lost or absorbed more readily than elsewhere; these can function as hydathodes when the plant is in a saturated atmosphere.

(2) Mosses (and leafy liverworts) in which there is no well differentiated conducting strand. These are termed "ectohydric" and are capable of absorbing water (and dissolved substances) through almost any part of the external surface of the shoot or thallus. In these there is no regular internal movement of water within the stem.

The ectohydric group probably embraces the great majority of the mosses and all the leafy liverworts. Some bryophytes, termed "mixohydric" by Buch, are transitional between the endohydric and ectohydric groups. Most of the terrestrial Marchantiales form a somewhat separate group, but as they

appear to absorb water and solutes entirely through the rhizoids and the lower surface of the thallus, they resemble the endohydric group.

Endohydric bryophytes, according to Buch, can be readily recognized by a number of features: for instance, they have a well developed basal rhizoid system, their young fully expanded leaves are difficult to stain with dilute solutions of basic dyes and the external cell walls are relatively impermeable to electrolytes. A further striking characteristic is that when air-dry the leaves only slowly become turgid, while in ectohydric species the leaves often "revive" in a few seconds. Endohydric mosses occur on loose substrata (soil or humus) and do not usually grow on rocks or bark.

The ability of an ectohydric moss to supply the tips of the shoots with water will depend to a large extent on the external conduction of water through capillary channels; it will, therefore, be a function of a large number of morphological features such as the arrangement and distance apart of the leaves, the presence of rhizoids or paraphyllia on the stem surface, and the branching and direction of growth. It may, therefore, be expected that the water economy of the plant will be closely related to its "growth form." From this point of view the studies of Gimingham and his collaborator Birse[39, 40] on the growth forms and "growth-form spectra" of mosses in various habitats are of particular interest. Birse[7] has shown in a recent paper that the distribution of different growth forms in the moss vegetation of a Scottish dune system is closely related to variations in ground water supply.

Besides conduction and absorption of water the drought resistance of the tissues themselves is certainly of great importance in the ecology of bryophytes. Much experimental work has been done on the resistance of mosses to extreme conditions of desiccation and both whole shoots and spores of various widely distributed species are known to be capable of remaining alive for long periods in an air-dry condition. Malta[68], for example, found that protonema could be grown from a 19-year old herbarium specimen of *Anoectangium compactum* and that spores of *Ceratodon purpureus* remained viable for 16 years. Such experiments provide evidence of the remarkable powers of drought resistance of some bryophyte cells and may have some bearing on the capacity for long-distance dispersal in the species concerned. What is perhaps of more immediate ecological interest is the demonstration by Höfler[53, 54, 55] and Herzog and Höfler[49] that different species of liverworts differ considerably in their drought resistance as measured by the percentage of their cells remaining alive after exposure to low humidity in a desiccator. According to their behaviour in the experiments the species could be arranged in a series agreeing closely with their range in relation to moisture in their natural habitats in the Austrian Alps. A similar study by Eva Clausen[32] of the distribution of hepatics in an area

in Denmark including woods, heaths, bogs, and other habitats also revealed a close relation between the ability of the cells to survive drought under experimental conditions and the moisture of the natural environment. This author concluded that it is the ability of the species to withstand desiccation, rather than "its ability to delay desiccation," which decides its range of habitats. Both Höfler and Clausen have found, as might be expected, that the drought resistance of a species is not a fixed value, but is affected, for example, by "hardening" treatments.

Another investigation showing the importance of water relations in determining the ecological range of bryophyte species is that of Overbeck and Happach[76] on the water-holding capacity and growth-rate in various species of *Sphagnum* found in the bogs of North Germany. In sphagna, differences in the water-holding capacity presumably depend on the morphological construction of the shoots, rather than on any feature of the cell physiology, but they might be expected to affect the growth rate by influencing the ability of the plant to continue its growth in dry periods. The growth rate (measured as growth in length in the field) varies from 3·3 to 10·7 cm/annum in *S. rubellum* to over 41·5 cm in *S. cuspidatum* f. *plumosum*, but higher growth rates would be attained if the plant always had a sufficient water supply. Great differences in water-holding capacity between the species were found; *S. rubellum* for example holds 46 g/100 ml volume, *S. magellanicum* 19 g and the less densely tufted *S. recurvum* 10 g. These facts throw some light on the position of the various species in the well-known "pool and hummock" pattern of the regeneration complex, the species of hummocks having, on the whole, greater water-holding power than those of the hollows; they also seem to have much slower growth rates.

The great sensitivity of bryophytes, especially such specialized types as the "hanging mosses" (Meteoriaceae) and epiphyllae of the tropics, to environmental conditions is undoubtedly largely governed by water-relations and there is room for much further work on the subject. Such research might have applications outside the limits of bryology proper. Thorold[97] it may be recalled, found a quantitative correlation in Nigeria between the occurrence of epiphytes (many of which are bryophytes) and the incidence of black-pod disease of cacao, which in the absence of suitable microclimatic data may be an observation of considerable practical value.

Studies of the growth-rate of a wide range of bryophytes are also certain to be valuable. Very few precise observations have so far been made, but there are indications that many bryophytes grow very slowly and that this is one of the important factors affecting competition between them and higher plants. A study by Tallis[95] of the autecology of the widely distributed and ecologically important moss *Rhacomitrium lanuginosum* includes carefully

collected data on its growth rate in different habitats and under different conditions. The interesting fact emerges that under British conditions the growth in length of this moss never exceeds 20 mm/annum and there is strong evidence that in some habitats, e.g. calcareous grassland, its slow growth is the reason that it is usually absent; it is unable to compete with the much faster-growing higher plants. On the other hand the growth rate of Sphagna, measured as yearly production of dry matter, is remarkably high; according to Overbeck and Happach[76] even *S. rubellum*, a relatively slow-growing species, grows about twice to four times as fast as such mosses as *Camptothecium* and *Hylocomium* spp.

The growth of many European bryophytes is markedly seasonal and in densely tufted mosses the clearly marked stratification of the tufts shows the size and number of the yearly growth increments. Hagerup[44] drew attention to this in a study of a large number of species in Denmark and came to the conclusion that most European bryophytes had two annual growth periods, one in spring from December to March, and another (following an early summer resting period of 1–3 months) from June or July to August or September. He found evidence that bryophytes in non-seasonal tropical conditions also showed periodic growth and concluded that the phenomenon depended chiefly on an internal "autonomic" rhythm and not on the annual cycle of climatic conditions. Lackner[60], working in the continental climate of East Prussia, arrived at different results and stated that most of the mosses studied by him showed only one annual growth period. The incidence of this appeared to be much more directly dependent on the environmental conditions and much less controlled by an autonomic rhythm than Hagerup had claimed. Jendralski[57] afterwards investigated a large number of species living in the relatively oceanic climate of the Rhineland. Though she found that some species which Lackner had found to have only one growth period in East Prussia had two under her conditions as in Denmark, she agreed with him in concluding that the periodic growth of mosses is largely controlled by external climatic conditions and is not autonomic. Romose[85] in a very thorough study of growth periods and dry weight gain in *Camptothecium sericeum* (*Homalothecium sericeum*), a common moss of walls trees and rocks, also showed that this species if kept moist grew uninterruptedly through the summer and had no autonomically determined summer resting period. The same is true of sphagna, according to Overbeck and Happach[76].

More observations on periodic growth in bryophytes in a wider variety of climates would clearly be interesting, but though periodic growth seems a very general phenomenon in both mosses and liverworts and may be influenced to some extent by some kind of inherent rhythm, it seems probable that the most important determining factors are the temperature and moisture of the external environment.

The mineral economy of bryophytes is a subject on which so little is known that a connected discussion is hardly possible. The few firmly established facts are, however, interesting and there is no doubt that this would be a promising field for research. Since there are various types of natural and semi-natural vegetation in which bryophytes (in most cases mosses) form a considerable proportion of the "biomass," e.g. the ground cover of some types of coniferous forest, "rough grazings," and moorlands, not to mention extreme examples such as raised bogs and the "mossy forests" of the tropics, the results of such studies are likely to be of practical value to agronomists and foresters. Here only a few probably significant points can be briefly mentioned.

It seems very likely that the mineral uptake, if not the mineral metabolism of bryophytes differs in some respects from that of higher plants. Since mosses and liverworts have no roots and the role of the rhizoid system as absorbing organs (as distinct from their mechanical functions) is controversial, it is generally assumed that in ectohydric species the gametophyte is able to absorb dissolved mineral substances over its whole surface. In certain specialized bryophytes, of which the sphagna and the Leucobryaceae are the best examples, a large proportion of the plant body consists of non-living "water-storing" cells, the significance of which is, at least in part, that the living cells are brought into close contact with a large volume of water from which they are capable of extracting nutrients, ions of which may be present in very low concentrations. The intimate mixture of non-living "water-storing" and living cells provides a very large interface between the two.

Though many bryophytes live under highly oligotrophic conditions, there are others which prefer eutrophic conditions or even grow on such substances as wet limestone rocks or gypsum deposits where there may be a high concentration of solutes in the surrounding water. It is noteworthy that species with the ability to grow on calcareous or other mineral-rich substrata tend to belong to particular families or smaller taxonomic groups such as the Tortulaceae, the Amblystegiaceae, and the genus *Bryum*, all of which are probably to be regarded as specialized and advanced from an evolutionary point of view. Bryophytes in general react sensitively to the chemical nature of their surroundings and the value of certain species as indicators of the presence of particular elements or ions, e.g. copper, is well known.

Some mosses appear to have the power of accumulating certain mineral substances. Tallis[95] has recently found that the moss *Rhacomitrium lanuginosum* contains a much higher percentage of iron than most flowering plants, even when growing on substrata which are not particularly rich in iron. There is also some evidence that bryophytes adsorb large amounts of phosphate; farmers in North Wales say that phosphate dressings should not be applied

to pastures where there is much moss mixed with the grass because the former takes up most of the phosphate and makes it unavailable to the other vegetation.

The uptake of mineral ions has been studied chiefly in *Sphagnum*. From the pioneer work of Paul, Skene, and others it has long been known that *Sphagnum* plants have the property of making neutral or weakly basic salt solutions acid. This is brought about by ion exchange and seems to depend on properties of the cell wall; it does not depend on any activity of the living cells and is as well shown by *Sphagnum* killed by heat or poisons as by living plants. This ion-exchanging capacity, which seems to play an essential part in the mineral nutrition of *Sphagnum*, has recently been re-investigated by Anschütz and Gessner[4] who find that the ionic exchange properties of the *Sphagnum* cell wall both quantitatively and qualitatively closely resemble those of synthetic exchange resins. The resemblance in behaviour probably depends on a similarity between a substance (or substances) in the cell wall and the artificial resins which may be physico-chemical rather than a real similarity in chemical composition.

Though this capacity for ion exchange is most highly developed in *Sphagnum* it is quite likely that it is shared to some extent by other bryophytes living under more or less oligotrophic conditions. The subject is of interest from various points of view and deserves much more investigation.

The possible importance of mineral uptake by bryophytes in some types of vegetation is shown by Tamm's valuable study of growth, yield, and mineral economy in *Hylocomium splendens*[98], a moss which often forms a nearly pure ground cover in certain types of coniferous forest in Scandinavia. Measurements of the growth of the moss in relation to light intensity, mineral supply, and other factors showed that at normal light intensities its yield is chiefly related to nutrient supply. The moss carpet appears to obtain most of its nutrients from atmospheric dust and from the rain-washings of the trees above. Owing to the absence of the latter, it is less well supplied with nutrients in the open than under a tree canopy. These observations seem to throw an interesting light on the possible importance of the moss layer in the economy of the forest as a plant community, as well as on the well-known harmful effect of collecting moss "litter" in woodlands.

EVOLUTION

A survey of bryology at the present day would be very incomplete without some reference, however brief, to modern views on the origin of the group and evolutionary tendencies within it. Though ideas now current on this subject differ considerably from those prevailing 40 or 50 years ago and there is perhaps now a greater measure of agreement on the main lines of bryophyte evolution, this is due mainly, but not entirely, to advances

outside the field of bryology, especially to progress in the study of algal life-histories and to increasing knowledge of the earliest known land plants, the Psilophytales. Evolutionary studies of the bryophytes themselves continue to lack the firm basis of a good fossil record. Comparatively few pre-Tertiary fossil bryophytes have been found and very few of these are known in sufficient detail to provide useful evidence of evolutionary trends. An important exception is the liverwort *Naiadita lanceolata*; of this Professor T. M. Harris gave an admirable account in his *British Rhaetic Flora* (1934)[45] which has greatly influenced subsequent discussions on bryophyte evolution. But because well-preserved fossil bryophytes are so scarce, except some of relatively recent date, it may be that the few that are known carry more weight in evolutionary arguments than they should.

The two chief alternative views on bryophyte evolution are quite well known and it is unnecessary to outline them here in more than a very few words.

According to the view which for convenience we can call the Up-grade Theory, the primitive bryophytes gametophytes were simple thallose plants similar to the "*Sphaero-Riccia*" of Lotsy[30, 63], an hypothetical plant which combined some features of the living genus *Sphaerocarpus* with some of *Riccia*. Such a plant by developing indentations in the "wings" of the thallus gave rise to a type of dorsiventral leafy liverwort with two rows of leaves and a third row of leaves (underleaves) was afterwards developed by the modification of mucilage hairs on the ventral surface of the thallus. In this way, according to the theory, were evolved erect-growing leafy liverworts with three more or less similar rows of leaves, such as the Calobryaceae and genera such as *Anthelia* and *Chandonanthus* among the Acrogynae. A plant of similar construction could also have been the ancestor of the Sphagnales and the true mosses; in both these groups the primitive gametophyte appears to have been radially symmetrical with three rows of leaves.

The sporophyte also, according to the Up-grade Theory, evolved from a simple to a complex type of construction, the primitive form being a mere "bag of spores" wholly dependent on the gametophyte for its nutrition, such as found in *Riccia*. This was believed to have evolved by a series of stages into a more complex type of sporophyte, such as is found in *Anthoceros* and most mosses, which has enough photosynthetic tissue to be partially independent of the gametophyte in its nutrition, and in addition often has elaborate spore discharge mechanisms.

The alternative view, which we shall label the Down-grade Theory, is almost the exact converse of the Up-grade Theory. On this the primitive gametophyte is supposed to be an upright plant with leaves in three rows. Dorsiventral leafy liverworts are regarded as being derived from such a radially organized plant by the reduction of one row of leaves. Thallose

types are derived from foliose, simple thalli like those of *Riccia* and *Sphaerocarpos* representing the extreme stage of reduction. The primitive bryophyte sporophyte, according to the Down-grade Theory, was fairly complex and was equipped with sufficient photosynthetic apparatus to make it at least to some extent nutritionally independent of the gametophyte. The nearest to this hypothetical primitive type among existing sporophytes is undoubtedly that of *Anthoceros*. The moss sporophyte has not departed from the primitive type so far as that of the majority of liverworts, but has some specialized features such as the peristome which are clearly advanced. The sporophytes of the liverworts, other than the Anthocerotales, show various stages of reduction, the extreme being reached, as with the gametophytes, in *Riccia* and *Sphaerocarpus*.

The two opposed theories outlined here are closely bound up with even more speculative views on the possible origin of the hypothetical primitive bryophytes and presuppose evolutionary changes of quite different kinds. The primitive "*Sphaero-Riccia*" of the Up-grade Theory implies the origin of bryophytes more or less directly from some kind of simple algal ancestor. Several versions of this theory are possible, the best known one being that expounded in Bower's *Origin of a Land Flora* (1908)[17]. According to this the algal ancestor had a haplobiontic life-cycle, the thallus being haploid and meiosis following immediately after sexual fusion. The evolution of the sporophyte generation is envisaged as a process in which more and more mitotic divisions are intercalated between fusion and meiosis, and more and more potentially spore-forming tissue becomes "sterilized" and diverted to other functions.

The Down-grade Theory, on the other hand, though it also regards the bryophytes as ultimately derived from algal ancestors, is usually taken to imply that the latter were plants which already had a diplobiontic life-cycle, i.e. that they already had an alternation of generations, probably of an isomorphic type (as in *Dictyota* among the brown algae and *Cladophora*, etc., among the Chlorophyta). After their migration on to the land the two generations may be supposed to have diverged in evolution, the one to become the independent gametophyte, the other the semi-parasitic sporophyte, both generations undergoing further evolutionary changes which, as already explained, mainly consisted of reduction. Since there is a wide gap between the hypothetical primitive bryophytes of the Down-grade Theory and any known type of alga, the theory admits of various views as to possible intermediate stages. Zimmermann[111] regards both the bryophytes and the pteridophytes as derived from some unknown type of early archegoniate land plant which he terms an alga, a view which is not far removed from the well-known "Thalassiophyta" theory of A. H. Church. Christensen[33] has expressed a view which is similar except that he thinks that the last common

ancestor of the Bryophyta and the known Pteridophyta should be termed a pteridophyte rather than an alga. Takhtajan[94] who lays much stress on the similarity between the sporophytes of the Devonian *Sporogonites* and *Horneophyton* and those of some modern bryophytes, suggests that the latter may be reduced descendants of the Psilophytales, a view which is much more plausible than the converse idea which has been put forward by some upholders of the Up-grade Theory, viz. that the primitive pteridophytes were derived from bryophyte ancestors with a sporophyte like that of *Anthoceros*. In spite of Campbell's observations on *Anthoceros* sporophytes which are supposed to have become independent of the gametophyte, it is very difficult to conceive any type of bryophyte sporophyte evolving into an independent plant.

At the present time various versions of the Down-grade Theory appear to be widely accepted and Up-grade views have few supporters. This is not the place to discuss the arguments for and against the two theories, but a few remarks are necessary on their implications for the taxonomy of bryophytes.

Most classifications of the Hepaticae have been based on the assumption that groups with simple sporophytes (Sphaerocarpales, Ricciaceae) are primitive and those with complex sporophytes (Anthocerotaceae) are advanced; gametophytes with three rows of equal or subequal leaves have also been regarded as more advanced than dorsiventral gametophytes with small underleaves or only two rows of leaves. Evans[34], however, in an interesting discussion of the classification of the Hepaticae has put forward a well thought-out scheme based on a down-grade theory. This and other modern views on the classification and phylogeny of the Hepaticae have been reviewed at some length by Fulford[36].

The mosses, though more numerous in species and genera than the liverworts, show a narrower range of structure in both gametophyte and sporophyte and are not a group in which phylogenetic conceptions can easily be expressed in classification. The classifications most widely used at the present day are largely based on that put forward by Fleischer in the *Musci der Flora von Buitenzorg*[35]. Though Fleischer's classification was certainly more natural than those which preceded it, a fundamental reassessment of the classification of the mosses seems overdue. For example, though it has long been clear that cleistocarpic mosses with very simple sporophytes such as *Phascum*, *Nanomitrium*, and *Ephemerum* are reduced and not primitive, this conclusion has not yet been embodied in the classification.

In all discussions on bryophyte evolution and classification the Anthocerotaceae necessarily occupy a central place. The large amount of attention which they have received in consequence has caused the differences between them and other liverworts to be overemphasized. This has led to the proposal

that the Bryophyta, instead of being divided into the traditional two classes, should be divided into three groups of equal rank, Hepaticae, Anthocerotae, and Musci. Though the Anthocerotales are undoubtedly isolated, the sporophytes of *Notothylas* approach those of other Hepaticae in some respects and there are perhaps other groups of bryophytes for which an equally strong claim for independent rank could be made. In spite of the superficial resemblance of their gametophytes to those of true mosses, the Sphagna, as Chalaud[31] has pointed out, resemble the Hepaticae in as many respects as they resemble the Musci. They occupy in fact an almost exactly intermediate position between the two groups. The conventional division into Hepaticae and Musci may well not correspond with any phylogenetic reality, but in the present state of our knowledge it is doubtful whether much is gained by attempting a division into three or more co-ordinate groups.

The study of bryophyte evolution remains now as always a fascinating subject for speculation, but unless more fossil evidence is forthcoming the only hope of progress must lie in looking for new types of evidence. One field from which evidence of a new kind has come is genetics. Burgeff[25] in his genetical studies of a number of *Marchantia* species obtained mutants and hybrids with characters closely resembling features found in *Dumortiera*, *Monoselenium*, *Riccia*, and other genera of the Marchantiales, so providing evidence supporting the view which Goebel had reached on purely morphological grounds that the simpler Marchantiales were derived from more complex types and not *vice versa*. Though it is difficult at present to foresee the outcome of the work on experimental morphology and morphogenesis in bryophytes which has been begun by Fitting, Bopp, and others it is not unlikely that such studies will ultimately throw a quite new light on phylogenetic problems.

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PTERIDOPHYTA

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FEW groups of plants have attracted the attention of botanists more than the Pteridophyta. The great interest they have aroused is due to various elements: their central position in the world of higher plants, their great antiquity, testified by particularly abundant fossil remains, the hope of discovering among them the forerunners of the higher vascular plants and, not least, the fact that they represent a pre-eminent field of study for the knowledge of general morphogenetic processes. However, even if these plants have been so intensely studied, several fundamental problems concerning their taxonomy and phylogeny still remain unsolved: both because the interrelations of single groups are in themselves hard to establish and require a deeper knowledge than is yet available, and because the fossil remains of the Pteridophyta, though more abundant than in other groups of plants, are not sufficient to give us a clear idea of the origin, evolution, and affinities of the various subdivisions.

This interest in the Pteridophyta has given rise to a profuse literature dispersed in a great number of books and periodicals and embracing all fields of botany. Since taxonomy represents the synthesis of all biological knowledge or, as Turrill[335] wrote, "the focal point of biology," our research cannot be limited to taxonomical works but we must also bear in mind the results of pteridological investigation in the fields of cytology, genetics, morphology, anatomy, palynology, physiology, geobotany, and phylogeny, in order to have our systems of classification based on the largest possible number of characters. Even if this is the goal we must have before us always, it is arduous to reach; apart from anything else the bibliographical research is becoming more and more difficult from year to year.

We cannot hope to understand the meaning of any present pteridological problem without an adequate knowledge of its antecedents. This is particularly true for the taxonomy of the Pteridophyta, which depends in so large a measure on the co-ordination of research on living and fossil plants. These considerations have induced me, before taking into account present problems and trends in the taxonomy of the Pteridophyta, to give a survey of our pteridological knowledge. Since, however, no historical account on Pteridophyta has so far been published, I have thought it convenient to combine the two things and to give a synthesis of our pteridological knowledge on an historical basis. This seemed to me particularly suitable in a

book which intends to commemorate an historical event as well as to give a vista on present and future researches. Thus my account will be divided into two parts: first the evolution of pteridological knowledge, and then problems and trends in the taxonomy and phylogeny of the Pteridophyta.

THE EVOLUTION OF PTERIDOLOGICAL KNOWLEDGE

Every taxonomic unit has its vicissitudes, but there are few groups of plants, or perhaps none, which have undergone so many changes in taxonomy and nomenclature as some groups of the Pteridophyta. Consequently the history of their classification is particularly complicated though interesting and informative.

The Pteridophyta, although mentioned by Greek, Roman, and Arab herbalists and naturalists, received little or no attention in ancient and mediaeval times, when medical virtues were the chief basis for plant classification. However, even in those times some people were attracted by the study of the morphology of plants; we find the first example of this in Theophrastus, who attempted an arrangement of plants according to their resemblance of habit, and a few other characteristics. But we must reach the Middle Ages with Albertus Magnus to find someone else who undertook plant studies along these lines, even if not very successfully.

Only in the 16th century do we perceive an approach to the plant classification which later on developed into taxonomic botany. Among the naturalists who flourished in that time, Brunfels, Bock, known also as Tragus, Gesner, Fuchs, and others, the most pre-eminent figure is Cesalpino, who is regarded as the first taxonomist, the father of plant taxonomy.

Andrea Cesalpino was the first to take into account for the purposes of classification the characteristics of the reproductive organs. He ordered plants on the basis of their habit, the structure of their fruit and seed, the presence of the ovary, the presence of bulbs and milky sap, the presence or absence of the seed and flower, etc. These concepts, expressed in his work *De Plantis*[55], as well as in his introductory letter of 1563 to the herbarium presented to Bishop Tornabuoni (cf. Caruel[51]), and his careful observations of living specimens, led him to segregate the plants bearing seeds from these devoid of seeds. He assembled the latter in a "genus, quod nullum semen molitur," described in the last part of his work (Liber XVI). In this group Cesalpino classified those plants which later on became the Cryptogams. Among them he included ferns, horsetails, and lycopods, treating the ferns first (". . . ut Filix, & quae illi affinia sunt,"), since he regarded them as the most advanced (". . . ., ad perfectiores accedunt magis; . . .").

Cesalpino had no immediate followers. Both Jean Bauhin and his brother Gaspard have left us some works very valuable in other respects, but their classifications were strictly artificial. For instance, G. Bauhin in his

Pinax[19] describes all the ferns together in Liber X, but classifies *Equisetum* in Liber I together with *Juncus*, *Cyperus*, *Sparganium*, etc. J. Bauhin and Cherler[20] deal with the pteridophytes in the same volume (Tomus III), but the different genera of ferns and fern allies are dispersed in four chapters of the book (Liber 35 to 38), mixed with several spermatophytes on the grounds of a very superficial resemblance. For instance, *Ophioglossum* and *Botrychium* are grouped with *Aloë*, *Sedum*, etc., on the basis of their succulent leaves; *Equisetum* with *Asparagus*, *Galium*, etc., as "herbae stellatae"; while *Marsilea* and *Salvinia* are placed together with *Nymphaea*, and other flowering aquatic plants.

In the second half of the 17th century, the development of optical instruments makes the first anatomical observations possible, and we find the first information on the anatomy of ferns in the works of Grew[128] and Malpighi[206], presented in "eâ ipsâ horâ" on the same day (7th December 1671) to the Royal Society of London (cf. Malpighi[206], App. p. 14; Grew[129] p. 4 of the Preface). Both described the sporangium and its dehiscence but Malpighi's observations are by far the more complete and technical. He described the indusium, the sporangium, the annulus, noticing that it was incomplete, and the dehiscence, and observed the colour of the spores. Moreover he gave a precise drawing (t. 51. f. 299) of the sporangium clearly showing its structure. Nearly at the same time Cole observed and described the sporangia and the spores of ferns, but his observations, described in a letter of 30th September 1669 were made known only in 1686 by Ray[269]. At that time Morison[227] first made the spores of ferns germinate, confirming the observations made, more than a century before, by Cordus[75], who was the first to have remarked that all ferns reproduce by means of the "pulvisculus" detached from the under surface of the fronds of ferns.

Towards the end of the 17th century, after nearly a hundred years, the way to taxonomical research opened by Cesalpino was resumed by other botanists: Morison, Rivinus, Ray, Tournefort. The research of these authors greatly improved taxonomical knowledge of flowering plants, and moreover had the merit of establishing the first systems of classification and laying the foundations of the taxonomical categories. However, as regards the vascular cryptogams, even though these authors gave a good contribution to the classification of single groups, the period marked a regression in the general arrangement of the Pteridophyta. For instance *Equisetum*, although clearly regarded by Cesalpino as a cryptogam, was classified by Tournefort[333] as well as by Ray[270], as a flowering plant together with *Spinacia*, *Cannabis*, *Lupulus*, etc. This point of view was resolutely opposed some years later by Dillenius[94] who stated that *Equisetum* must be regarded as a fern. Like Ray and Tournefort, he treated the Lycopods as belonging to Musci.

Later on Dillenius studied this group very carefully and in his *Historia Muscorum*[95] distinguished as distinct genera *Selago*, *Lycopodium*, *Selaginoides*, *Lycopodioides*, and *Calamaria*. This was an arrangement quite noteworthy for his times. Almost simultaneously B. De Jussieu[87] described the germination of the spores of *Pilularia* and discussing the taxonomical position of this genus, clearly expressed the opinion that it must be classified among the ferns.

In the 17th century pteridological knowledge was chiefly based on European plants, but at the beginning of the 18th several extra-European pteridophytes were described and illustrated thanks to the works of Plumier[254, 255] on American ferns, of Rheede[276] on Indian plants, and of Plukenett[253] and Petiver[245, 246] on plants from different parts of the world.

The knowledge acquired by Cesalpino, Bauhin, Ray, and Tournefort, and several others was taken up by Linné, whose merits are known to everybody. In his *Species Plantarum*[199] and in the fifth edition of the *Genera Plantarum*[200] which immediately followed it, Linné arranged the genera of Pteridophyta rather roughly but, nevertheless, he was able to take up the best of what each of his predecessors had achieved, so that Linné's arrangement of the Pteridophyta was reasonably sound for his time, even if we regard it now as poor and artificial. He included all the Pteridophyta in his Classis XXIV: "Cryptogamia." *Equisetum*, all the ferns, and *Isoëtes* formed the group of "Filices," while *Lycopodium* was referred to the "Musci." In these two books Linné recognized seventeen genera and 213 species of Pteridophyta. He based his classification of the Pteridophyta on the arrangement of sporangia (in spikes, or on the leaf, or near the basis of the leaf-stalk) and on the shape, position, and other characteristics of sori.

The time following the publication of the *Species Plantarum* was dominated by Linné's authority. His so-called "sexual system," although so clearly artificial, was adopted in nearly all countries with the exception of France. There it had strong opponents in Adanson, Lamarck, and Bernard and Antoine Laurent De Jussieu, the founders of the natural method in taxonomy, and the earliest exponents of that pre-Darwinian era which culminated in the publication of Darwin's *Origin of Species*[79] in 1859.

Adanson was the first to present a natural system and had a pre-eminent place in the development of systematic botany. In his book *Familles des Plantes*[4] he subdivided the vegetable kingdom into fifty-eight families, on the basis of both the vegetative and reproductive characteristics of plants. His system marked a great advance in comparison with the Linnean classification, and some of his families still stand in modern classifications, but as regards the members of the Pteridophyta his arrangement was decidedly unsatisfactory. He placed *Equisetum* among the conifers; *Isoëtes* in the

family of "Arum" together with *Ruppia*, *Zostera*, *Arum*, etc.; *Lycopodium* in the family of mosses like Linné, *Salvinia* among the hepatics, and established a family for the ferns. In spite of all this, we must remember that Adanson was probably the first to take into account the presence or absence of the indusium ("enveloppe"), as well as its shape and structure, in the classification of fern genera.

A. L. De Jussieu in his *Genera Plantarum*[86] proposed a natural system which undoubtedly was better than Adanson's. He proposed three primary divisions: Acotyledones, Monocotyledones, and Dycotyledones. The "ordines naturales" (our families) of Monocotyledons and Dicotyledons were clearly differentiated, described and named; several of them correspond exactly to the families of present-day classifications. The group of the Acotyledones is a strange mixture of cryptogams and phanerogams. However, contrary to Adanson's treatment, the members of the Pteridophyta are assembled again as in the Linnean system, and are distributed: *Lycopodium* in the order of Musci but in the special group "Musci spurii"; the ferns, *Isoëtes*, and *Equisetum* in the order of Filices including in it also *Zamia* and *Cycas*.

The last decade of the 18th century was eventful for pteridology. In 1791 Schreber[288] classified all the Pteridophyta into two orders: Miscellaneae (*Equisetum*, *Lycopodium*, *Porella* ·an hepatic·, *Salvinia*, *Marsilea*, *Pilularia*, *Isoëtes*) and Filices (all the remaining ferns). Thus *Lycopodium* was segregated for the first time from mosses and found its proper place among the Pteridophyta. In 1793 J. E. Smith[300] published the first attempt at the classification of ferns based on the structure of the sporangia, dealing with the so-called "Filices dorsiferae." These he subdivided into "Annulatae" and "Thecatae" according to the presence or absence of the ring of the sporangia. In 1794 Lindsay made known his observations on the germination of the spores of ferns[197] (already observed more than a hundred years before by Morison[227] and afterwards by B. De Jussieu[87]) and of the spores of *Lycopodium*[198] (according to Smith[301] already seen by Fox in 1799). His experiments on ferns, described and illustrated in his paper, confirmed the nature of the spores which previously had been regarded as pollen grains by most botanists. In 1799 Hedwig[133] considered the spores as different from the seeds and, dealing with ferns, introduced the term "spora" and hence "sporangium"; two terms which have still kept exactly the same meaning. In 1799 Bernhardi[23] published the first account of his studies on fern classification, and described some new genera. As chief distinctive characteristics he utilized the presence or absence of the annulus, the dehiscence of the sporangium and the presence or absence of the indusium as well as its structure. The introduction of these characteristics is of great importance since they influenced nearly all 19th century fern classifications.

The interest in the Pteridophyta increased greatly in the following years stimulated by the discovery of a lot of new plants from tropical countries and the southern hemisphere. In 1801, in the same journal, Swartz[325] described the genus *Psilotum*, and Bernhardi[24] the genus *Tmesipteris*, the only two members of the present-day Psilotopsida, a class of Pteridophyta of outstanding interest. Besides these, the same authors described several important genera of ferns. The following year Willdenow[347] presented a preliminary account of his classification of the Pteridophyta, which found its definitive form some years later. In this paper he established a group consisting of the genera *Salvinia*, *Marsilea*, *Pilularia*, and *Isoëtes* under the well-known name Hydropterides, still adopted by many taxonomists for the living heterosporous ferns. The same group in the same year was named Rhizocarpae by Batsch[18], a name probably inspired by the Rhizospermae previously introduced by Wiggers[346] for *Pilularia* and *Isoëtes*.

In the following year L. C. Richard (in Michaux[221]) subdivided the Cryptogamia into six main groups: Filices, Hepaticae, Equisetaceae Lycopodaceae, Musci, and Lichenaceae, establishing for the first time two independent main divisions of Pteridophyta: Equisetaceae (for *Equisetum*) and Lycopodaceae (for *Psilotum* and *Lycopodium*). In the same year Brisseau Mirbel[40] classified the present Pteridophyta into four groups ("familles"): Lycopodia, Filices, Marsileae, and Equiseta. It should be noted that Mirbel, in dealing with the Lycopodia (subdivided into six genera, five of which new and attributed to Palisot de Beauvois) and the Marsileae (including *Pilularia*, *Marsilea*, *Salvinia*, and *Isoëtes*) probably utilized the homomorphism and dimorphism of the sporangia for the first time as diagnostic characteristics, although ignorant of the true nature and meaning of these organs. Thus in 1803 three of the four primary groups of the living Pteridophyta recognized in modern times were already established.

An important event for Pteridology was the publication of Swartz's *Synopsis Filicum*[326] in 1806 which represents the first taxonomical book entirely devoted to ferns. Swartz based his system of classification on the mode of dehiscence (sporangia with or without annulus, or opening otherwise) and on the presence or absence of the indusium. Thus he subdivided the ferns into three primary groups: "Gyratae" (with the subdivisions: "Soris Nudis" or "Indusiatis"), "Spurie Gyratae" ("Capsulis Rimatis") and "Agyratae" (with the subdivisions: "Capsulis Multilocularibus" or "Bivalvibus"). He recognized thirty-eight genera of ferns with 710 species, besides numerous doubtful ones. Swartz dealt also with the groups of *Lycopodium*, *Tmesipteris*, and *Psilotum* (sixty-eight species) which he treated under the new name "Lycopodineae." In this manner he sanctioned the independence of these plants from the other pteridophytes already proposed by Richard[221], Brisseau-Mirbel[40], and Palisot de Beauvois[243].

In his Prodrome on mosses and Lycopods[244] presented to the "Institut National" on the 1st of May 1803, but published only in 1805 Palisot split *Lycopodium*, segregating from it the well-known genus *Selaginella*, and other genera. These had already been described in the meantime by Brisseau-Mirbel[40], who attributed them to Palisot.

Another notable book is that of Schkuhr[284], the value of which is due to its 192 fine coloured plates, and to the fact that numerous pteridologists have quoted its illustrations as a reference in the identification of species. It represents the first pictorial work entirely devoted to the illustration of ferns. One year later Willdenow[348] published Vol. 5, Part 1 of the 4th edition of Linné's *Species Plantarum* which deals with the Pteridophyta. This book is a good conspectus of the various species known at that time, but the classification is rather retrogressive. Willdenow based it on superficial characteristics, and hence distributed ferns and lycopods in a very artificial manner. He recognized fifty-three genera, and 1155 species subdivided into six groups: Gonopterides (*Equisetum*), Stachyopterides (Lycopsida pp., Psilotopsida and Ophioglossaceae), Poropterides (*Marattia, Danaea*), Schismatopterides (*Angiopteris*, Gleicheniales, Osmundales, Schizaeales), Filices (Filicidae), Hydropterides (*Isoëtes*, Marsileidae and Salviniidae). At exactly the same time (Spring of 1810) R. Brown published his *Prodromus Florae Novae Hollandiae*[43], in which he gave the first account of the flora of Australia, describing eight new genera and numerous new species of Pteridophyta, assembled in a system like that of de Candolle.

The general system already sketched by de Candolle[88] in 1805, was improved and published by him[85] in 1813, and in it he pointed out the importance of the vascular system in taxonomy. He assembled all the present-day Pteridophyta in a single group, and classified them as "Endogènes ou Monocotylédonés, B. Cryptogames" of the primary group "Végétaux vasculaires ou Cotylédonés." Thus de Candolle was the first to recognize that the Pteridophyta are better classified in a group with the Spermatophyta than with the lower plants.

In the remaining decades of the so-called pre-Darwinian period taxonomical research was chiefly directed to the definition and classification of the genera and families of the Pteridophyta, especially of ferns, rather than to their general classification. Great attention was paid also to morphology, anatomy, geobotany, and especially to palaeobotany. In fact at that time the first palaeobotanical papers were published, and in 1820 appeared Stenberg's work[311] which represents the starting-point for the nomenclature of fossil plants.

An eminent figure of this time was Kaulfuss, who published two remarkable papers: one[171] in 1824, in which ten new genera and numerous new species are described, and the second[172] in 1827 in which he gives a careful

description of the germination of the spore, and of the development of the prothallus and young plant. However, he did not observe any sexual part. Besides giving an exhaustive review of the subject, Kaulfuss in his second paper proposed a good system of fern classification in which the characteristic of circinnate or straight vernation is taken into consideration for the first time.

A new systematic arrangement of the Pteridophyta appeared in 1827 in vol. 4 of Sprengel's *Systema Vegetabilium*[304], in which he described all the species of Pteridophyta known to him (1627 species), arranged in seventy-four genera, and subdivided into nine main groups (plus a first group, the "Rhizantheae," consisting of a flowering plant, *Rafflesia*). The nine groups were Rhizospermae, Equiseteae, Lycopodeae and six other groups of ferns. The system is an improvement compared with that of Willdenow, but the splitting of ferns into seven groups of the same rank as the Equiseteae and Lycopodeae make it rather artificial. In the same year another general account of the Pteridophyta (Equisetales excluded), was published by Desvaux[91] who established a system of classification based on personal observation. Although constructed on the characteristics of sori and sporangia only, it was better than Sprengel's.

A promising period for the iconography of Pteridophyta was opened in 1827 with the publication in instalments of the splendid folio volumes of Hooker and Greville's *Icones Filicum*[165] consisting of 240 plates with descriptive letterpress. One year later the publication of another splendid folio work was undertaken, Blume's *Flora Javae*[31], which contains eighty-eight plates of ferns, and some interesting remarks on certain genera. The editions with coloured plates of Hooker and Greville, and of Blume, together with Schkuhr's book[284], which was later on continued by Kunze[179], are probably the finest illustrated works on the pteridophytes. However, speaking of fern illustration, we must not forget the great contribution given to this branch of pteridology by Hooker[157, 158, 159, 160, 161, 162] and by Fée[107, 110, 111, 112].

The study of fossil plants which had been already undertaken by some naturalists, attracted the interest of Ad. Brongniart, who so greatly contributed to the knowledge of fossil plants as to be considered the founder of palaeobotany. In 1828 he undertook the publication of his greatest work *Histoire des végétaux fossiles*[42], in which he introduced the comparative study of fossil and living plants, and proposed an interesting system of the vegetable kingdom, in which it was divided into six classes: "Agames, Cryptogames celluleuses, Cryptogames vasculaires, Phanérogames gymnospermes, Phanérogames angiospermes monocotylédones and dycotylédones." All the pteridophytes were referred to the "Cryptogames vasculaires," and in each group the study of fossil plants was introduced by an exhaustive

account of the group's living members. He paid particular attention to the classification of living ferns, and also proposed a good classification of the venation of the leaves. Furthermore we are indebted to Ad. Brongniart for his subdivision of the earth's history[41] into the following four periods of vegetation: (*a*) of the great vascular cryptogams; (*b*) of the vascular cryptogams and conifers; (*c*) of the cycads and vascular cryptogams; (*d*) of the dicotyledons and monocotyledons. Speaking of the earliest palaeobotanists we must also mention Witham, who was probably the first to investigate the anatomical structure of fossil plants[350, 351], and Goeppert, author of some famous works such as the *Systema Filicum fossilium*[124] and *Die Gattungen der fossilen Pflanzen*[125].

The first attempt to utilize vegetative characteristics as well, for the classification of the Pteridophyta, was made by Gaudichaud[120], who must also be credited with being the first to attempt the subdivision of polypodiaceous ferns. His book contains several interesting observations and new ideas, but he did not adequately study the application of these characteristics to fern classification, and moreover was so unmethodical as regards taxonomy and so confused in his exposition, that his classification turned out rather artificial, and the meaning and the delimitation of the single groups is often obscure and vague. The use of vegetative characters was also attempted by Schott in his *Genera Filicum*[285], in which the importance of the venation for the taxonomy of genera is stressed; but the work was soon interrupted.

In 1836 two works of basic importance for the taxonomy of the Pteridophyta were issued: the first two instalments of Endlicher's *Genera Plantarum*[102], and Presl's *Tentamen Pteridographiae*[262]. The great system of classification of plants proposed by Endlicher had the merit, besides many others, of establishing for the Pteridophyta the same taxonomic position in the plant-kingdom as that which is acknowledged by most modern taxonomists. He classified them in a group named "Protophyta" (to which Cycads are also referred), belonging to the primary division of the "Cormophyta," which was very conveniently established and properly defined by him. As regards the classification of the true Pteridophyta, Endlicher adopted the four classes previously established: Equiseta, Filices, Hydropterides, and Selagines (the Lycopodineae of previous authors), but he properly treated *Isoëtes* as a member of the lycopodiaceous classis, leaving only Salviniaceae and Marsileaceae in the Hydropterides. Endlicher was also one of the first taxonomists to classify fossil and living plants in the same system; he was particularly successful in thus dealing with the class of lycopods. Endlicher's system of the Pteridophyta greatly influenced later classification and was rather advanced. In fact, if we compare it with the most modern systems of living Pteridophyta, the only differences we find are the exclusion from the

class of lycopods of *Psilotum* and *Tmesipteris*, which are now kept as an independent class, and the inclusion of the Hydropterides among the ferns.

The publication, in 1836, of Presl's *Tentamen Pteridographiae*[262] marks another important event in pteridological history. It deals with gleichenioid, cyatheoid, and polypodioid ferns only, classifying them into 112 genera and about 1500 species. Apart from the numerous new genera and the innumerable new combinations, the value of this book chiefly depends on Presl's entirely new system of classification, in which, together with the characteristics of the sporangia and sori, he made use of all the vegetative and reproductive characters known to him whether morphologic or anatomic, particularly those of the venation of the leaves and the vascular bundles in the leaf-stalk. The result of this method, which had already been unsuccessfully introduced by Gaudichaud[120], and by Schott[285], was excellent. Presl completed and improved this system of classification in some later papers[263, 264, 265, 266] dealing with the other ferns. His publications still remain a source of interesting taxonomical ideas. Unfortunately, Presl's advanced concepts were followed by few pteridologists and the true and great value of his system was wholly acknowledged only a century later.

The way opened by Presl to pteridological research was followed by Fée and Smith. The former published several books, some of them of a certain importance as monographic works[107, 108, 109], but his greatest publication is *Genera Filicum*[110], dealing with the family of Polypodiaceae (including the cyatheaceous ferns). Fée in this work enumerated more than 2100 species subdivided into 188 genera. He followed Presl's system, but introduced new characteristics in classifying the genera, such as the number of the cells of the annulus, and the form of the spores. But the number of cells of the annulus is not a good diagnostic characteristic, and furthermore Fée's knowledge of the shape of the spores was insufficient, so that his classification did not much improve upon Presl's system; nevertheless it greatly enlarged our pteridological knowledge.

J. Smith published two works on fern classification. The first[298] was written without knowing Presl's book (cf. Smith[299], p. 33). The arrangement of the 143 genera described was based on the characteristics of the sporangia and sori and proved to be rather artificial. The second work[299] was published more than thirty years later when Smith had largely adopted Presl's views. In it he recognized 220 genera of ferns, and based his system on circinnate or straight vernation, the mode of growth of the caudex and its direction, the attachment of the fronds, articulated with the caudex or adherent to it, the position and structure of the annulus, the venation of the fronds, the shape and position of sori, the presence or absence of indusium, and other less important characteristics. By combining these characters he succeeded in delimiting natural genera and groups which still stand today.

His work, like that of Presl, was overlooked in later years, but his ideas are now generally accepted, and, like Presl, Smith is regarded as a pioneer of modern pteridology.

If Presl did not receive the attention he deserved from his contemporaries, this was due to the influence excercised at the time by W. J. Hooker whose preference for large genera, based solely on the characteristics of the reproductive organs, is well-known to all pteridologists. These conservative concepts led him to mass hundreds of species under a single generic name, regardless of their dissimilar vegetative characteristics and anatomical structure. Thus he retained the old Swartzian classification of ferns, reducing Presl's and Smith's genera to subgenera and sections. In spite of this, Hooker remains one of the most distinguished of pteridologists. Among his most interesting books, some of which we have already mentioned, three are particularly memorable. *Genera Filicum*[157] consists of 120 coloured plates, each containing both natural-sized and magnified illustrations of portions of fronds showing soral characteristics, accompanied by corresponding letterpress giving the description of each genus; altogether 135 genera are illustrated and described, many being derived from Presl[262], and twenty from Smith[298]. The book was compiled without a deep knowledge of the genera accepted in it, so that it reflected Hooker's concepts only in part. Indeed several of the genera so finely and clearly illustrated in the book were later on rejected by him. *Species Filicum*[158] consists of five volumes in which about 2400 species, subdivided into sixty-three genera, are described, and about 520 of them illustrated. *Synopsis Filicum*[163, 164], completed after Hooker's death by Baker, contains more than 2200 descriptions of species belonging to seventy-five genera. Both the books reflect Hooker's conservative preference for large genera, and their value lies chiefly in his descriptions of the species, more than 600 of them new, and on his critical remarks about them.

Hooker's ideas were adopted by Baker whose activity was chiefly devoted to analytical research. Besides completing the first edition of Hooker's *Synopsis Filicum*[163], and taking care of the second one[164], he published several papers in which many new species of Pteridophyta are described. He also studied the families of Cyatheaceae and Polypodiaceae for Martius's *Flora Brasiliensis*[15] and published a *Handbook of the Fern-allies*[16].

Other pteridologists of the mid-19th century are Spring and Moore. Spring published a monograph on the Lycopodiaceae (incl. *Psilotum* and *Tmesipteris*)[305] which must be mentioned for its value as a descriptive work, but which has no importance from the point of view of general taxonomy. Moore, whose name is well-known for various papers on cultivated plants and for his fine book of illustrations of British ferns, published together with Lindley[226], is the author of the first *Index Filicum*[225] which

unfortunately remained incomplete. The book also contained a section dealing with classification, in which Moore recognized numerous genera (180 of ferns and six of lycopods). This part is interesting for its descriptions, synonyms, and illustrations of genera, but the classification is based on old concepts and thus artificial.

I have dealt with Presl, Fée, Smith, Hooker, and others, out of the chronological sequence, in order to follow the two opposite tendencies which dominated the field of pteridological taxonomy in the middle of the 19th century. But in the meantime morphological studies had thrown new light upon the organography of Pteridophyta. As already mentioned Kaulfuss[172] in 1827 had described the germination of the spores. In 1828 Bischoff[30] pointed out that spores, unlike seeds, did not contain any part of the future plant; he concluded that spores and seeds are different, and proposed that the seed-plants should be named "Spermophyta" and the plants with spores "Sporophyta."

In 1834 Pietro Savi in a short note on *Salvinia*[281], though using an improper terminology, actually described and illustrated the germinating microsporangium ("granello pollinico") with male prothallia and antheridia ("budelli"), and the spermatozoids ("granellini"); the latter, however, were not described but only noticed because of their rapid movements. Savi also described and illustrated the female prothallus with the archegonia ("borse"), provided with their neck of four cells and the ovum ("germe"). He correctly supposed that the spermatozoids penetrated into the hole in the centre of the four cells of the neck, and thus operated the fecundation of the ovum. In 1844 Nägeli[228] in a more appropriate manner described and illustrated the antheridia and the spermatozoids of ferns. Finally in 1848 Leszczyc-Sumiński[190] most accurately described and illustrated the archegonium, the entrance of the spermatozoids into the neck canal, the process of fecundation, and the development of the embryo.

In 1851 all these discoveries found a conclusion and at the same time a confirmation in the publication of Hofmeister's book on the development of the higher cryptogams[141, 142]. It was a milestone in the history of Pteridology. Hofmeister's book is the first detailed and complete account of the life-cycle of Pteridophyta with descriptions and illustrations of their prothalli, sexual organs, and stages of development. Hofmeister not only studied the life history of members of all classes of living Pteridophyta (except the Psilotopsida), but also investigated the Bryophyta and to some extent the Conifers. These observations enabled him to demonstrate that essentially the same events take place in the life-cycle of the archegoniate plants, whether Bryophyta or Pteridophyta, and to conclude that two generations although differing greatly in form and size, alternate one with another, the phases being respectively sexual and non-sexual.

Besides this book, Hofmeister published several other publications, among them his *Allgemeine Morphologie*[143], in which he is clearly seen to be a pioneer of experimental morphology—a branch afterwards extensively developed by his follower Goebel.

Hofmeister's work was the starting point of a new period of research in plant morphology which greatly enlarged the boundaries of pteridological knowledge, and at the same time threw light on some facts of general biological interest. Bower[39], and recently Manton[212], have discussed the development of research in morphology which followed Hofmeister's discoveries, while Williams[349], and recently Wetmore and Wardlaw[344] and Wardlaw[343] have given a review of research in experimental morphology and in morphogenesis. Thus, I think, I need only mention a few basic events and those studies which more strictly concern the classification of Pteridophyta.

The new discoveries did not have an immediate effect on pteridological taxonomy. Mettenius, although a pupil of Hofmeister's, based his studies on the external morphology and on the microscopic features of pteridophytes, especially on the development of the sori, but gave no great importance to their life-cycle. His best taxonomical works are *Filices Horti Botanici Lipsiensis*[219] and a series of monographic papers on some genera of ferns[220], in which he was more interested in finding affinities than differences, and therefore made his genera or groups so large and comprehensive that they became artificial. Aware of the importance of vegetative characters, he proposed in the former work[219] a classification of the various kinds of venation, more complete than that of Ad. Brongniart[42], which is still in use. But Mettenius's greatest taxonomical merit is his classification. In it he laid down the families in a general seriation which is still considered the best as regards the affinities between the different families. Mettenius arranged his sequence beginning from Polypodiaceae and ending with Ophioglossaceae, and this sequence was adopted by many later botanists. However, in 1890 Campbell[48] on purely comparative grounds, recognized the Eusporangiates as the more primitive ferns, and the Leptosporangiates as the more advanced. Campbell's hypothesis was soon supported by Bower[35] with palaeontological evidence and with other morphological remarks, and now everybody agrees that the order of Mettenius's sequence of families must be inverted, but when so inverted, it is entirely in accordance with modern views on the course of fern evolution.

Hofmeister's discovery found its first application in taxonomy in the classification which Sachs proposed in his *Lehrbuch der Botanik*[280] published in 1868. Here the Pteridophyta, still named "Gefässkryptogamen," were subdivided, according to the kinds of spores, into two primary groups, isosporous and heterosporous pteridophytes. And they were further

subdivided, chiefly on the basis of the features of the prothalli and of the position of the sporangia: the isosporous into "Farne," "Equiseten," and "Ophioglossen"; the heterosporous into "Rhizocarpeen" and "Lycopodiaceen." This system is clearly artificial, as is sufficiently proved by the inclusion of the homosporous genera *Lycopodium*, *Phylloglossum*, *Psilotum*, and *Tmesipteris* into the heterosporous group of Pteridophyta. Sachs justified this incongruity in his classification by the imperfect state of knowledge at that time, but actually it is due to the adoption of homospory and heterospory as characters of primary importance, while they have not so great a value. Equal importance was given to the same characters by Caruel[52, 53, 54] who, however, split the lycopodiaceous plants into two groups, and proposed to classify the Pteridophyta (named by him "Protallogamae") into "Heterosporeae," with the orders of "Rhizocarpariae" and "Phyllocarpariae" (heterosporous ferns and lycopodiaceous plants respectively), and "Isosporeae" with the orders "Conariae" (the homosporous lycopods), "Calamariae" (Equisetaceae), and "Filicariae" (homosporous ferns). This system, morphologically speaking, is better than that of Sachs, but undoubtedly it is more artificial, because in it heterosporous ferns and lycopods are segregated from the homosporous ones.

Sachs's classification of the vascular cryptogams, which about that time were named "Pteridophytae" by Cohn[66], was greatly improved by Prantl[259] who, regarding heterospory and homospory as of secondary importance, proposed a better classification of this division. He divided the Pteridophyta into three classes: Filicinae, Equisetinae, and Lycopodinae, the first and the third being further subdivided into Isosporeae and Heterosporeae. This classification was adopted also by Luerssen[202], Eichler[100], and van Tieghen[337]. The latter in his system of the Pteridophyta included the fossil plants, too, and also subdivided the Equisetinae into homosporous and heterosporous.

The theory of evolution put forward in 1859 by Darwin in his *Origin of Species*[79] had been rapidly accepted by the majority of botanists, but it only showed its influence on taxonomy several years later, partly owing to the difficulty of applying evolutionary concepts to classification, and partly owing to the prestige of the previous natural systems. At an early stage Sachs had summarized the principles of evolution in his *Lehrbuch* but he did not apply them to his own classification and so it is not till 1880–1881 that we find the first signs of Darwin's influence.

One of the first works in which taxonomy is examined in the light of evolutionary concepts is De Saporta and Marion's book *L'Évolution du Règne Végétal*[89, 90], the first volume of which, devoted to the cryptogams, was published in 1881. In this book the authors study the evolution of the plant kingdom along lines which agree so completely with the most modern

concepts and methods of phylogeny, as to present a phylogenetic diagram of the evolution of ferns through the geological ages, which, we must not forget, was probably one of the first phylogenetic diagrams. Furthermore, De Saporta and Marion investigated certain problems of organogenesis in the same way as they are dealt with in a paper of the "New Morphology."

The follower of Hofmeister, Goebel, a great German morphologist, of whom I have already spoken, was among the earliest evolutionists. He contributed enormously to the morphology of Pteridophyta. It was at this same time that Goebel pointed out another characteristic of great morphological and phylogenetical importance. Goebel[121] investigated the development of the sporangia, in order to trace the origin of the sporogenous tissue. This study, besides containing some other interesting observations, enabled him to ascertain that the sporangia originated either from one parent-cell or from a group of them. Accordingly he distinguished two groups of vascular plants, which he named respectively "Leptosporangiaten" and "Eusporangiaten." He attached great importance to these characters and divided the vascular plants into two groups: the Leptosporangiates, consisting of all homosporous and heterosporous ferns except that Ophioglossales and Marattiales, and the Eusporangiates, including the Ophioglossales and Marattiales, all the remaining Pteridophyta, and the Gymnosperms and Angiosperms. On the basis of the origin of the sporangia and other characteristics of the sporogenous tissues, Goebel expressed the opinion that the Leptosporangiates could not be the ancestors of seed-plants. On the other hand he suggested a derivation of the conifers from the lycopods (a suggestion which has again found support in these last years; cf. Lam[180]) and of the cycads from Marattiales. In spite of the value of these characteristics Goebel's classification is clearly artificial since he attached too great an importance to them. This fault was also noticed by Luerssen[203] who left the three classes of the Pteridophyta unaltered, and subdivided the homosporous ferns into two groups: Leptosporangiatae and Eusporangiatae. This was the first step towards the subdivision of ferns into the primary groups Eusporangiatae and Leptosporangiatae which, regardless of homospory or heterospory, was the basis of fern classification at the turn of the century. These two groups, with the addition of the intermediate group of the Protoleptosporangiatae, are still accepted by several taxonomists.

In the meantime morphological research had also made progress. The facts so excellently described and illustrated by Hofmeister had shown the succession of the different phases of the life-cycle, but had not explained its inner meaning. Interest in this problem was stimulated by the discovery of apogamy and apospory. Apogamy was discovered in 1874 by Farlow[106] in ferns and its biological significance was discussed by de Bary[84] a few years later. Apospory, although already experimentally produced in mosses

by Pringsheim[267] and Stahl[306] in 1876 was ascertained in ferns in spontaneous conditions by Druery in 1884 and was studied by him[97, 98] and by Bower[33, 34]. These discoveries threw new light on the basic facts of alternation, but the inner mechanism of the life-cycle remained without an explanation until 1894. In that year Strasburger[322, 323], helped by the achievements of the cytological analysis he had introduced himself, recognized the periodic reduction of the number of the chromosomes in the life history of all plants which show sexuality, and concluded that the alternating generations rest on two events: syngamy, resulting in a doubling of the chromosome-number, and meiosis or reduction, by which that number is halved and the original chromosome-number is re-established. Thus the alternation of generations recognized by Hofmeister was at length shown to be based upon a cytological cycle.

In the two last quarters of the 19th century, after the publication of de Bary's book[82, 83], the plant anatomy of the Pteridophyta also attracted the interest of botanists. Great advances were rapidly made especially in the knowledge of the vascular structure, thanks to the British school of plant anatomists, headed by Bower, and to the French school, headed by van Tieghem, to which we owe the introduction of the concept of the stele[338, 339]. The progress of the anatomical research of the time, as well as of later decades, is well summarized in publications by Schoute[286, 287], Bower[36, 39], and Tansley[329], to which I refer the reader.

During this same score of years great attention was devoted also to the study of palaeobotany, stimulated by the discovery of new fossils, and by the theory of evolution which was spreading rapidly. It was then that the study of fossil plants shifted from geology to botany, and underwent its modernization chiefly because of the publication of several textbooks and reference books which appeared in that period and in the first decade of the 20th century, such as the works by Renault[275], Solms-Laubach[302, 303], Seward[294], Zeiller[352], and Scott[290, 291]. The progress of palaeobotanical studies will be described in another part of this book and need not be dealt with here, but I cannot pass over in silence the names of Renault, Williamson, Stur, Zeiller, Kidston, C. E. Bertrand, Seward, Potonié, Lignier, and Scott, who greatly contributed to our knowledge of the morphology, anatomy, phylogeny, and taxonomy of fossil pteridophytes.

The end of the century marks another basic event in the history of pteridology: the publication of the volume on the Pteridophyta of Engler and Prantl's *Die natürlichen Pflanzenfamilien*[104]. This work represents a complete synthesis of all previous pteridological knowledge, and in spite of the taxonomical arrangement of some groups, which is regarded now as unnatural, its unrivalled value as a standard work is still recognized by all pteridologists. The volume was compiled in collaboration by Sadebeck,

Diels, Potonié, Bitter, Pritzel, and Hieronymus. Following the system previously proposed by Engler[103], the Pteridophyta were treated as a subdivision of the "Embryophyta asiphonogama" (previously Engler[103] had more conveniently named them "Embryophyta zoidiogama") which correspond to the Archegoniatae. They are subdivided as follows:

Class I. Filicales: 1. Filicales leptosporangiatae ((*a*) Eufilicineae; (*b*) Hydropteridineae); 2. Marattiales; 3. Ophioglossales. Fossil Filicales in general and doubtful fossil allies with them.

Class II. Sphenophyllales.

Class III. Equisetales: 1. Euequisetales, 2. Calamariales.

Class IV. Lycopodiales: 1. Lycopodiales eligulatae, ((*a*) Lycopodiineae, (*b*) Psilotineae); 2. Lycopodiales ligulatae, ((*a*) Selaginellineae, (*b*) Lepidophytineae, (*c*) Isoëtineae).

Appendix: Cycadofilices.

The system adopted in this work does not differ much in its arrangement of main groups from the systems proposed in the previous thirty years by other taxonomists, whom I have mentioned; however, some orders and families like that of the Polypodiaceae underwent a complete rearrangement, so that the work is important because of its classification as well as the great amount of data it contains. But one of the book's greatest merits was the inclusion in a single system of both fossil and living plants. Besides greatly improving the understanding of the affinities of the various groups, this was a valuable stimulus to the comparative study of fossil and living plants, and also to a closer collaboration between taxonomists and palaeobotanists. Engler and Prantl's system composed of groups based on resemblances and differences, and arranged hierarchically to form a progressional series, is not, however, a phylogenetic system in the modern sense.

Almost concurrently with this volume of *Pflanzenfamilien*, Jeffrey[166, 167], on the basis of some anatomic features, proposed splitting the Pteridophyta and classifying the vascular plants into two groups: Lycopsida, including "Lycopodiales" and "Equisetales," and Pteropsida, consisting of Ferns, Gymnosperms, and Angiosperms. Jeffrey's system found few followers among botanists of his time, and was more widely adopted later on, after some improvements.

An important event of the first years of the 20th century was the discovery of certain fossils, which made it possible to know the true nature of those plants, combining cycad-like and fern-like characters, which Potonié[258] had assembled under the name of Cycadofilices. In 1904 Kidston[173] discovered fragments of fronds of *Neuropteris heterophylla*, a species of Cycadofilices, attached to some seeds. In the same year after a preliminary communication[241], Oliver and Scott[242] gave a full statement of the evidence

that the seeds of *Lagenostoma lomaxi* could have belonged to no other plant than *Lyginodendron*, a member of Cycadofilices known through its vegetative organs only. As a result of these discoveries Oliver and Scott concluded that *Lyginodendron*, while retaining many of the filicinean characters, had fully attained the level of a Palaeozoic gymnosperm in the organization of its seeds. Consequently they recognized the presence in the Palaeozoic of "Fern-like Spermatophytes," for which they established a distinct class with the name of Pteridospermeae. Thus the great complex of Palaeozoic plants combining filicinean with gymnospermous features was transferred from the Pteridophyta into the Spermatophyta.

In 1905–1906 Christensen published his *Index Filicum*[58]. It is a good deal more than a list of generic and specific names, since Christensen pointed out the genera and species which he regarded as good. Thus it is an index and at the same time a nomenclator, brilliantly prepared with a well-balanced conception of the species, and also with extreme accuracy. In the Index and in the supplements[59, 60, 61] he followed the system adopted in Engler and Prantl's *Pflanzenfamilien*, though the arrangement of genera in the third supplement was largely changed.

Until the end of the 19th century *Psilotum* and *Tmesipteris* were classified among the lycopodiaceous plants, but in 1900 Scott[290] suggested, albeit confusedly, that they were more nearly allied to the Sphenophyllales than to the Lycopodiales. This opened the way to different opinions on the affinity of these plants. In 1908 Sykes[327] proposed "to place them in a separate cohort, the Psilotales," a proposal which was sanctioned in 1911 by Seward[294], who treated them as a main group of the same rank as his Sphenophyllales, Lycopodiales, and Filicales. Thus, after more than a century from their description, the psilotinean plants become independent from the other Pteridophyta with which they had been unnaturally associated.

The great activity in the field of palaeobotany in the first twenty years or so of the century had a profound influence on pteridological thought. In 1904 Lignier published a paper on the origin and evolution of Equisetales and Sphenophyllales[191] which previous authors had treated as two distinct classes. He came to the conclusion that, although differing in some important characteristics, the Equisetales and the Sphenophyllales belong to one group, for which he proposed the name of "Articulées." Lignier's views were accepted by subsequent taxonomists and this group was adopted in all later systems but its name was changed to that of Sphenopsida. In this paper[191] and in others[192, 193, 194, 195, 196], Lignier developed his theory ("théorie du mériphyte") of the morphological evolution of land plants. He supposed that the most primitive terrestrial ancestors of vascular cryptogams had a small stem ("cauloïde") divided in regular dichotomies, provided

with small appendices ("Phylloïdes"), ending in terminal sporangia bivalved with a longitudinal dehiscence. He indicated *Psilophyton* as the best model of this primitive type among the plants known to him. Further he supposed that, in the course of evolution, the stems and the leaves had originated through the collective sympodization of the cauloïds, with the formation of appendicularized complexes of cauloïds ("mériphytes"), and through a cladodification and a dorsiventralization of some groups of small terminal cauloïds on these appendicularized meriphytes. He named[192, 195] the plants which underwent these modifications "Phyllinées," and those which did not "Phylloïdées." He referred mosses and lycopodiaceous plants to the latter, and regarded the other higher plants as belonging to the "Phyllinées"; these in their turn were subdivided into four groups: "Macrophyllinées" (Ferns, Pteridosperms, and Cycads), "Microphyllinées" (Conifers and perhaps Chlamidosperms), "Mesophyllinées" (Angiosperms) and "Articulées" (Sphenopsida).

In 1916 Halle in his paper on the "Lower Devonian plants from Röragen in Norway"[130] described together with other new plants, some new fossils of the Devonian pteridophytes *Psilophyton* and *Arthrostigma*. These genera had been described already by Dawson, in 1859[80] and in 1871[81] respectively, on material from the Devonian of Gaspé in Canada, but had not received the attention they deserved. Halle had the merit of stressing the botanical interest of these Devonian plants and of discussing the origin of microphyllous and megaphyllous plants in the light of this new knowledge. More important than this was the discovery by Mackie in 1913 near Rhynie in Scotland of certain isolated blocks of chert containing remains of Devonian vascular plants. These were studied by Kidston and Lang[174] and referred to three new genera *Rhynia*, *Hornea*, and *Asteroxylon*. The study of these fossils enormously enlarged our knowledge of the Devonian plants, above all of their internal structure, thanks to the wonderful preservation of the material. It led Kidston and Lang to recognize for them, and for other Devonian plants previously described, the new class of the Psilophytales. Later on knowledge of the Devonian flora was greatly extended thanks to the researches of Lang, Kraüsel and Weyland, Dorf, Stockmans, and Höeg (cf. Höeg[139], Croft and Lang[76] and Leclercq[187]); but Halle's and Kindston and Lang's discoveries marked the beginning of a new era as far as the Devonian plants were concerned, and offered an excellent ground for speculation on the origin of vascular plants, to which Lignier's theory had previously opened the way.

Among other facts worthy of note in the first decades of the 20th century the publication of some important works of Pteridology should be mentioned. In 1913 Jongmans undertook the publication of the part of the *Fossilium Catalogus*[170] dealing with plants, which is still in progress. Several fascicles

on fossil pteridophytes have been already issued. Between 1915 and 1918 vol. 2 of the second edition of Goebel's *Organographie der Pflanzen*[123] appeared; it dealt with the Pteridophyta, and in it the great German botanist summarized all the knowledge assembled during his long productive life, devoted to plant morphology.

Between 1923 and 1928 Bower published his important book *The Ferns*[37] in which he condensed the experience attained throughout a life of research on the morphology, anatomy, and phylogeny of the Pteridophyta. Not only is it an excellent compendium on the phylogeny of ferns but it is also a valuable work on organogenesis, as well as a good guide to comparative research. It is not a book of taxonomy in the strict sense of the word, since no system of classification is followed or proposed, and in point of fact his subdivision of the ferns into "Simplices, Gradatae, and Mixtae" was not intended as taxonomical classification. However, it offers excellent grounds for a phylogenetic system; such a system is already sketched in Bower's phyletic scheme for the primitive ferns. We must only regret that the third volume dealing with the "Polypodiaeceae" s.l. is not as satisfactory as the other two, of which the first gives an analytical examination of the criteria of comparison, and the second is devoted to the eusporangiates and the less advanced leptosporangiates. Speaking of Bower we cannot pass over in silence his valuable book *Primitive Land Plants*[39], published during the last years of his life, in which he contributed in so large a measure, probably more than any other botanist, to our knowledge of the phylogeny of the Pteridophyta.

In 1927 Hirmer published his *Handbuch der Paläobotanik*[136] most of which deals with fossil Pteridophyta. The profound palaeobotanic erudition of its author, the considerable amount of data assembled in it and the richness of its illustrations, make it an extremely valuable and useful work; but its value depends also on the system of classification of the fossil Pteridophyta here proposed by Hirmer, which, with some amendments, has since been followed by almost all authors. Hirmer's book is undoubtedly the most exhaustive and detailed treatise on the taxonomy of fossil Pteridophyta hitherto published. Finally, we must mention *Die Phylogenie der Pflanzen*[353] in which Zimmermann put forward his Telome theory, largely based on the hypothesis of the morphological evolution of higher plants, previously advocated by Lignier[191, 192, 195]. This theory was accepted by many authors, and was a good basis for a better understanding of the organogenesis of some structures, and at the same time it gave a great impulse to speculative interpretations, though not all of these were equally deserving of attention.

In 1928 Němejc[233] had published a study on the fossil *Noeggerathia* and related genera, and had concluded that they were "a quite independent group

in the system of the Pteridophyta." In 1931 he[234] proposed to name this group Noeggerathiales and to consider it "of the same cardinal systematic value as f. inst. the Filicales, Lycopodiales etc." Thus a new classis was added to the Pteridophyta.

Another important event was the discovery of the fossil plants *Baragwanathia*, *Yarravia*, and *Hedeia*, which proved the existence of vascular plants in the Silurian age. This discovery, illustrated by Lang and Cookson[184], and by Cookson[68], was particularly interesting since *Baragwanathia* is clearly a member of the lycopodiaceous stock, while *Yarravia* and *Hedeia* are members of the psilophytaceous complex. Thus this discovery revealed the occurrence, already in the Silurian, of two distinct classes of Pteridophyta: the Lycopsida and the Psilophytopsida. This suggests the possibility of the co-existence of other classes of vascular plants in the Devonian, an hypothesis which is supported by the recent palaeopalynologic researches of Radforth and McGregor[268].

In 1938 Verdoorn edited the *Manual of Pteridology*[340], designed chiefly to give taxonomists a view of the state of knowledge in all fields of pteridology, but at the same time intended to offer botanists a collection of essays, surveying the most interesting aspects of modern pteridological research, and showing the most recent systems of classification of the various classes of living and fossil Pteridophyta. Subdivided into several parts according to the different branches of pteridology, each assigned to an outstanding specialist, this book resulted in a synthesis of the greatest interest and usefulness.

In 1929 Copeland had undertaken a revision of *The Oriental Genera of Polypodiaceae*[69], with the intent of giving a classification of them more in accordance with modern phylogenetic concepts. His essay was incomplete, since it was limited to the oriental genera, but it opened a new period of research on the taxonomy of ferns which is still in progress. This does not seem the place to consider the development of the new and fertile points of view to which Copeland's paper gave rise, since they will be discussed more in detail in the coming pages, but I cannot omit all mention of the papers of Christensen[62], Ching[57], and Holttum[151], which have so largely contributed to the modern advances in fern taxonomy, nor of the *Genera Filicum*[74] in which Copeland has collected the results of his studies. It is regarded as the best standard book on the taxonomy of fern genera.

Until 1950 cytological studies were the least advanced in all pteridology. What little had been done in this field was summarized in the two chapters by Atkinson on cytology[14] and by Döpp on caryology[96] in Verdoorn's *Manual of Pteridology*, but all these data were so fragmentary that it was impossible to utilize them for taxonomic purposes. In 1950 Manton published her book *Problems of Cytology and Evolution in the*

Pteridophyta[209] whose merits are not due merely to the wealth of data supplied, but also to the logical co-ordination of her research and to the fact that she had clearly defined the problems to be solved. This book was the starting-point of much cytological and cyto-taxonomical research on the vascular cryptogams, and in the last few years thanks to Manton's school and to other isolated botanists, cytologic knowledge of the Pteridophyta has developed enormously. But Manton's researches are to be valued for another reason: they have proved how much cytology can help taxonomy when investigations are carried out with a suitable method and a clear vision of the aims to be attained.

The most recent palaeobotanical discovery is that of *Aldanophyton*, a lycopodiaceous plant of the Cambrian described by A. N. Kryštofovič[178]. Apart from the evidence that vascular plants were already present in that period, the discovery of this pteridophyte, closely allied to the Silurian *Baragwanathia* and the Devonian *Drepanophycus*, has a particular value since it shows that the Lycopsida were already relatively advanced then; a fact which implies a long previous period of evolution. On the other hand the occurrence in the Cambrian of *Aldanophyton*, which is more complex in structure than the Devonian Psilophytopsida, leads us to regard as very improbable the derivation of all the Pteridophyta from the Psilophytopsida postulated by many botanists, and emphasizes the distinction of lycopodiaceous stock from psilophytaceous.

Another important discovery is that of a new genus of living Isoëtaceae, described in 1957 by Amstutz[6] under the name of *Stylites*. It was found on a moist and limy substrate around the boggy margins of a small glacial lake near Caprichosa (in central Peru) at an elevation of 4750 m by Amstutz herself. Unluckily the specimens were badly collected and much about this genus remains to be known.

Finally, I will mention the most outstanding publications of recent years. The first is the 12th edition of Engler's *Syllabus der Pflanzenfamilien*[218], in which the section on the Pteridophyta was written by Reimers. The classification adopted, the descriptions of the various taxa, the quantity of data supplied, and the illustrations, make it a valuable and practical compendium of taxonomic pteridology; however, it is to be regretted that the classification of living ferns, particularly of the leptosporangiates, is so conservative, and the families so ill-defined. In 1955 Andrews published the *Index of Generic Names of Fossil Plants*, 1820–1950[8]. This work is designed to cover all plants, but so large a number of fossils belong to the Pteridophyta that it is quite a useful manual for the pteridologist.

In recent years palynological research has begun to fill up another gap in pteridological literature. In 1950 Knox published a paper on the spores of Lycopsida[175], in 1955 Harris produced an account of the spores of New

Zealand Pteridophyta[132], and in 1957 Erdtman published *Pollen and Spore Morphology/Plant Taxonomy*[105]. The latter contains many illustrations of spores of the Pteridophyta, and when completed with the descriptions it will become a foundation for research on the palynology of the Pteridophyta, which up till now has had to rely on imperfect and dispersed illustrations and data.

Finally, I will mention a paper of mine[252] in which I have tried to establish a classification of the higher taxa of living and fossil Pteridophyta.

PROBLEMS AND TRENDS IN THE TAXONOMY AND PHYLOGENY OF PTERIDOPHYTA

In the previous pages we have followed the development of our knowledge up to the present day. Now we must examine the situation of research in the fields of the taxonomy and phylogeny of Pteridophyta.

When dealing with this subject we must consider first of all that the study of living pteridophytes is so profoundly linked to that of the fossil ones that the two fields of research cannot be kept any longer distinct. Thus instead of speaking of fossil and living plants it appears more correct to speak of ancient and modern Pteridophyta.

Our knowledge of the modern pteridophytes is not quite satisfactory, but for some groups certain fundamental concepts are universally admitted and they offer us good grounds for ascertaining the trends which determined the course of their phylogeny and for indicating clearly enough their relationship. However, some points are still in the dark and certain gaps must be filled. As regards the ancient Pteridophyta the situation is quite different. Latterly palaeobotanical research has tremendously enlarged our knowledge, but unfortunately it is still defective. On the other hand it has carried investigation so far back into the past that a point has now been reached in which the fossils are so scanty and incomplete as to make of our scarce knowledge a fascinating field for the purest conjecture and speculation.

From this profound ignorance of ours concerning the origin and evolution of the Pteridophyta in the first periods of their existence, from the gaps in our achievements, and from the paucity of our knowledge of other facts derive all problems, uncertainties of interpretation, hypotheses, theories, suppositions, and conjectures which characterize present-day pteridology.

In this section of my paper, I have thought it best to subdivide the subject-matter under various headings according to the taxonomical groups recognized in my most recent paper[252], beginning with the Pteridophyta in general and turning later on to their higher taxa. It was originally intended in this article to deal only with the living vascular cryptogams, but my reluctance to deal with the living Pteridophyta without taking into

consideration the fossil ones led me to touch upon some palaeobotanical problems as well, although in the most concise manner possible.

The Taxonomical Position of the Pteridophyta

There are various modern systems of classification of the vascular cryptogams, but many of them differ only in detail, while a few disagree on basic principles.

The most widely adopted system of classification is that in which the vascular cryptogams are assembled in a single group, under the name of Pteridophyta, and treated as a main unit, usually with the rank of a division, equal in importance to that of the Bryophyta or Spermatophyta. This grouping of the vascular cryptogams all together is the result of two hundred years of pteridological study, and therefore may be regarded as the classic system for the Pteridophyta.

At the turn of the 19th century Jeffrey[166, 167], on the basis of some anatomical characters, proposed that this unit should be abandoned and that the vascular plants should be subdivided into two "great primitive stocks": Lycopsida, consisting of Lycopodiales and Equisetales, and Pteropsida consisting of ferns, gymnosperms, and angiosperms. Jeffrey's views were subjected to strong criticism which induced him to publish other papers[168, 169], in which he defended his proposal and was more careful to stress the characteristics of the groups he had established. In spite of this criticism, Scott[291] adopted Jeffrey's views, but he added the new group Sphenopsida to the original Lycopsida and Pteropsida. Later on other groups were added to these three. This classification of vascular plants into different main groups, one of them including both ferns and seed-plants, was adopted by several botanists, such as Zimmermann[353], Eames[99], Darrah[78], Tippo[332], Arnold[12], and Boivin[32]. However, they did not all adopt the same number of groups, nor use the same names and ranks for them.

Another trend is represented by those botanists who classify vascular plants into different main groups without referring them to one or more groups of higher rank. When the various groups are phylogenetically well delineated a system of this kind is logical and suitable. We may mention, for instance, that of Berry[25], who subdivided the vegetable kingdom into nine "phyla." In the first, the "Thallophyta," he assembled, very improperly, all the lower plants, and in the second, the Bryophyta, the mosses and hepatics. The vascular plants were classified into the remaining seven phyla: Pteridophyta, Arthrophyta, Lepidophyta, Pteridospermophyta, Cycadophyta, Coniferophyta, Angiospermophyta. This system, worked out in 1917–1918, before or nearly simultaneously with Kindston and Lang's description of the Devonian plants from Rhynie chert, so strictly agrees with the latest views in

taxonomy as regards the distinction of the various groups of the higher plants that with the addition of the groups that have been recognized since it could be published now. Benson's system[22] reflects the same tendency. He recognizes five divisions: Spermatophyta, Pteridophyta, Sphenophyta, Lycophyta, and Psilophyta, but they are not well delimited and the system appears rather defective.

Takhtajan's system[328] of the "Division Telomophyta" (the Cormophyta of other authors) is based on the same principle and at the same time on Jeffrey's classification of Pteropsida. Independently from the importance of the vascular system, he recognizes six "phyla": Psilopsida, Bryopsida, Lycopsida, Tmesopsida, Sphenopsida, Pteropsida (ferns, gymnosperms, and angiosperms). As far as the Bryopsida are concerned their taxonomical position is based on the author's assumption that they, as well as all the vascular plants, derive from the psilophytes.

Finally, we must mention Rothmaler's system[278], in which the psilophytes are segregated from the other vascular cryptogams, and the Anthoceropsida from the Bryophyta, while the Cormobionta are subdivided into five divisions: Psilophyta, Anthocerophyta, Bryophyta, Pteridophyta, and Spermatophyta.

All these systems are based, or should be, on the phylogeny of the vascular cryptogams, so that I think it advisable to pass in review the various theories on the phylogeny of the Pteridophyta, in order to try to ascertain which of these systems is the soundest.

The origin of vascular cryptogams is a problem that has been discussed at length, and several theories have been put forward. However, all of them are based on the comparative morphology of living and fossil plants. Since a fossil plant which can be considered a forerunner of the Pteridophyta is still wanting, none of these theories is exempt from a certain degree of speculation, and perhaps this is the reason why some authors leave out this subject and others hint at the ancestors of the Pteridophyta in vague terms. Other botanists, on the contrary, have paid great attention to this problem, the majority of them being in favour of the origin of the Pteridophyta from algal ancestors, while a few suggest an independent origin or a bryophytean ancestry.

Since the theories of the origin of the Pteridophyta, though based partly on pure speculation, have had a certain influence on some taxonomical views, I think it convenient to summarize the principal trends of the subject.

The theory of the origin of the Pteridophyta from the Bryophyta was put forward by Campbell[49], who supposed that the ancestor of the vascular cryptogams was a type more or less like the Anthoceropsida. This hypothesis received but little support from later botanists. Bower[39] pointed out that "the Anthocerotales appear as a suggestively synthetic Archegoniate type,"

Smith[296, 297] supported Campbell's hypothesis, and finally Campbell[50] himself resumed his original idea. However, a bryophytean origin of the Pteridophyta does not appear very probable.

Another idea on the origin of the vascular cryptogams is expressed by Bower[36], who thinks that there is no good reason for regarding algae as being in the actual line of descent of archegoniate forms. More recently he has confirmed[39] his opinion, and has stated that the Archegoniatae "stand aloof from any known Thallophytic origin, unless there be some remote connection with Isokont Green Algae. They will be best studied as an independent evolutionary innovation on land, rather than as a direct extension of a Thallophytic Flora from aquatic to sub-aerial habit."

A different opinion is expressed by many botanists who point to the algae as the ancestors of the vascular cryptogams. However, some of these botanists think that the evolution was polyphyletic, while others support a monophyletic origin.

A polyphyletic theory is put forth by Arber[11], who maintains that the Sphenopsida, Pteropsida, and Lycopsida represent three different lines of descent, each derived from thallophytic algae of a distinct type. To them he adds a fourth independent group, the Psilotales, also of algal origin, developed long after the other three ". . . possibly in Mesozoic times or even later." Another moderate polyphyletic theory is that of Gregus[126]. He imagined that a part of the Psilophytopsida and Lycopsida originated from the Chlorophyceae; that a part of the Psilophytopsida and Lycopsida, and the Psilotopsida and Filicopsida derived from the Phaeophyceae; and finally that the Sphenopsida originated from the Rhodophyceae through the Characeae. Apart from any monophyletic or polyphyletic consideration, Greguss's phylogenetical ideas, as already pointed out by Lam[181], are based on an insufficient knowledge of the morphology of living and fossil Cormophyta.

A higher polyphylesis of the vascular plant is strongly supported by Church in his essay on the "Thalassiophyta and the Subaerial Transmigration"[64], in which he gives a vivid picture of the transmigration as he imagine it to have happened. Church postulates a highly polyphyletic conception of the course of evolution. He believes that all the main lines of evolution must have been differentiated in the sea at a very early time from extinct large seaweeds, called by him the Thalassiophyta. He is inclined to think that the lines of descent of the existing groups of land plants may be traced back to the flagellated organisms of the sea, wholly independently of one another. Equally in favour of a highly polyphyletic origin is Andrews[7, 9]. He expresses the opinion that in Devonian times and probably earlier the primitive vascular plants were highly polyphyletic, and that "they were radiating out in many directions a few of which became definable as

lycopods, articulates, coenopterids, etc." He suggests that they represent numerous lines of evolution from the algae, rather than just three or four, and he thinks that this view receives support from the existence of plants like *Protosalvinia*, *Prototaxites*, and *Crocalophyton*, which represent the efforts in the struggle to evolve vascular forms, but which can find their proper place neither among the known vascular plants nor among the algae.

A polyphyletic origin of the Pteridophyta is quite reasonable, but I do not see why we must admit so high a degree of polyphylesis. At all events it would be convenient to have some idea, however rough, of the independent lines of descent. But neither Church[64] nor Andrews [7, 9] give us information on this point, and they are rather vague about the ancestors from which the lines come. Moreover, they base their views on speculative arguments rather than on comparative study. Finally, as regards *Protosalvinia*, *Prototaxites*, and *Crocalophyton* and the Nematophyta in general, which represent the first unsuccessful attempts to become vascular plants along lines different from that of our land-plants, their existence does not favour the hypothesis of a higher polyphylesis of our vascular plants. On the contrary, if we bear in mind that these lines of descent are represented by plants which differ from each other as well as from our vascular plants, whereas our land-plants have many characteristics in common, we see that there is confirmation of a monophyletic origin of our vascular plants, rather than evidence pointing to a higher polyphylesis.

A monophyletic origin of the vascular cryptogams from algae is advocated by several botanists. Schenck[283] maintains the origin of the Bryophyta and Pteridophyta from phaeophyceous forerunners. Through an interesting comparative study, he presents several arguments in favour of his hypothesis. But we cannot help observing that the Phaeophyta differ greatly from the Pteridophyta in their pigments, products of assimilation and cytochemical properties in general, and in their characteristic motile elements, whether zoospores or gametes, which bear laterally attached flagella, the one pointing forwards and the other backwards. Moreover they are almost exclusively marine algae. These differences are of such fundamental importance that a derivation of the Pteridophyta from a phaeophyceous stock appears very unlikely.

The theory of the vascular cryptogams originating from chlorophyceous ancestors seems sounder. Fritsch has supported this view in some very interesting papers[115, 116, 117, 118]. On the grounds of a morphological comparison between the Algae and the higher plants, he suggests that the vascular plants were derived from heterotrichous forms of the Chlorophyta, endowed with some capacity to resist desiccation, and closely resembling the Chaetophorales of the present day. Fritsch points out that these forms of Chaetophorales show a tendency towards longitudinal division of the

cells, include a number of more or less specialized terrestrial genera, like *Fritschiella*, and are also represented in the littoral region of the sea. These forms of green algae do not show any advanced member comparable with the highly evolute types of the brown and red algae, and have only reached the simple heterotrichous evolutive level of these. Fritsch properly observes that the only adequate explanation for the absence of more specialized forms of the green algae in the sea, is that all the more advanced forms developed towards a terrestrial, rather than a marine life, and gave rise to the higher plants. Fritsch's views have received support from a recent study of Chadefaud's[56], in which the evolution of algae and its importance for understanding the origin of the higher plants is discussed in the light of new investigations on comparative morphology. In his opinion the higher plants would be, fundamentally, highly advanced green algae, some of rhodomeloid type, others of fucoid type. The arguments adduced by Fritsch and Chadefaud in favour of the origin of the Pteridophyta from the green algae are remarkably cogent and, indeed, among the algae of cellular type the Chlorophyta alone possess chloroplast pigments, photosynthetic mechanism, and products of assimilation comparable to those of the higher plants. We must also bear in mind that the green algae show a larger diversity of forms of organization and higher evolutive potentialities than do the brown and red algae. All these considerations point to the Chlorophyta as the most probable algal ancestors of the Pteridophyta.

The monophyletic theories we have discussed so far seem to agree in a direct derivation of the Pteridophyta from their algal forerunners, but some botanists hypothesize the existence of an intermediate group, originated from algae, which gave rise to the higher plants. Such a group, if it ever existed, has not yet been found, so that it is purely conjectural. Lignier[192, 195] suggests that the Pteridophyta sprang from an hypothetical group, the "Prolycopodinées," which were derived from another hypothetical group, the "Prohépatiques," originating in their turn from algal ancestors, the "Paracutleriées," similar to the present Cutleriales (Phaeophyta). Tansley[329] maintains that the pteridophytes derive from an hypothetical group, named "Protopteridophyta" which had its forerunners in the green algae.

On the grounds of this review of the principal theories regarding the origin of the Pteridophyta, it seems to me that the soundest hypothesis is the one according to which the Pteridophyta have a monophyletic origin and derive from ancestors closely resembling the present-day Chlorophyta.

This monophyletic origin is supported by the affinity of the biological organization of the different classes of the Pteridophyta, which may well be regarded as indicating that they spring from a common stock. These classes share several fundamental characters. Both the generations of the life-cycle are independent, but very different in size and organization. The

gametophyte is minute, anatomically less differentiated, but nevertheless able to nourish the sporophyte in its first stages after the development of the embryo so that we have a partial parasitism of the sporophyte on the gametophyte. The sporophyte is dominant, well evident, anatomically highly differentiated, and provided with vascular tissues. The ovum is borne in the archegonium, and the motile spermatozoids are produced from the antheridium. The fecundation takes place only through water, since no vector organ is produced. The spores germinate after they become detached from the sporophyte, and no true seed is present. Other characters which the Pteridophyta have in common are the histological structure of the vascular tissues, the features of the stomata, and the origin of the root from the spindle.

These characteristics of the classes of vascular cryptogams demonstrate on the one hand that the Pteridophyta are a well defined phylogenetical unit, and on the other that they are sharply characterized in comparison with the Bryophyta and with the Spermatophyta as well.

Now that we have examined the origin of the Pteridophyta and seen which are their distinctive characteristics, we are in a better position to judge which system of classification appears the soundest.

Since we recognize that the vascular cryptogams have a monophyletic origin and are well characterized and delimited, hence easily definable in terms of taxonomy, we consider that systems like those of Berry's or Benson's, and from this point of view Takhtajan's too, are not well founded. It appears illogical to treat the various groups of vascular cryptogams as independent divisions without a taxon of higher rank to assemble them. Moreover, it would seem to be defective from the practical point of view too, as is clearly proved by Benson, who does not recognize such a group of higher rank, but ends by assembling his divisions of vascular plants into a group named "Pteridophytes" of which he even gives the characteristics.

As regards the other systems which derive more or less from Jeffrey's views, it seems to me that they are based on an incongruity. While they keep distinct some groups like the classes of the Pteridophyta which have many important characteristics in common, they classify ferns and seed-plants together in spite of the considerable differences between them. The differences on which the distinction of Psilopsida, Lycopsida, Sphenopsida, and Pteropsida (ferns and spermatophytes) is based, are less important than the differences that occur between the ferns and the spermatophytes, which, on the contrary, are assembled in a single group, the Pteropsida. Therefore, it follows that these systems are based on criteria which are not well balanced. Some of the differences between the above-mentioned main groups are obvious, but the chief anatomical difference, the absence or presence of foliar gaps, originally advocated by Jeffrey to segregate the Lycopsida from the Pteropsida, is hardly reliable. As pointed out by Bower[38] this difference is

"a phenomenon of size and proportion rather than an inherent racial character." But the greatest fault of these systems is the assembling of ferns and spermatophytes in a single group equal in importance to the Lycopsida or Sphenopsida. It is not easy to claim that the spermatophytes derive from Filicopsida, since some gymnosperms are as ancient as the most ancient ferns, if not more ancient still. Florin[114] has shown that the Cordaitopsida, Ginkgopsida, Coniferopsida, and Taxopsida undoubtedly belong to the same natural group (the Coniferophytina) but "they constitute parallel evolutionary lines which probably were already separated from each other in Upper Devonian or Lower Carboniferous times. At all events a clear differentiation can be seen as far back as the available fossil records go." Moreover, it is probable that gymnosperms and angiosperms do not belong to the same line of descent within the Spermatophyta as supported by Mägdefrau[205], Andrews[7], Lam[180] and others. It is quite reasonable to recognize lycopsids, sphenopsids, psilopsids, pteropsids, etc., as groups of the same taxonomical value, but we do violence to phylogeny and taxonomy as well, when in one of these groups we also include the Spermatophyta. In the course of evolution the ferns and the spermatophytes showed they possessed a completely different perspective power as is clearly proved by the fact that starting from almost the same geological period, the ferns attained at most heterospory, while the spermatophytes reached the status of seed.

As regards Takhtajan's and Rothmaler's systems they start evidently from the assumption that the Psilophytopsida are the forerunners of all the higher plants, the Bryophyta included; but such a hypothesis, as we shall see in the coming pages, is open to serious objections. As regards the Bryophyta, they are sharply distinguished from the vascular plants by their life-cycle, the absence of a vascular system, their habit, and other important characteristics. Their derivation from the Psilophytopsida or other pteridophytic groups, as suggested by Takhtajan[328], Steinböck[310], Christensen[63] and others, is hardly justifiable. Therefore, I think that these systems should not be followed.

In the course of evolution the higher plants, holding different biological potentialities, attained three distinct evolutive levels. Some did not achieve the differentiation of a vascular system and, being only partially fitted for land conditions, were unable to reach a considerable size. Some achieved a vascular system and, being better adapted to sub-aerial life, attained great dimensions, but were unable to free themselves completely from the aquatic environment and to reach the status of seed. Others gained the sub-aerial world successfully, attained an efficient protection of the vital reproductive organs and produced true seeds. In the classification of the higher plants these three evolutive levels correspond to the Bryophyta, Pteridophyta, and

Spermatophyta respectively, and if taxonomy is to reflect phylogenetical concepts, these three divisions must stand as the fundamental units of the system of the Cormobionta. On the grounds of the absence or presence of a central cylinder of vascular tissue (stele), which is of basic biological importance in order to free the plants from the aquatic habitat, these three divisions can be classified into the two categories of higher taxonomical rank (legiones) which I have recently proposed[252]: the Bryophytonta (Bryophyta) and the Stelophytonta (Pteridophyta and Spermatophyta).

To sum up, since the classes of the Pteridophyta have several fundamental characters in common which sharply distinguish them both from the Bryophyta and the Spermatophyta, I believe that we are entitled, as I have already concluded in a previous paper[252], to adopt the Pteridophyta in its classic sense as a single great taxonomical unit including all the vascular cryptogams.

The Higher Taxa of the Pteridophyta

The vascular cryptogams, whether treated as a single unit, the Pteridophyta, or classified together with the other vascular plants, are subdivided into various groups, but not all botanists agree as to their number, rank, and name.

All contemporary botanists recognize at least four groups, the most widely adopted names for which are Lycopsida, Sphenopsida, Psilopsida, and Pteropsida. Zimmermann[353], Eames[99], Smith[296, 297], Darrah[78], Campbell[50], Tippo[332], Arnold[12, 13], and Lam[180, 181] accept these four groups only. Wettstein[345], Takhtajan[328], and Reimers[274] treat *Psilotum* and *Tmesipteris* as an independent group, the correct name for which as a class is Psilotopsida. Hirmer[136] and the author of the present paper[252], in addition to the five taxa already named, recognize a sixth taxon, the Cladoxylales in Hirmer's system and the Noeggerathiopsida in my system. Seven main groups are adopted by still other botanists; Němejc[234] and Rothmaler[278] adopt the same six groups as Hirmer, to which the former adds the Noeggerathiales and the latter the Isoëtopsida; Seward[295] recognizes the groups Filicales, Equisetales, Sphenophyilales, Lycopodiales, Isoëtales, Psilotales, and Psilophytales. Finally, among the botanists who only take living plants into consideration, Lawrence[185] adopts five groups: Articulatae, Lycopodiinae, Psilotinae, Isoëtinae, and Filicinae. The same five groups are recognized by Boivin[32] too although with different names and the rank of division instead of that of classis. Benson[22] adopts only four groups, since he includes the Isoëtales in the Lycophyta.

In conclusion the groups which have been recognized in these systems as higher taxa (classes or divisions) are nine, namely (with the ending of classis in *-opsida*): Lycopsida, Isoëtopsida, Sphenopsida, Equisopsida, Noeggerathiopsida, Psilotopsida, Psilophytopsida, Cladoxylopsida, and Filicopsida.

This short review of the best known systems shows how deeply botanists disagree on the classification of vascular cryptogams. This is chiefly due to the fact that the classification of the Pteridophyta is based on fossil plants rather than on living ones, and that we do not know the extinct vascular cryptogams well enough; so that the affinity between the various groups is liable to different interpretations. However, recent discoveries have thrown new light on the phylogeny of the Pteridophyta, and I think it useful to deal with the problem of the interrelationships within the Pteridophyta, in order to try to reach some conclusion as far as the taxonomy of the Pteridophyta is concerned.

If we glance through modern phylogenetic literature and examine the phylogenetical diagrams outlined by various botanists, we shall notice that two trends dominate the field of phylogenetical studies as regards the Pteridophyta. Some authors state that vascular cryptogams derive from the psilophytean plants, and hence are monorheithric; others deny it and recognize, apart from their monophyletic or polyphyletic origin, more than one line of descent within the Pteridophyta.

Zimmermann[353], Eames[99], Höeg[139, 140], Smith[296, 297], Darrah[78], Mägdefrau[205], Takhtajan[328], Däniker[77], and other botanists, who regard the Psilophytopsida as the ancestors of all the vascular cryptogams, base their hypothesis on the morphological characteristics of these plants, and above all on the remarkable simplicity of the Rhyniales. But already in 1923 and 1924 Scott[292, 293] had admitted that this simplicity might not be wholly primitive. Browne[45] opposed Scott's suggestion, but the doubt as to the primitiveness of the Rhyniales became stronger after the discovery of *Baragwanathia*, which is provided with vascularized leaves, although it is older than the aphyllous Rhyniales. Martens[215] brought forward the hypothesis that the aphyllous character of the Rhyniales was not primitive, and Leclercq[186, 187] came to the conclusion that the Psilophytales do not represent the ancestors of the vascular cryptogams. The recent discovery of the Cambrian lycopodiaceous genus *Aldanophyton*, as observed also by Leclercq[188], has strengthened this conclusion.

As I have already pointed out [252], the present state of palaeobotanical knowledge does not allow us to regard the Psilophytopsida as the common source from which the Pteridophyta sprang. I am inclined to think, in agreement with Chadefaud[56], that the Psilophytopsida have no direct descendant among the other classes of vascular cryptogams, and that they represent one of the lines which in the Upper Devonian were already running parallel to each other, a line which became extinct early on. The Psilophytopsida show us one of the patterns of the evolutive course in early times and their study is extremely informative, but they are not the ancestors of the Pteridophyta.

Andrews[7, 9], Leclercq[186, 187, 188], Chadefaud[56], Becquerel[21], Lam[180], the author of the present paper[252], and others, all of whom deny the origin of the classes of the Pteridophyta from the psilophytaceous stock, admit that at present no group is known which can be indicated as the forerunner of all the Pteridophyta, and that the groups known to us can be traced very far back in the past.

The ancient members of the Lycopsida are the Cambrian *Aldanophyton*, the Silurian *Baragwanathia* and the Lower and Middle Devonian *Protolepidodendron*, and *Drepanophycus*, *Protolepidodendropsis*, and *Bergeria*. These genera and others of later Devonian times, among which *Colpodexylon* described recently by Banks[17], prove that the Lycopsida had attained great development in that period. The earliest indisputable fossils of the Sphenopsida are presented by the genera *Calamophyton* and *Hyenia* from the Middle Devonian. Perhaps the ancestors of the Sphenopsida are to be found in the Lower Devonian *Climaciophyton* studied by Kräusel and Weyland[177], and in *Sphondylophyton* described by Schultes and Dorf[289], but these plants are not sufficiently known to be referred confidently to the Sphenopsida. The Psilophytopsida include several ancient genera, the oldest of which are the Silurian *Yarravia* and *Zosterophyllum*, the Lower Devonian *Bucheria*, *Cooksonia*, *Psilophyton*, and the enigmatic *Gosslingia*, and the well-known Middle Devonian *Rhynia*, *Horneophyton*, *Asteroxylon*, and *Pseudosporochnus*. As regards the Filicopsida, they are represented by a certain number of genera in Devonian times. I consider as belonging to the oldest known ferns the Middle Devonian *Arachnoxylon*, *Reimannia*, and *Iridopteris*, as well as the Devonian plants of which Banks has undertaken the study and Leclercq[189] has given a short description. But I am convinced, as I have already remarked[252], that other Devonian genera such as *Protopteridium*, *Aneurophyton*, *Cladoxylon* (the genus on which Cladoxylopsida are based), *Xenocladia*, *Schizopodium*, *Pietzschia*, *Asteropteris*, *Archaeopteris*, and other apparently related plants, all of which are regarded by certain botanists as ferns, do not belong to the line of descent of Filicopsida, but represent the primitive members of the Pteridospermopsida. As to the other classes of the Pteridophyta, no fossil of theirs has been found to be present in pre-Carboniferous ages.

The conclusion we may draw from this brief survey is that Lycopsida were present in the Cambrian, that Lycopsida and Psilophytopsida were already distinct in the Silurian, and that Lycopsida, Sphenopsida, Psilophytopsida, and Filicopsida were already running as independent lines of descent in the Middle Devonian. Consequently, since we have accepted the monophyletic origin of the Pteridophyta—and the antiquity of these lines of descent, which have retained many fundamental characters in common throughout many millions of years supports this view—we are led to admit, together with

Leclercq[187, 188], Lam[180, 181], and Thomas[331], that the common ancestor of the Pteridophyta should be found in the Cambrian age. Therefore the antiquity of the Pteridophyta would appear to be greater than was expected some time ago. But this antiquity should not surprise us. Among the living members of the vascular plants we find the remnants of independent lines of descent, which branched off as secondary lines from the main one within the classes of the Pteridophyta at a very remote time; for instance the Lycopodiidae and Selaginellidae are independent since the Carboniferous. This denotes that the differentiation took place very early in every rank of the evolutive lines. Accordingly nothing prevents our thinking that the differentiation of the main lines of the Pteridophyta took place from a common stock in the Cambrian or pre-Cambrian age.

If we consider that the earliest structurally preserved fossil algae according to Tyler and Barghoorn[336] go back to about 1300 million years and probably earlier, we must conclude that algae had existed before the advent of the first Pteridophyta for at least 900 million years, and probably more. We do not know how the evolutionary processes took place, and we have no idea of the time required by a main group to attain its dominance in the course of evolution, since the time probably differed from one group to another and from one age to another. However, I do not think it rash to admit that in these 900 million years the vascular cryptogams may well have evolved from their common algal ancestor. Accordingly, even though four lines of descent of the Pteridophyta were already running parallel in the Middle Devonian, this need not prevent us acknowledging a monophyletic origin of the vascular cryptogams.

Returning to the Pteridophyta groups, from what has been said we are bound to infer that the four groups already independent in the Devonian ought to be recognized as distinct main taxa.

Since as just noticed I regard *Cladoxylon* and related genera, as I have already suggested, possibly as members of the pteridosperms rather than of the Pteridophyta, four groups remain to be dealt with. The segregation of the Isoëtopsida from the Lycopsida advocated by Lotsy[201], Seward[295], Rothmaler[278], Lawrence[185], Reed[272], Boivin[32], and others appears very questionable; and even more so is the inclusion of *Isoëtes* in the Eusporangiate ferns proposed by Campbell[50], an idea which appears groundless. If we take into consideration the only living members of the Lycopsida, the difference of *Lycopodium* and *Selaginella* from *Isoëtes* is striking but when we study also fossil lycopods, we find no profound gap to justify distinguishing a class or division. Mägdefrau's study[204] on *Nathorstiana* has strengthened this view. I agree with Walton[342] that the Triassic *Pleuromeia*, the Cretaceous *Nathorstiana*, and the living Isoëtaceae form a line of descent which underwent a progressive reduction in size from the Mesozoic age to

the present time. Possibly these plants find their forerunner in the arboreous Permo-Carboniferous Sigillariaceae.

Equally untenable is the segregation of Equisetales from the Sphenopsida as a distinct higher taxon of the Pteridophyta, supported in modern times by Seward[295] and Boivin[32]. In the last century Sphenophyllales and Equisetales were kept distinct, but thanks to Lignier[191] they were at last brought together, and this assemblage appears to be justified by comparative morphology, and is adopted by most modern botanists.

The taxonomical position of the Noeggerathiopsida is still controversial. Němejc[233, 234] pointed out that they differ in several important characters from the other vascular cryptogams and proposed that they should be regarded as an intermediate class between the Articulatales and the Lycopodiales. Browne[44] maintains that their nearest affinity is to the Sphenophyllales; and her opinion is shared by Emberger[101], and Arnold[12] who, however, treat them as an independent group, and by Lam[180] who includes them in the Sphenopsida. On the contrary Hirmer[137, 138] classifies *Noeggerathia* and related genera as a main group of the Filicopsida. While Halle[131] regards them "as an isolated group of *pteridophyta incertae sedis*." While waiting for new fossils to make us better acquainted with this group, I think it convenient to treat it as I have already done[252] as an independent class, the Noeggerathiopsida.

The last group consists only of the two living genera *Psilotum* and *Tmesipteris*. These genera have been referred to the Lycopsida, Sphenopsida, or Psilophytopsida, or treated, following Sykes[327], as members of an independent group. They show no close relationship to the other groups of vascular cryptogams, and I think it better to keep them as an independent group. Takhtajan[328] calls them Tmesopsida instead of Psilotopsida, probably in order to avoid confusion with Psilopsida and Psilophytopsida; but if one of these names must be changed, it ought to be the name of the fossil plants since the name of the living group has priority over the name of the fossil one. The name Rhyniopsida proposed by Rothmaler[278] for them could be very convenient since *Rhynia* is the best known genus of the class and is a very short name too.

To conclude, it seems to me that six groups of the vascular cryptogams are worth keeping as distinct and, when treated as classes, they should be named Lycopsida, Sphenopsida, Noeggerathiopsida, Psilotopsida, Psilophytopsida, and Filicopsida.

In the coming pages we shall deal with the taxa of these six classes. They are listed in an order which has no phylogenetical or taxonomical significance, and is not intended to express a particular affinity or any sort of derivation of one group from another. I have attempted to group these plants in subdivisions, as I did[252] for the Spermatophyta. I have tried, for instance, to

distinguish two groups, microphyllous and megaphyllous pteridophytes, and I have made other tentative groupings bearing in mind other characters, but I have not reached a satisfactory arrangement and I leave this task for the future.

The fossil remains of the Pteridophyta are so numerous and involve so many problems that it is impossible to consider them here; I could only add very little to what I wrote in my recent paper[252] in which some general concepts were discussed and a classification of the higher taxa of the Pteridophyta presented. Accordingly the following pages will be almost exclusively devoted to the living vascular cryptogams.

LYCOPSIDA

The Lycopsida were one of the most important components of the Carboniferous forests. At present they are represented by few genera, not all closely related to each other, which are treated as members of three different subclasses or orders. Most botanists recognize four genera of living Lycopsida: *Lycopodium*, *Phylloglossum* (Lycopodiales), *Selaginella* (Selaginellales), and *Isoëtes*, to which we must add the genus *Stylites* recently described by Amstutz[6] (Isoëtales).

Lycopodiales and Selaginellales are represented by fossils which extend as far back as the Carboniferous (*Lycopodites*, *Selaginellites*, etc.). They show no clear relationship to the Palaeozoic Lepidodendridae, and a derivation from the Protolepidodendridae appears more acceptable. The Lycopodiales, homosporous and devoid of the ligula, differ greatly from the Selaginellales, heterosporous and ligulate. Moreover, the first cytological investigations show that the former have a rather high chromosome number, while the Selaginellales, unlike nearly all the Pteridophyta, have a low number. Manton[209] thinks that the high chromosome numbers of the pteridophytes are, in a sense, secondary, and that only a few genera have retained the simple nuclear state shown by their low chromosome number. She interprets this state as a primitive condition. Finally, there is a certain amount of evidence that Lycopodiales and Selaginellales have been running as independent lines for a long time, possibly since the Carboniferous. These are the reasons why I prefer to regard them as two subclasses: Lycopodiideae and Selaginellidae. As regards the Isoëtaceae, as I have already pointed out, they may possibly derive from the Palaeozoic Sigillariaceae, through the Mesozoic *Pleuromeia* and *Nathorstiana*. Consequently they are to be classified in the subclass of the Lepidodendridae and treated as an order of it.

Lycopodiidae—Among the living Lycopodiidae, the monotypic genus *Phylloglossum* from Australia and New Zealand is recognized by all botanists. As regards *Lycopodium* there is a tendency nowadays to revive the ideas of

Dillenius[95] and Palisot de Beauvois[244], and to split it into two or more genera.

Herter[134] in 1922 subdivided *Lycopodium* into two genera in accordance with the subgenera *Urostachya* and *Rhopalostachya* proposed by Pritzel in the *Pflanzenfamilien*[104]. He named these two genera *Urostachys* and *Lycopodium*. The former name was very improperly established, since this genus had four other names previously published (*Selago* Boehm. non L., *Mirmau* Adans., *Huperzia* Bernh., *Plananthus* Pal. Beauv.) and one of these should be adopted. Herter's genera are the same two genera recognized about fifty years before by Trevisan[334] under the names of *Lycopodium* and *Huperzia*. Herter's genera were adopted with the same names in Nessel's monographical work[235], and by Herter himself in his *Index Lycopodiorum*[135].

Rothmaler[277] proposes a further splitting of the Linnean genus *Lycopodium*. He subdivides the Lycopodiales into two families: Urostachyaceae with the single genus *Huperzia* (= *Urostachys* Herter) and Lycopodiaceae with the genera *Lycopodium*, *Diphasium*, *Lepidotis* and *Phylloglossum*. More recently Rothmaler[279] appears inclined to recognize a third monotypic family for *Phylloglossum* ("Phylloglossacées").

As already pointed out by Trevisan[334] in the last century and supported by Herter[134], Rothmaler[277], and Fuchs[119], *Huperzia* (or *Mirmau* or *Urostachys*; the correct generic name not being established as yet) is sharply distinct from the other members of *Lycopodium* and should stand as an independent genus on morphological ground. Cytologically (Ninan[240]) the chromosome number which occurs in most examined species is $n = 136$; but $2n =$ *circa* 260 and *circa* 405 have also been counted. They perhaps derive from a hypothetical basic number 17. If so *Huperzia* is characterized by a high polyploidy.

As regards the other three genera recognized by Rothmaler, the morphological characteristics do not constitute such important differences as those between them and *Huperzia*, but it is significant that cytological investigation, although still in its early stages, seems to support Rothmaler's views. According to the data supplied by Manton[209] and Ninan[240], Rothmaler's genera possess different chromosome numbers. *Lycopodium* (*sensu stricto*) has $n = 34$, which is referable to a hypothetical basic number 17, equal to that of *Huperzia*, but the two genera appear characterized by a low and a high polyploidy respectively. *Lepidotis* has chromosome numbers $n = 78$ and 104, which indicate an origin from a hypothetical basic number 13. *Diphasium* has $n = 24$–25 and 48, which may derive from a hypothetical basic number 12 (chromosome numbers in multiples of 11 would also appear to be present, but this datum needs confirmation). If we consider the chromosome numbers of the species of *Lycopodium* given in Table II of Ninan's

paper, we shall see that the correspondence between the cytological data and Rothmaler's genera is perfect. Thus the complete cytological dissimilarity between the different members of *Lycopodium* (*sensu lato*) pointed out by Manton[209] finds a clear and logical explanation. On the strength of these facts I think that Rothmaler's genera ought to be adopted, but not his families; in fact the Urostachyaceae and the Lycopodiaceae have the same basic chromosome number, while, on the contrary, three different basic numbers are counted in the Lycopodiaceae alone.

Thanks to Knox's paper[175] the spores of the Lycopodiaceae are well-known, and according to their characteristics I have tried to see if the palynological features bear out the segregation of the four genera proposed by Rothmaler; but I have found that the groups established by Knox correspond only in part to Rothmaler's genera, and the only distinction possible is of *Huperzia* from the other three genera. No better result has emerged from a similar comparison with the groups of Harris[132] based in part on different features.

Rothmaler's suggestion of establishing a new family for the monospecific *Phylloglossum* does not seem an idea to be pursued. *Phylloglossum* appears to be a distinct genus; its ovoid fleshy tuber-like storage organ, simple leaves crowded in a pseudowhorl, siphonostelic stem, and mesarch xylem warrant a generic rank. However, *Phylloglossum* is undoubtedly allied to the *Lycopodium* complex, and embryogeny (Thomas[330], Holloway[147]) indicates that it is closely related to the group of *Lycopodium cernuum* (*Lepidotis*).

In conclusion, I am not averse to accepting the four genera recognized by Rothmaler (*Huperzia*, *Lycopodium*, *Lepidotis*, and *Diphasium*) as distinct genera, but I prefer to regard all of them, together with *Phylloglossum*, as members of a single family, the Lycopodiaceae.

Selaginellidae—The large genus *Selaginella* (more than 600 species) is the only living one of the Selaginellidae. Rothmaler[277], following Palisot de Beauvois[244], has split it into the three genera, *Selaginella*, *Lycopodioides*, *Didiclis*; but they are not sharply delimited morphologically. It seems to me that *Selaginella* is a well-characterized taxonomical unit, which, in spite of its large number of species, can be kept as a single natural genus. Even Alston, who knew *Selaginella* better than anyone else, recognized one genus only. The cytological evidence, although there is very little of it in proportion to the number of species, appears to be in favour of this view. The various species of *Selaginella* already investigated, belonging to different subgenera, show a very close cytological similarity. Unlike the other genera of the Pteridophyta (with the possible exception of *Isoëtes*), they possess a low chromosome number ($n = 9$, and occasionally a multiple of it) which evidently represents the basic number.

Isoëtales—This order includes two living genera only: *Isoëtes* and *Stylites*. Pfeiffer[247] and Grenda[127] who have published two monographic papers on the Isoëtaceae, Reed who has produced an *Index Isoëtales*[272] and, so far as I know, all contemporary botanists, agree in considering *Isoëtes* as morphologically uniform, and regard it as a natural generic entity. In spite of this, the few species investigated cytologically show an evident dissimilarity. Chromosome numbers $n = 10, 11, 22, 33, 54$–56 and $2n =$ not less than 100, were counted (Döpp[96], Manton[209], and Abraham and Ninan[3]). This dissimilarity can be explained perhaps by a polyploidy of some species derived from a basic haploid number 11 actually present in the genus; while $n = 10$ (and $2n = 20$) counted only in one species, *Isoëtes hystrix*, could be due to aneuploidy probably originated from $n = 11$. But further investigation is needed.

The genus *Stylites* was described very recently by Amstutz[6]. Its elongate caudices, deeply bilobed, each bearing apparently unbranched fleshy roots along one side only, and its sporangia, attached far above the basis of the short and broad sporophylls, are very interesting characters. Unfortunately, owing to the lack of complete and well collected material, this genus is imperfectly known, although very promising.

SPHENOPSIDA

The Sphenopsida are a large and diversified group of vascular cryptogams which attained their peak in the Upper Carboniferous when they were abundantly represented in the forests by the slender, climbing or prostrate Sphenophyllaceae and by the giant tree-like Calamitaceae. The only living vestige of the Sphenopsida is the genus *Equisetum*, one of the oldest of the existing vascular plants. It stands out from the Sphenophyllales, which disappeared during the Triassic, while it is closely related to the Calamitaceae and Asterocalamitaceae. Together with these two the Equisetaceae form the order of the Equisetales. They are not the direct descendants of the Calamitaceae, which became extinct at the end of Palaeozoic; possibly these two groups derive from a common ancestor in ancient Carboniferous times, or the Equisetaceae may have developed as an offshoot of the primitive calamitean stock.

The genus *Equisetum* is represented by fossil species as far back as the Upper Cretaceous, and is closely related to *Equisetites* (Lower Cretaceous to Carboniferous) and *Phyllotheca* (Lower Cretaceous to Upper Carboniferous). These three genera together with *Schizoneura* (Jurassic to Upper Carboniferous) and perhaps *Neocalamites* (Triassic) form the family of Equisetaceae.

Equisetum is widely distributed from the tropics to the arctic regions (cf. Schaffner[282]) and occurs in wet, as well as in the driest, habitats. It is regarded as a natural genus, which, according to Milde[223, 224], can be

subdivided into two sections or subgenera: *Equisetum* (= Malacocaulon) and *Hippochaete* (= Sclerocaulon). Recently Rothmaler[277], following Milde[222], has split the genus, and has adopted the genera *Equisetum* and *Hippochaete* corresponding to the two subgenera or sections mentioned. The chief differences of these two genera consist in the position and structure of the stomata. However, the genus is uniform, natural and small, so that I do not see any serious reason for splitting it. Moreover, almost 50 per cent of the species belonging to both the subgenera have been examined cytologically and they are proved to be strikingly uniform as regards their chromosome number ($n = 108$) though the subgenus *Hippochaete* has larger chromosomes than the subgenus *Equisetum*. Manton[209] concludes her cytological study by saying that "As we find them now, the Horsetails give the impression of being a very ancient and very stable group, still able to make new species by genetical means though doing so only slowly, but long out of the habit of giving rise to new generic types."

NOEGGERATHIOPSIDA

This class is represented only by fossil plants, which range from the Upper Carboniferous to the Triassic. As I have already remarked, the taxonomical position of Noeggerathiopsida is uncertain, these plants being imperfectly known and their features standing apart from those of all other vascular cryptogams. Even the interrelationship of the various members of the class is not clear. I have[252] tentatively referred *Tingia* and *Tingiostachya* to the Noeggerathiopsida as a subclass, the Tingiidae; but the degree of affinity of this group to *Noeggerathia* and its closely related genus *Plagiozamites* is not clear.

We need further morphological comparative studies to solve the problems concerning the phylogeny and taxonomy of the Noeggerathiopsida, but above all more abundant and better preserved material.

PSILOTOPSIDA

This class consists of the two living genera *Psilotum* and *Tmesipteris*, the former distributed throughout tropical and sub-tropical lands from New Zealand and Australia as far north as Florida, South Carolina, and Japan; the latter occurring in the Australasian countries, Philippines, Polynesia, Melanesia, and New Zealand.

Psilotum and *Tmesipteris* are sharply distinct. The aerial shoots in *Psilotum* are several times and strictly dichotomously branched, while in *Tmesipteris* they are unbranched, though occasionally a dichotomy may be observed; the sterile lobes of the fertile appendages in *Psilotum* are reduced, scale-like, subulate, and devoid of vascular tissue and stomata, while in *Tmesipteris* they are well developed, leaf-like, flattened, vascularized, and with numerous

stomata; the spore-producing apparatus consists of three sporangia in the former, and of two in the latter; gametophytic and sporophytic gemmae are present in *Psilotum*, but not in *Tmesipteris*; conducting tissues are found in robust gametophytes of *Psilotum*, but not in the other genus. These and other characteristics justify keeping these two genera as members of two distinct monotypic families, the Psilotaceae and the Tmesipteridaceae.

In spite of these differences *Psilotum* and *Tmesipteris* share many fundamental and peculiar characters. The spores are monolete, bilateral, rather thick-walled. The gametophyte is subterranean, elongated, cylindrical, branching dichotomously once or more, with an indefinite apical growth, bearing numerous stiff hair-like rhizoids; it is saprophytic and mycorrhyzic with endophytic fungus. The antheridia and archegonia are intermixed and scattered over the entire surface of the gametophyte, so that there is no differentiation into reproductive and vegetative regions. The antheridia are spherical protuberances strongly projected from the surface of the gametophyte body. The spermatozoids are spiral and multiciliate. The embryo is very simple and consists of foot and shoot only. The young embryo is totally rootless and leafless—a condition not found in any other vascular plant. The foot develops from the inner, the hypobasal, cell formed by the first division of the zygote, and has a strongly haustorial nature. The shoot, which originates from the epibasal cell, in its first stages is a simple spindle which grows from one apex only; later on it shows dichotomous growing apices which arise in an indefinite manner. The sporeling, when it has become independent, breaks away from its foot which remains attached to the gametophyte. The sporophyte is rather unspecialized. Its rhizome is so strikingly similar in general appearance to the gametophyte that a close microscopical examination is necessary to ascertain its nature. It is rootless, clothed with hair-like rhizoids, and continues into the aerial stem which has no true leaves. It bears decurrent fertile and sterile appendages which are regarded as small branches of the stem more or less modified. The spore-producing apparatus is clearly terminal on the fertile appendage and consists of two or three sporangia arranged around a central axis, each of them being supplied separately with a reduced vascular trace (cf. Bierhorst[29]). At the basis of the sporangia the fertile appendage bears two separate sterile lobes more or less developed. No true tapetum is present.

A comparison of these characters with those of the other vascular cryptogams shows that the Psilotopsida possess a complex of features of a striking simplicity, which is interpreted as due either to primitiveness or to reduction; but embryogeny is in favour of the first of these alternatives. For instance, it has been stated that the rhizome has lost its roots in the adaptation to saprophytic and epiphytic life, but the total absence of root in the young embryo is in favour of a primitive condition. Moreover the cylindrical, subterraneous

gametophyte with indefinite apical growth, without a differentiation into fertile and sterile regions, the strictly dichotomous branching, the absence of true leaves, the terminal position of the sporangia, all concur in pointing to a primitiveness of the Psilotopsida. The comparison with characteristics of other primitive pteridophytes confirms this conclusion.

Among their various features, the Psilotopsida has one which is particularly interesting: the extreme similarity of the rhizome and the gametophyte. I have already said that they can only be distinguished by a careful microscopic examination to ascertain the presence or absence of the sexual organs. A resemblance of this kind, though not so marked a one, is shown also by *Ophioglossum*, which has roots and prothallia closely alike in form and other characters; it likewise possesses a cylindrical, perennial subterraneous gametophyte. Since both these plants are among the most ancient of the living pteridophytes, we may conclude that this resemblance of the subterranean part of the sporophyte with the gametophyte is a primitive character.

Holloway, to whom we are much indebted[144, 146] for our knowledge of the psilotaceous prothalli, collected many rhizomes and gametophytes of *Psilotum triquetrum* (= *P. nudum*) on Rangitoto Island (New Zealand), in different localities and in different years; on these he carried out a very careful study[148, 149]. He discovered that the larger of these gametophytes possessed a well-defined conducting strand, while the slender ones had no vascular tissue. Holloway's investigation established that: "The strand originates at the apex; it is discontinuous, fading out and reappearing usually several times in the length of a few millimetres; it has a distinct limiting endodermis; and in regions of the gametophyte well behind the apex it commonly possesses 1–3 centrally placed annular or scalariform tracheids." He estimated that the strand makes its first appearance at the growing apex when the progressive widening has attained a diameter of at least 1 mm. Holloway observed that sexual organs in the usual large number and some healthy well-grown and normal embryos were borne in the large strand-bearing gametophytes, in which he also observed an abundant accumulation of starch. Holloway's observations have been confirmed recently by Bierhorst's research[27, 28] on cultivated gametophytes of *Psilotum nudum*.

The presence of tracheids in apogamous prothalli of ferns is well known (Lang[182], Steil[308, 309]) and it is regarded as one of the proofs of apogamy in ferns. But the occurrence of vascular tissue in the normal gametophyte is a character unique among vascular plants. It is interpreted by Holloway as due, either to some abnormal nuclear condition in the large gametophytes, or to physiological changes taking place in the gametophyte as it increases in size, or to the persistence in it of an archaic feature.

The first interpretation was not confirmed by the cytological examination carried out by Manton[208] on Holloway's specimens. Both vascular and non-vascular gametophytes were seen to be cytologically diploid, and the sporophytes tetraploid. A condition which appears normal and is not in contradiction with other chromosome investigations (cf. Manton[209], Ninan[236]).

The second interpretation involves the assumption that lignified tracheids and an endodermis, hitherto regarded as peculiar to the sporophyte, can arise in the gametophyte in response to special physiological conditions. Such a possibility appears improbable and there is little to warrant such an assumption.

The third interpretation is the soundest, all the more so as the occurrence of vascular tissue is accompanied by a distinct endodermis. This endodermis, the discontinuous manner in which the vascular tissue occurs in the gametophyte and its presence only in large prothalli, are indicative of a vestigial structure rather than of a teratological feature. A vestige of archaic features in a plant like *Psilotum*, which possesses many primitive characters, is logical, and need not surprise us. Furthermore it is significant that an axial tissue of elongate cells, though not a vascularized one, is found in the elongate subterranean and mycorrhyzic prothalli of *Helminthostachys zeylanica* (Lang[183]) and in *Lycopodium* (*Huperzia*) *billardieri* (Holloway[145]) which are undoubtedly two ancient plants.

All these considerations support the view that the occurrence of the vascular tissue and the endodermis in the large gametophytes of *Psilotum* is due to the persistence of an archaic feature.

The presence of vascular tissue in the gametophyte is particularly interesting since from the phylogenetical point of view it has a general significance. When we consider that in these plants the gametophyte, together with a striking apparent similarity to the rhizome of the sporophyte, possesses a vascular tissue and an endodermis, we must admit that *Psilotum* provides strong evidence for the "homologous" theory, concerning the nature and origin of the sporophyte, which assumes that sporophyte and gametophyte were essentially alike in the primitive vascular plants, and that both occurred in the ancestral stock of land plants. The "homologous" theory, which had its first foundation in Lignier's theory on the morphological evolution of land plants[191, 192, 195], has been strongly supported by Eames[99]. The theory has been further strengthened by Stebbins's genetic views on the origin of the diploid state and on the alternation of generation[307]. At present the "homologous" theory seems more acceptable than the "antithetic" theory, which was strongly advocated by Bower[36].

If we wish to draw a conclusion from all this, it will be that the Psilotopsida are characterized by a marked primitiveness, and possess many peculiar

features which make them a clearly defined natural group, well distinct from all other classes of the pteridophytes, ancient and modern. Arber[11] is inclined to regard them as an independent group which "appeared on the scene" long after the other pteridophytes, ". . . possibly in Mesozoic times or even later." But when we compare the Psilotopsida with the other living pteridophytes, some of which are the direct descendants of Palaeozoic plants, we must conclude that they are far more ancient than supposed by Arber. Some botanists maintain that the Psilotopsida derive from the Psilophytopsida, but in the latter the sporangia have an entirely different structure and the manner in which they are borne is completely different. They differ also in anatomical characters and no fossil link between them has been found. The Psilotopsida are undoubtedly among the most ancient of living plants unless, indeed, they are the most ancient. They are the survivors of an ancient conservative group, of whose geological history nothing is known.

PSILOPHYTOPSIDA

I have already had several opportunities of speaking of these plants and I only wish to add that the Psilophytopsida represent a rather heterogeneous complex of fossil plants. Höeg[139, 140], Darrah[78], Arnold[12], Leclercq[187], Andrews and Mamay[10], Andrews[9], and many other palaeobotanists agree on this point. Accordingly, the present classification of the Psilophytopsida must be regarded as liable to undergo considerable modification in the future.

Höeg[139, 140], believes that two groups may be distinguished: the spinous Psilophytopsida and the spineless ones, but a subdivision of this sort would lead to an artificial system, since the presence or absence of spines does not appear to be in agreement with other important characters, such as the position of the sporangia. Leclercq[187] emphasizes the difficulties that beset the characterization of *Psilophyton*, and shows that the whole class suffers from troubles similar to that of the genus. As far as the spore-producing apparatus is concerned, she recognizes two groups, the first one with the sporangia borne at the end of the terminal naked branches, the second one with specialized fertile branches, consisting of loose terminal spikes with rows of erected sporangia. But Leclercq does not present this subdivision as a system, and whether the position of sporangia reflects real affinities or not is uncertain. On the other hand there are other characters which seem important for taxonomical purposes.

At present in the Psilophytopsida only two groups appear well established: the Rhyniales and the Zosterophyllales. They are different from each other, but are two well-characterized units. With the exception of these two basic groups, all the other members of the Psilophytopsida are imperfectly known

and artificially delimited. Accordingly, for the time being any arrangement of these plants is provisional, and the classification of the Psilophytopsida into a natural system is a task for the future.

FILICOPSIDA

This class is the largest of all modern Pteridophyta. The Filicopsida are usually subdivided into two groups, the Eusporangiatae and the Leptosporangiatae, a distinction established by Goebel[121] on the basis of the origin of the sporangia. But these groups appear to be rather artificial since they include some ferns, for instance the Ophioglossales and the Marattiales, which have the sporangia originated in the same way, but are not closely related. Moreover, the origin of sporangia does not offer us a sharp distinction, as is clearly demonstrated by the existence of an intermediate condition, for which the creation of a third group, the Protoleptosporangiatae, was necessary (Hirmer[136]). Consequently, I think it is better to drop the Eusporangiatae, Protoleptosporangiatae, and Leptosporangiatae as main taxonomical units, and base the higher taxa of ferns on a complex of characteristics, rather than on one only.

Recently I have subdivided[252] the class of the Filicopsida into seven subclasses, namely Primofilicidae, Ophioglossidae, Marattiidae, Osmundidae, Filicidae, Marsileidae, and Salviniidae, and in dealing with the ferns I shall follow this classification.

Primofilicidae—The Primofilicidae consist of Palaeozoic ferns which appear to have no direct affinity with the living members of the Filicopsida, with the possible exception of the Marattiidae. Since all these are fossil ferns I shall not deal with them here, nevertheless I wish to quote the publications of Posthumus[256, 257], Hirmer[136], Bertrand[26], and Emberger[101], who have paid great attention to this group, and the recent paper by Leclercq[189] in which some problems of the Primofilicidae are discussed. Furthermore, I wish to mention Surange's investigation on the spore-producing apparatus of *Stauropteris burntislandica*[324]. He has demonstrated that the spindle-shaped structures, formerly interpreted as "glands" and named *Bensonites fusiformis* are actually megasporangia which were terminal on the ultimate branchlets of the complex non-laminar ramifications of *Stauropteris burntislandica*. The discovery of the heterospory in a "fern" displaying several archaic features raises doubts about the affinity and the taxonomical position of *Stauropteris*, which I have regarded[252] as the most advanced among the Primofilicidae, but which might be a member of the primitive group in line with the evolution of the Pteridospermopsida.

Ophioglossidae—They include a few genera which have many characters in

common and constitute a well-defined natural group. They differ greatly from the other subclasses of ferns in the leaves which have straight (non-circinnate) vernation and stipular sheaths, in the sporangia arranged in spike-like organs, terminal (fundamentally) on leaf divisions and each provided with a vascular supply at its base, in the gametophyte which is subterraneous, radial (cylindrical to ovoid), mycorrhizic, with indefinite apical growth and scattered sexual organs.

The Ophioglossidae show a condition similar to that of the Psilotopsida. Their features are clearly indicative of a marked primitiveness, but no fossil record surely belonging to them is known. Scott[292] suggests an affinity of these ferns, though a somewhat remote one, with the Zygopteridales (Primofilicidae), but, as he rightly observes, the comparison of a recent group with a Palaeozoic one is apt to be misleading. On the basis of the morphological nature of the "fertile spike" an affinity between Ophioglossidae and Lycopodiidae was supposed (Bower[36]), but comparative studies have shown that the spike-like organs of the Ophioglossidae are of pinna-nature, and this affinity is now regarded as groundless. Copeland[74] suggests that these plants descend directly "from ancestors most nearly represented, among surviving plants, by *Anthoceros*." But such a derivation appears very rash. In conclusion, I think that we can agree with Bower[37] that the Ophioglossidae "appear to have terminated as a blind evolutionary series, and they stand today as an imperfectly modernized relic of the Palaeozoic flora."

The number of the genera is not well established. The majority of botanists adopt three genera: *Helminthostachys*, *Botrychium*, and *Ophioglossum*, and Clausen in his monograph[65] follows this line. Nakai[229, 230] recognizes four genera, the fourth being *Ophioderma* subdivided into two sections Cheiroglossa and Eu-Ophioderma. Masamune[216] has described a new genus, *Japanobotrychium*, but it does not appear worthy of generic distinction. Copeland in his *Genera Filicum* accepts the three universally adopted genera and *Rhizoglossum*. I am in favour of keeping *Cheiroglossa* distinct[248], in addition to Copeland's four genera. However, the problem of the delimitation of the genera remains open. In this problem cytology can help us very little, since the data are insufficient and an extremely high polyploidy, which makes counting and its interpretation difficult, characterizes these genera. Abraham and Ninan[2] have counted 631 bivalents and 10 fragments (or very small univalents?) at the first meiotic metaphase in *Ophioglossum reticulatum*.

The relative antiquity of the genera has been discussed at length, but no agreement has been reached. The monotypic *Helminthostachys* stands as an isolated genus and probably is more ancient than the other genera. Bower[37] and Eames[99] regard *Botrychium* as the most primitive, and *Ophioglossum*

as the most advanced. This is the conclusion drawn from the comparative study of the sporophyte; but the gametophyte appears more advanced in the former genus than in the latter, a condition which calls for further investigation.

Marattiidae—They are a small group of ferns occurring in tropical humid forests of both hemispheres. They were unnaturally classified together with the Ophioglossidae to form the Eusporangiatae, but they are better treated as a distinct subclass. The Marattiidae differ from the other ferns in several characteristics. The leaves have a circinnate vernation, and thin stipular enlargements. The tissues are traversed by numerous lysigenous mucilage canals. The large massive sporangia, exindusiate and exannulate, are separated or fused in radial or linear synangia; they are borne, perhaps owing to a phyletic slide, on the underside of the leaves and on the back of veins; they have thick walls provided with stomata and an eusporangiate origin. The tapetum derives from the wall tissue. The gametophyte is dorsiventral, perennial, thick, green, but provided with an endophytic fungus, and often bearing adventitious buds at the edges. The first division of the zygote is transverse and the embryo is erect.

The Marattiidae appear intermediate between the Ophioglossidae and the other modern ferns (Osmundidae, Filicidae, etc.), but they are not closely related to them, and neither can the Ophioglossidae be the ancestors of the Marattiidae, nor can the latter be the forerunners of the other more advanced ferns.

The Marattiidae are certainly a primitive group and this is substantiated by the numerous fossils, clearly related to them, which date back to the Palaeozoic age. Mamay in a recent paper[207] has suggested a derivation of the Marattiidae from the exannulate Carboniferous genus *Chorionopteris* (Primofilicidae, Anachoropteridales) and has also produced a phyletic diagram of the Marattiidae. Mamay's paper contains many fruitful ideas, but his arguments are not entirely convincing and concerning the origin and evolution of the Marattiidae much remains to be known.

The Marattiidae consists of a few living genera, but botanists do not agree on their number nor on the number of families to which they belong. Bower[37] recognizes only one family with seven genera referred to three different groups; Christensen[62], six genera subdivided into two families, Copeland[74], six genera assembled in a single family. Recently I was dealing with the nomenclature of the Marattiidae[250] and I recognized seven genera classified into four families. As regards the number of the genera, the only problem is whether *Protomarattia* is entitled to generic distinction or not. As I have remarked[250] this genus was misinterpreted but when correctly understood it represents an independent genus.

As regards the number of the families, I am of the opinion that the seven genera should be referred either to a single family or to four families, since otherwise the characterization of the families is difficult. Copeland[74] prefers the first alternative, while Reimers[274] adopts the second one. I agree with the latter and I am of the opinion that it is better to recognize four families. Cytological investigation so far is insufficient to support this view, though it is interesting to note (Manton and Sledge[214] and Ninan[237]) that *Angiopteris* which is considered more primitive has a chromosome number $n = 40$ and 80, while *Marattia*, which appears to be more advanced, has $n = 78$ (probably derived from a hypothetical basic number 13). We may have to wait a long time before having a sufficient karyological documentation, since some plants are growing in regions of difficult access. For the time being I prefer to classify the living Marattiidae as follows: Angiopteridaceae: *Angiopteris, Macroglossum, Archangiopteris*; Marattiaceae: *Marattia, Protomarattia*; Danaeaceae: *Danaea*; Kaulfussiaceae: *Christensenia*. They might constitute more than one order, but the creation of new orders can be proposed only when our knowledge of fossil records is better.

Osmundidae—The osmundaceous ferns are usually treated as an order of the Leptosporangiatae, but Hirmer[136] has segregated them from the other ferns and created the new group of the Protoleptosporangiatae, since they are intermediate, as regards the origin of the sporangia, between Eusporangiatae and Leptosporangiatae. The osmundaceous ferns differ both from the Marattiidae (eusporangiate) and the Filicidae (leptosporangiate) in many important features. The leaves have a winged base with expansions covered with glandular hairs. The stem is massive, complex, and formed by a small stele, surrounded by a thick dark-coloured cortex of sclerenchyma, and by persistent leaf bases showing the characteristic C-shaped bundles in cross section. The development of the sporangium is inconstant: it may originate from a single cell, or from several, the initials being either conical or cubical. The sporangia are non-soral, exindusiate, large, globose or pyriform, and without a true annulus, but with a mere cluster of thick-walled cells near the distal end. They dehisce by a longitudinal slit running from these cells across the top to the ventral side. The tapetum has two or three layers, the spores are very numerous and chlorophyll-bearing, and they soon lose their power of germination. The germination is of the bipolar type. The gametophyte is large, fleshy, flat, with a projecting thickened midrib on the lower side, long-living, and often bearing adventitious buds. The antheridia are large, complex, very numerous, and borne on the margin as well as on the dorsal surface of the prothallus; their walls consist of many chlorophyllous cells, one of which serves as an operculum for the dehiscence. The spermatozoids are numerous (about 100 or more). The archegonium

has a straight neck tapering from a heavy base; the canal cells and egg contain a large amount of starch. The embryo is prone and its early segmentations are different from both the leptosporangiates and the eusporangiates.

These characters prove that the Osmundidae differ from all other ferns in several important characteristics of the sporophyte and gametophyte. The latter has been exhaustively studied by Stokey and Atkinson[319] in recent years. Bower[37, 39] suggests that Plagiogyriaceae derive from the Osmundaceae, and Holttum[151] accepts this suggestion, and thinks that perhaps a part of the Adiantaceae also take origin from these ferns. But both these derivations are improbable, and the structure of the gametophyte (Stokey and Atkinson[320]) does not confirm them. Consequently, since the osmundaceous ferns appear sharply distinct and show no clear affinity to any other fern, Reimers[274] following Hirmer's view[136] has raised this group to the rank of subclass under the name of Osmundidae and I prefer to follow him.

The osmundaceous ferns are represented only by a few living species belonging to three genera, distributed in temperate and tropical regions all over the world. They are the relicts of a group which appears to have lost its evolutionary potentialities. This is also proved by the rare variation in the structure of the gametophyte among the species (Stokey and Atkinson[319]), by the striking constancy of the chromosome number which is $n = 22$ in all the osmundaceous genera, and by the lack of a polyploid series (Manton[209], Ninan[238], Brownlie[47]).

The Osmundidae are a primitive and isolated group not closely related to the other ferns. It was supposed that they derived from the Botryopteridales (Primofilicidae). Such an origin is uncertain, but the osmundaceous ferns extend back to the Palaeozoic age. Since remote times, perhaps since that age, they run as a line of descent independent both from the eusporangiates and the leptosporangiates. Its few living species are the last survivors of this conservative and primitive evolutionary line.

The Osmundidae are intermediate between the eusporangiates and the leptosporangiates, but only morphologically: not from the point of view of their phylogeny and palaeontological history. This is why I prefer to keep them as an independent class, even though they are not so sharply distinct from the Filicidae as they are from the Ophioglossidae and the Marattiidae.

Filicidae—I have given the distinctive features of the previous three groups of ferns, in order to show that they are important enough for these groups to be considered as subclasses. However, I think it superfluous to quote the distinctive characteristics of the Filicidae, which are those of the leptosporangiate homosporous ferns well known to all.

The Filicidae are by far the richest in genera and species among the ferns, and are the group of the Pteridophyta best represented in the present age.

They consist of about three hundred recognized genera of living ferns whose delimitation and classification is very difficult. In the past these genera were grouped into a dozen families, and even quite recently Christensen[62], Reimers[274], Smith[297] and Benson[22] adopted only a few families; but with the splitting up of the old "Polypodiaceae," the number of families has considerably increased. However, grouping the genera into families, and these into orders, presents considerable difficulties, and pteridologists are very far from agreeing in their classification. In the last twenty years many papers on the Filicidae, covering every field of pteridology, have been published, and they have greatly contributed to clearing up the affinities between fern genera. There have been investigations of particular importance on cytology, palynology, and the structure of the gametophyte, which have disclosed a new and promising source of information for taxonomy and phylogeny. All this work has laid the foundation for several systems of fern classification, such as those of Christensen, Ching, Dickason, Holttum, Copeland, Reimers, Alston, and for mine. It would be very interesting to examine these systems in detail, but it would require far more space than that allotted to the Pteridophyta in this book, and I must confine myself to a few comments on them.

Christensen's system[62] is rather conservative. Within the limits assigned here to the Filicidae, he recognizes eleven families, one of which, the Polypodiaceae, is subdivided into fifteen subfamilies. Reimers[274] follows Christensen's classification in its main lines and adopts thirteen families one of which, the Polypodiaceae, consists of fourteen subfamilies. All these ferns are grouped into a single order, the Filicales.

Ching[57] only takes into account the ferns previously referred to the composite family "Polypodiaceae." His classification is largely based on Presl's system[262]. He classifies the polypodiaceous complex into thirty-three families, which are grouped into five "series," and one isolated family: the Didymochlaenaceae. These series are established by Ching according to his concepts of the evolution of ferns as summarized in his phylogenetic diagram. The five series and the supposed ancestral stock (quoted here in brackets) are the following: Pteroid-Gymnogrammeoid series and Lindsayoid-Davallioid series (Dicksonioid stock); Thelypteroid-Asplenioid series (extinct ancestral stock); Cyatheoid-Aspidioid series (Cyatheoid stock); Dipteroid-Polypodioid series (Dipteroid stock). Ching's system was bitterly criticized by Copeland[73] but it contains many fruitful ideas, in part adopted by Copeland himself some years afterwards[74].

Dickason[92, 93] proposed his system of fern classification in two papers devoted to the ferns of Burma. He makes an interesting comparison between the classification of the polypodiaceous ferns adopted by Diels[104], Bower[37], Copeland[74], Christensen[62], and Ching[57], and examines the principal

characters of ferns in general, which according to him show the phyletic patterns of variation among the leptosporangiate ferns. He concludes his study by recognizing five orders of ferns, the third of which, the Filicales, corresponds (Osmundaceae excluded) to my Filicidae. The order of the Filicales is subdivided into forty-two families of living ferns, assembled to form twelve groups of families, half of which are belonging to the polypodiaceous ferns. Dickason regards the position of the sori as very important, but, instead of the marginal or superficial position of them emphasized by Bower[37], he attaches great importance to whether the position of the sori is apical on the veins, or whether it is lateral on them and located on the abaxial side of the leaf. According to these two different positions of the sori he subdivided the twelve groups of families into three sections: groups A-E with sori lateral on the veins, groups H-L with sori apical on the veins, and groups E-G with sporangia scattered on elongate receptacles which follow the veins and sometimes extend between them. The terminal or lateral position of the sori on the veins is certainly important, but probably not so important as Dickason thinks, and the groups based by him on these features are artificial.

Holttum[150] at first proposed a system devoted to the polypodiaceous ferns, and later[151] extended it to all the leptosporangiate ferns. He recognizes fourteen families, one of which, the Dennstaedtiaceae, consists of eleven subfamilies. The interrelations of the various families and subfamilies are shown in a phylogenetic diagram included in the second paper[151]. Holttum's system is undoubtedly a great improvement on Christensen's. For instance, the segregation of the Thelypteridaceae from Aspidiaceae is certainly a good thing and cytological evidence (Manton and Sledge[214]) has confirmed it. However, some groups delimited by Holttum are clearly artificial. His Dennstaedtiaceae, for instance, consist of groups of genera which are not closely related.

Copeland[74] assembles all the leptosporangiate ferns, both homosporous and heterosporous, into the order of the Filicales. The ferns corresponding to the present Filicidae are subdivided into sixteen families, which include 290 genera in all. Copeland has a clear conception of the delimitation of genera, and agrees well enough with Ching in this respect. He adopted several of Presl's and J. Smith's genera too. But as regards the families, Copeland's classification is really defective. His family of the Pteridaceae, like that of the Aspidiaceae, is a strange mixture of genera, whose affinity is certainly remote. Moreover, from the taxonomical point of view these families cannot be defined.

Alston[5] presented his views on the classification of the polypodiaceous ferns in a short paper, in which he also proposed the new families of the Athyriaceae and of the Lomariopsidaceae. The paper is very concise and is

devoted chiefly to the African ferns. It shows its provisional nature clearly, but most unfortunately Alston's premature death has put an end to any hope of his system being fully elaborated. Nevertheless, even in this succint form, his classification is highly interesting and shows fresh ideas which appear full of promise for future development. Alston emphasizes the taxonomical importance of the presence of hairs or scales on the rhizome, the structure of the spores, the number and the features of the bundles, and the chromosome number. He presents a classification which, in my opinion, agrees with the phylogeny of ferns better than any previous system.

In the classification I have proposed recently[252] the Filicidae, which include the homosporous leptosporangiate ferns, are classified into fourteen orders and thirty-seven families, five of which consist of fossil members only. The subdivision of the subclass of the Filicidae into orders must be regarded as provisional, and probably their number will be reduced. However, I have preferred to propose a subdivision of the subclass of the Filicidae into various orders, each including families which appear clearly related, rather than merging numerous families, some of which show no close affinity, into a single order. Orders and families are disposed in a sequence which does not involve a derivation of one order from the other.

The Filicidae form a group of ferns which do not show a close affinity to each other. Bower[37, 39] supposes that all ferns originated from the Coenopteridaceae (= Primofilicidae) and suggests that the ferns here treated as the Filicidae represent five independent lines of descent. According to him the polypodiaceous ferns derive from three different sources, the Schizaeaceae, the Osmundaceae, and the Gleicheniaceae. Eames[99] agrees in part with Bower, but he suggests a derivation of the polypodiaceous ferns indirectly from schizaeaceous and gleicheniaceous ancestors. Holttum[151] supposes that all the leptosporangiates derive from a hypothetical primitive fern, of which he gives the characteristics. He claims that three groups derived from it: the "Primitive Marginales," the Osmundaceae, and the "Primitive Superficiales"; these groups gave rise to the different families of the leptosporangiate ferns. Holttum's views do not appear to differ greatly from those of Bower, but he believes in a different derivation of the various families and subfamilies from the three ancestral groups.

Dickason[92] appears in favour of a monorheithric origin of the leptosporangiate ferns but does not give further information. Ching[57] recognizes "five or six distinct lines of evolution" which he suggests are originated by five different stocks, three of them indicated as Dipteroid, Cyatheoid, and Dicksonioid, and each of the other two as "Extinct Ancestral Stock." No information is given as to their origin. Copeland[74] only occasionally discusses the phylogeny of the families adopted in his system, so that it is difficult to form an idea of his phylogenetic concepts.

I think that the Filicidae have a common origin, even if a remote one, but I know of no fossil or living fern group which may be regarded as their ancestor. It was suggested that the Osmundidae were the forerunners of the Schizaeales and Gleicheniales, but the hypothesis of such a direct descent is hardly tenable. This does not exclude the possibility that in a remote past these ferns may have originated from a common source. There is little evidence to suggest that the Schizaeales or the Gleicheniales are the direct forerunners of the other Filicidae. My opinion is that the Filicidae derive from a common ancestor with marginal sporangia, hence nearer to the Schizaeales than to the Gleicheniales. From this common source two lines of descent took origin: one, the line of the marginales, with an evolutive trend towards a marginal position of the sporangia; another, the line of the superficiales, with an evolutive trend towards superficial sporangia. The line of the marginales gave rise to secondary lines; one with scarce evolutive potentialities became the Schizaeales, while others with a wider perspective power gave origin to the remaining marginal leptosporangiate ferns. The line of the superficiales developed into secondary lines with different evolutionary power. The most conservative of these became the Gleicheniales and the Matoniales, while the richest in evolutive potentialities gave origin to the superficial leptosporangiate ferns. The heterosporous living ferns probably derived from ancestors which had branched off from the line of the marginales.

After this brief survey of contemporary systems of fern classification and the principal phylogenetic theories, I think it necessary to deal briefly with the orders and most important families of the Filicidae following my recent paper[252].

The Schizaeales is an ancient and well-defined group which ranges from the late Lower Carboniferous, where it is represented by the genus *Senftenbergia*, up to the present age. Reed[271] has given a good conspectus of the fossil and living members of the order; they are classified into eight families, four of which consist chiefly of living genera. I agree with Reed in treating these ferns as an order, but I do not follow him in his excessive splitting of genera. There is not much cytological data and the monoploid numbers (*Lygodium* $n = 29, 30$; *Anemia* $n = 38$; *Schizaea* $n = 77$) are known for only three genera of the Schizaeales (Manton and Sledge[214] and Lovis[201 bis]). Perhaps research in this field will throw up new facts for the taxonomical understanding of these ferns, but for the time being I prefer to recognize only the four genera adopted by Prantl[261], and Bower[37], who studied the morphology of these ferns very carefully. From the point of view of nomenclature the living genera of the Schizaeaceae have been recently revised in a paper of mine[249]. As regards the number of families, on the basis of the structure of the gametophyte, flattened or filamentous, the living

members can be subdivided into two families. But for the time being I think it more convenient to wait for the gametophyte to be better known. The Schizaeales are regarded by some botanists as the ancestors of the marginales, but a direct derivation of the latter from the former is improbable. I would tend rather to believe that Schizaeales and marginales represent lines of descent derived from a common schizaeoid ancestor, but provided with different evolutive perspective power, the Schizaeales being the more conservative of these lines.

The Pteridales in my view[252] consist of eight families: Pteridaceae, Negripteridaceae, Sinopteridaceae, Cryptogrammaceae, Parkeriaceae, Gymnogrammaceae, Adiantaceae, and Vittariaceae. As it is here constructed the order includes the Pteridoideae Lepidopterides, the Gymnogrammoideae, and the Vittarioideae of Christensen[62]; the majority of the Pteroid-Gymnogrammeoid series of Ching[57]; the families of groups F, G, and part of those of group H of Dickason[92]; the Adiantaceae and part of the Pteridoideae of Holttum[150, 151]; part of the Pteridaceae (genera no. 31–63) and the Vittariaceae of Copeland[74]; and the Adiantaceae and Vittariaceae of Alston[5]. I wish to point out that I exclude from the order of the Pteridales all the pteridaceous genera belonging to the Chaetopterides (*Pteridium*, *Paesia*, etc.); I include them provisionally in the Dennstaedtiaceae following Alston's suggestion[5]. The families of this order appear to be clearly related and they form a uniform and well-delimited group. This is confirmed also by the cytological evidence, as clearly pointed out by Manton in a recent paper devoted to the "Pteridaceae"[213]; and indeed most genera of the Pteridales have a chromosome number $n = 29$ or 30 or multiples of these. The only obviously discordant element from the cytological point of view is *Ceratopteris* (Parkeriaceae) which has $n = 77$ (Ninan[239]) but the morphology of the sporophyte as well as of the gametophyte (Stokey[314]) shows that it is definitely related to the other Pteridales. Although it has not yet been thoroughly investigated the structure of the gametophyte of the Pteridales seems to show no great differences, except for the Vittariaceae which according to Stokey[314] have a gametophyte sharply distinct from that of any known higher fern. However, in other respects they show affinity with the other Pteridales, particularly, as I have already pointed out[251], with the Adiantaceae. And, indeed, Holttum[150, 151] merges gymnogrammeoid and vittarioid ferns into a single family, the Adiantaceae. Although they are less closely related to the remaining Pteridales than the other families of this order are to each other, I include both the Parkeriaceae and the Vittariaceae in the order. As regards the origin of the Pteridales, they probably derive from a schizaeoid ancestor, and represent a branch of the evolutive line of the marginales, a branch with a wide perspective power which appears to be clearly, even if not closely, related to the Schizaeales.

The Dicksoniales, as constructed in my recent paper[252] consist of three families: Dicksoniaceae, Dennstaedtiaceae, and Lindsaeaceae. The first two families appear to be closely allied, but the affinity of the third is less close. Kramer[176], who has recently revised the American species of *Lindsaea* monographically, recognizes that the alliance of the lindsaeoid ferns to the dennstaedtioids is not very close, and that the alliance to the davallioids is even less evident. Nevertheless, I think that the relationship between the Lindsaeaceae and the Dennstaedtiaceae is clear enough to justify their inclusion in the same order. Holttum[150, 151] has included in his Dennstaedtiaceae several unrelated groups of genera which I would rather refer to other orders. Besides the genera usually comprised in the Dennstaedtiaceae *sensu stricto* I tentatively include in this family the pteridaceous ferns called Chaetopterides (*Pteridium*, *Paesia*, etc.). As regards the cytological aspect in the Dicksoniales there is a striking diversity of chromosome numbers which could be indicative of a remote affinity of their members. The interpretation of the cytological data, as noted by Manton[213] too, is very difficult and a comparative study of the morphology and the cytology are needed. From the view point of the gametophyte too, the Dicksoniales show some dissimilarities. The Dicksoniaceae (Stokey[312]) are uniform, but according to Conard[67] there is a considerable gap between the gametophyte of *Thyrsopteris*, or even of *Culcita*, and that of *Dennstaedtia*—a much larger gap than that between *Dennstaedtia* and *Pteridium*. The Dicksoniales are ancient ferns, and fossils belonging to the Dicksoniaceae date back to the Jurassic. Like the other marginales, they probably originated from a schizaeoid ancestor; in any case the relationship with the Schizaeales is remote.

The Davalliales consist of two families only: the Davalliaceae and the Oleandraceae. These two families (or subfamilies, as certain botanists prefer to regard them) are considered as closely allied. Some pteridologists, among them Copeland[74] and Alston[5], go so far as to regard them as a single family: the Davalliaceae. On the contrary Dickason[92, 93], on the basis of the position of the sori, apical on the veins or lateral on them, regards *Nephrolepis* as allied to the Davalliacese, and *Oleandra* as related to the Aspidiaceae. The affinity of the Davalliales is not clear; according to most botanists they are related to the Dicksoniales, while Alston[5] suggests an affinity with Polypodiaceae. From the point of view of cytology the chromosome number $n = 40$ and 41 counted respectively in the Davalliaceae and Oleandraceae, would suggest a relationship with the Aspidiaceae and Lomariopsidaceae. However, I have placed them next to the Dicksoniales, since from the morphological point of view they appear to be less distantly related to them than to any other order.

The Hymenophyllales are a very well-defined group adopted by all botanists. The greatest problem of the Hymenophyllales is the delimitation

of their genera. Most pteridologists recognize only two genera, while Prantl, who has produced a good account of the morphology and taxonomy of the Hymenophyllaceae[260], recognizes seven genera, and Copeland, who has published three great works on this family[70, 71, 72] adopts many genera: perhaps the number of thirty-three or thirty-four genera adopted by him is excessive, but several groups are well delimited and are entitled to generic rank. This is confirmed by the various chromosome numbers, $n = 11, 13, 18, 21, 22, 26, 27, 28, 33, 34, 36$, which are counted in this order (Manton and Sledge[214], Mehra and Singh[217 b18], Brownlie[46, 47]) and may derive from the basic numbers 7, 9, 11, 13, 17. Research work on the cytotaxonomy of the group is needed in order to interpret the significance of these numbers. The Hymenophyllales are a primitive specialized group probably isolated since remote times. Their relationship is not clear, but very likely they belong to the marginal series and take origin from schizaeoid ancestors.

The Gleicheniales are primitive ferns which are represented in the Upper Carboniferous by *Oligocarpia*, a fossil genus recently revised by Abbott[1]. The living members form a single family which includes few genera. Pteridologists do not agree on their number: Christensen[62] accepts five genera, Copeland[74] recognizes six genera, Nakai[232], in a new classification of the Gleicheniaceae, subdivides the family into eight genera referred to three subfamilies, and Holttum[155, 156], in two recent papers devoted to the Gleicheniaceae, adopts three genera: *Stromatopteris*, *Gleichenia* (with three subgenera), and *Dicranopteris* (with two subgenera), assigned to two subfamilies. He excludes[153] from the Gleicheniaceae the genus *Platyzoma* which he considers a gymnogrammeoid fern. Personally I follow Holttum's classification, but I would rather raise his subgenera to generic rank. This appears to agree with the present cytological evidence, different chromosome numbers being present in the family, namely *Gleichenia sensu stricto* $n = 20$ (Brownlie[47]); *Hicriopteris* $n = 56$ (Mehra and Singh[217]); *Sticherus* $n = 34$ (Brownlie[47] and Walker ex Manton[213]); and *Dicranopteris* $n = 39$ and 43 (Manton in Holttum[152] and Walker ex Manton[213]). While displaying so much variety in their cytological features, the Gleicheniaceae show great uniformity in the structure of the gametophyte (Stokey[313]). The origin of the Gleicheniaceae has been discussed recently by Holttum[156]. Probably Gleicheniales and Schizaeales have a common origin, but since the latter appear to be somewhat more primitive, a derivation of the Gleicheniales as a branch of the evolutive line of the forerunners of the Schizaeales—rather than an origin from a common ancestor—cannot be excluded. Probably Gleicheniales had no direct descendant, and the so-called superficiales ferns are to be regarded as derived from the forerunners of the present Gleicheniales, and hence as originated from gleichenioid ancestors.

The Cyatheales include few genera which are classified into one or two

families. I have subdivided[252] them into Lophosoriaceae (= Protocyatheaceae Bower) and Cyatheaceae, following Bower[37]. The gametophyte of the cyatheoid ferns is uniform and *Lophosoria* differs from the true Cyatheaceae only in details (Stokey[312, 314]). But these families possess several important characters of the sporophyte which set them apart, the Lophosoriaceae displaying a certain number of primitive characters. The delimitation of the genera of the Cyatheaceae is difficult and calls for further study. Holttum[154] has recently emphasized the importance of the structure of the scales, and shown that Copeland's classification[74] of oriental genera should undergo some amendments. From the cytological point of view only high chromosome numbers ($n = 69$ and 70) have been counted in Cyatheales (Manton and Sledge[214], and Brownlie[47].) The interpretation of these numbers is very puzzling since they do not seem to be in agreement with the taxonomical separation of genera. The Cyatheales seem clearly related to the Gleicheniales: the structure of the gametophyte (Stokey[312]) supports this view, and Holttum's researches[156] confirm it. The affinity is not very close, but it is evident, and the origin of the Cyatheales from the ancestors of the modern Gleicheniales is beyond doubt.

The Loxsomales were placed in my system[252], following Bower[37], among the orders of the series of marginales. Goebel[122] suggested an affinity with the Cyatheaceae. A recent study by Stokey and Atkinson[321], published when my paper[252] had already been written, has added further evidence in favour of a relationship between Loxsomales and Cyatheales, and has shown that they are at the same evolutive level; accordingly I prefer to place this order next to that of Cyatheales. Stokey and Atkinson's research has confirmed the affinity of *Loxsoma* and *Loxsomopsis*. The Loxsomales are an isolated group; they are certainly primitive ferns, and this is also proved by the geographical distribution of their sole genera *Loxsoma* of New Zealand and *Loxsomopsis* of Central and Southern America.

The Aspidiales is one of the largest orders. I have referred[252] to it the five families Thelypteridaceae, Aspleniaceae, Athyriaceae, Aspidiaceae, Lomariopsidaceae. This order includes the Asplenioideae, Woodsioideae, Dryopteroideae, and Elaphoglossoideae of Christensen[62]; the families of the Cyatheoid-Aspidioid series, and part of those of the Thelypteroid-Asplenioid series of Ching[57]; the Thelypteridaceae, Asplenioideae, Lomariopsidoideae, Dryopteroideae, Tectarioideae, and Athyrioideae of Holttum [150, 151]; the Aspidiaceae and Aspleniaceae of Copeland[74]; and the Aspleniaceae, Thelypteridaceae, Athyriaceae, Aspidiaceae, and Lomariopsidaceae of Alston[5]. If we consider the cytology of the Aspidiales, we find the following chromosome numbers: Thelypteridaceae $n = 36$, 35, 34, 31; Aspleniaceae $n = 36$; Athyriaceae and Aspidiaceae $n = 41$, 40, 42 and Lomariopsidaceae $n = 41$ (Manton and Sledge[214], Alston[5], Manton[213]). So

construed this order consists of a complex which, although various, does in fact share some fundamental characters, as already remarked by Alston[5]. Holttum[151] refers nearly all the families of this order to the marginales as subfamilies of his Dennstaedtiaceae, but I do not agree with him, and I consider this order as belonging to the superficiales and hence as originated from gleichenioid ancestors.

The Blechnales consist of the single family Blechnaceae which includes few genera. They are primitive ferns the affinity of which to other orders is not clear. The possibility of a relationship with the Aspleniaceae and with the Athyriaceae has been put forward, but nothing confirms these suggestions. Cytology indicates no particular affinity. Several chromosome numbers are present in this order, namely $n = 34, 33, 32, 28, 35$, and four of these occur in the genus *Blechnum*. The number $n = 73$ was counted (Mehra and Bir[216 b18]) in *Stenochlaena* which according to Holttum[150] belongs to the Pteridoideae, while Copeland[74] refers it to the Blechnaceae. Cytological research does not solve the problem, but Stokey and Atkinson's investigation on the gametophyte of this genus[315] has shown that *Stenochlaena* is allied to *Blechnum* and not to *Acrostichum* (Pteridales). The same conclusion is reached by Mehra and Bir[216 b18] on the basis of other features. The Blechnales can be regarded as an isolated and primitive group, probably derived from gleichenioid ancestors.

The Matoniales can be traced back as far as the Rhaetic in which they were represented by the genus *Laccopteris*. The living descendants belong to the genera *Matonia* and *Phanerosorus*, which form the sole family of the order. The only known chromosome number is that of *Matonia*, $n = 26$ (Stokey and Atkinson[316] and Manton[210, 211]). The Matoniales are clearly related to the Gleicheniales and even the structure of the gametophyte (Stokey and Atkinson[316]) confirms this affinity, but they attained a higher evolutive level. Their derivation from gleichenioid ancestors is certain, but probably rather remote in time. This is proved by the type of branching in *Matonia* which does not occur in living Gleicheniales. The Matoniales are certainly related to the Polypodiales, and particularly to the Dipteridaceae, but the Matoniaceae stand apart from them for their frond architecture (cf. Wagner[341]), stelar structure, soral features, and for the presence of the umbrella-shaped indusium. Moreover, the fossil Matoniales and Dipteridaceae were already distinct in the Rhaetic. This is why I keep the Matoniales distinct from the Polypodiales as an order. They probably represent the survival of a primitive conservative branch of the line of the superficiales.

The Polypodiales consist of the four families Dipteridaceae, Cheiropleuriaceae, Polypodiaceae, and Grammitidaceae. The Dipteridaceae are the most primitive and their fossil members date from the Rhaetic. This family is sharply distinct and represents a conservative type without direct

descendants. It has probably a common origin with Matoniales from gleichenioid ancestors. The Cheiropleuriaceae is another ancient family. They were united with the Polypodiaceae in a single family, but they are distinct enough to deserve family rank. The structure of the gametophyte investigated by Stokey and Atkinson[318] gives reliable evidence of this distinction, and shows that the Cheiropleuriaceae are more closely related to *Dipteris* and *Matonia* than to the Polypodiaceae. Probably they represent a family more advanced than the Dipteridaceae, but still somewhat primitive. Their derivation from dipteroid ancestors is very probable. As regards the other two families, Holttum[150, 151] considers them as derived from two different lines of descent, and Alston[5] emphasizes their differences; but they show a clear relationship which is confirmed by cytological investigation, the commonest chromosome number in both the Polypodiaceae and Grammitidaceae being $n = 37$, with minor divergences to 36 and more rarely 35 (Manton and Sledge[214], Brownlie[47], and Manton[213]). Ching[57] has created a monotypic family, Platyceriaceae, for the genus *Platycerium*, but neither cytology (*Platycerium* has $n = 37$ like the other Polypodiaceae) nor the structure of the gametophyte (Stokey and Atkinson[317]) support the recognition of this family, and *Platycerium* is better regarded as one of the primitive members of the Polypodiaceae. Ching[57] and Dickason[92, 93] recognize another family, the Loxogrammaceae, represented by the genus *Loxogramme* which would seem to be an aberrant member of the polypodiaceous ferns. Whether this genus forms an independent monotypic family or should be merged into the Polypodiaceae is uncertain. It possesses a chromosome number $n = 36$ (Manton and Sledge[214]), which is present in the Polypodiaceae. This indicates that its affinity is to the Polypodiales, and not to the Vittariaceae as suggested by Ching[57]. Both the Polypodiaceae and Grammitidaceae are advanced ferns, evidently related to the Cheiropleuriaceae, and hence of dipteroid origin; but this affinity is not very close and a gap between the Dipteridaceae and Cheiropleuriaceae on the one hand, and the Polypodiaceae and Grammitidaceae on the other is evident. This gap might suggest the splitting of the Polypodiales into two orders, but the affinity between the two groups seems to me clear, and I prefer to adopt a single order.

The Plagiogyriales consist of one family and one genus only. They represent an isolated type whose affinity with other ferns is not clear. In the past *Plagiogyria* was associated with the Pteridoideae, Blechnoideae, and Cyatheaceae, until Bower[37] created a distinct family for it suggesting an affinity, although a remote one, with the Osmundaceae. But there is no probative evidence to support this view, and no indication of its possible affinities is supplied by the study of the structure of the gametophyte made by Stokey and Atkinson[320]. However, their research has confirmed that

Plagiogyria is a primitive fern. Because the Plagiogyriaceae represent an isolated group I have treated them as an order, but its taxonomical position is uncertain, although their origin from schizaeoid ancestors appears more probable than that from gleichenioid ones.

The Hymenophyllopsidales represent another group "incertae sedis." Copeland[74] looks upon their only genus *Hymenophyllopsis* "as a fern of Pteridaceous ancestry" and suspects an affinity with *Orthiopteris*. But for the time being no definite taxonomical position can be upheld. *Hymenophyllopsis* shows a remarkable simplicity, but whether this is due to reduction or to primitiveness is uncertain.

Marsileidae—They were formerly assembled with other heterosporous living ferns, the Salviniidae, to form the Hydropterideae, on the grounds of their adaptation to aquatic life and their heterospory. Copeland[74], Lawrence[185], and other contemporary taxonomists still adopt this group, but a better knowledge of these plants has shown that the Marsileidae and Salviniidae are not related, and that their similarities are due to homoplasy. Consequently the group of the Hydropterideae must be regarded as unnatural and is not entitled to recognition. I have treated the Marsileidae and the Salviniidae as two subclasses, but they have been recently regarded as two classes, Marsileata and Salviniata, by Nakay[231] and Reed[273].

The Marsileidae consist of a single family with three closely related genera, *Marsilea, Regnellidium*, and *Pilularia*. No sure fossil records of the Marsileidae are known. They retain some important primitive characters, while being rather advanced in others features. In comparison with the Salviniidae, the heterospory of these ferns appears to be less advanced, since the Marsileidae produce in the same sorus both megasporangia and microsporangia. In many of their characters the Marsileidae show an affinity to the Schizaeales, and on these grounds several authors when treating them as a family, assign to the Marsileaceae a taxonomical position next to the Schizaeaceae. I do not intend to disregard this affinity, but I think that it is remote, and that the Marsileaceae are not the direct descendants of the Schizaeales. Probably they derive from a schizaeoid ancestor, but the two orders had an entirely different perspective power, as is clearly shown by the conservative trends of the Schizaeales and the rich evolutive potentialities of the Marsileidae. This consideration and the fact that the Marsileidae in the course of evolution attained heterospory, warrant a segregation of the present group as a subclass.

Salviniidae—They include the two genera *Salvinia* and *Azolla* which are usually associated in a single family, but I agree with Christensen[62] and Bonnet[32 bis] that they are distinct enough to be classified into two different families, Salviniaceae and Azollaceae. In the course of adaptation to the

floating life they attained great specialization and at the same time a reduction in size and structure. They have attained the highest degree of heterospory among living ferns. In *Salvinia* the sporocarps contain only one type of sporangia from the beginning; the megasporocarp possesses several megasporangia, in which only a single megaspore comes to maturity. In *Azolla* the sporocarps in the first stage of ontogeny contain megasporangia and microsporangia, but later on one of them aborts and when mature the sporocarps are monosporangiate and bear either megasporangia or microsporangia. The megasporocarp contains only one megasporangium which bears a single megaspore.

The Salviniidae are relatively young. According to Florin[113] *Salvinia* can be traced back to the Eocene and was fairly common in the Middle Tertiary. *Azolla*, although rarer, was likewise present in the Tertiary. The affinities of the Salviniidae are obscure; a relationship with the Hymenophyllales has been suggested, but even if it exists, it is certainly remote and undoubtedly indirect. However, the origin of the Salviniidae from schizaeoid ancestors appears sound.

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GYMNOSPERMAE

By W. B. Turrill

The gymnosperms have long been considered as a group of seed-bearing plants distinguished from the angiosperms by having naked ovules and seeds, that is to say the ovules are not enclosed in an ovary and the seeds are not enclosed in a pericarp. Pollination is direct in the sense that the pollen grains (or at least the pollen tubes) reach the nucellus of the ovule without the intervention of stigmata and styles through which the pollen tubes have to penetrate. The nakedness of the ovules was clearly recorded by Robert Brown in 1828[14, 15]. Until recently it was generally accepted, and expressed in schemes of classification, that the Gymnospermae formed a group co-ordinated with the Angiospermae. From time to time suggestions have been made for splitting the Gymnospermae into a number of major groups taxonomically equivalent one to another and to the angiosperms. Though it is not our concern here, it has to be remembered that proposals for segregating the angiosperms into groups, other than dicotyledons and monocotyledons, have also been made. The gymnosperms are a heterogeneous assemblage and there can be no doubt that they should be divided into phyla that have high hierarchical value. It may not yet be possible to reach wide agreement as to the contents and arrangement of these phyla and any classification proposed must, therefore, be tentative and can, at best, do no more than express present knowledge and conclusions, usually associated with some subjective elements. In many respects the classification proposed by Johansen[66] in 1951 has much to recommend it. He accepts, in the following sequence, the phyla and orders:

Phylum Pteridospermophyta
  Order Cycadofilicales
Phylum Cycadophyta
  Order Bennettitales
  Order Cycadales
  Order Nilssoniales
  Order Caytoniales
Phylum Ginkgophyta
  Order Cordaitales
  Order Ginkgoales
Phylum Coniferophyta
  Order Voltziales
  Order Coniferales
Phylum Ephedrophyta
  Order Gnetales.

This scheme could be improved in several respects to bring it into line with the latest conclusions of experts. Thus, the Caytoniales might be moved from the Cycadophyta to the Pteridospermophyta and the Taxales raised to an order equivalent to the Coniferales.

For convenience of general coverage the heading Gymnospermae (gymnosperms) is here retained, and can so far be justified in that the segregated

phyla are, in all proposed classificatory schemes studied by the writer, placed near together and, in linear classifications, between the Pteridophyta (or whatever name be used) and the Angiospermae (sometimes called Anthophyta, etc.). In dealing with the gymnospermous groups below Johansen's classification will be followed with some modifications.

The importance of the gymnosperms cannot be gainsaid. While the dominant vegetation of the land over the greater part of the earth is composed at the present time of angiospermous species, the conifers ("soft-woods") dominate the forests in a wide belt right round the globe in the northern part of the North Temperate Region between the treeless zone of the Arctic Region and the broad-leaved deciduous forests to the south. They also often form extensive belts or altitudinal zones in mountain regions far to the south of the conifer belt. Economically they are of very great importance in providing timber and wood pulp and they are planted in many parts of the world under schemes of forestation and reafforestation. Botanically, the interest in the group is several-fold. They are all woody plants but in size range from the tallest known trees to dwarf shrubs. The diversity of their vegetative parts is very great and that of their reproductive devices even greater. They are, in many points of structure and details of behaviour, intermediate between vascular cryptogams and angiosperms. That the history of many of the groups is better known than is that of the angiosperms is one of the main reasons of their importance to botanists. Several of the major groups are extinct and are known only from a study of their remains in Palaeozoic or Mesozoic strata. These remains, however, are in part well preserved and in part have yielded a great deal of information by the application of modern techniques of palaeobotany. It has been by painstaking treatment and examination of gymnospermous fossils that the details of structure, and even to a certain extent of the probable life-histories, of extinct phyla and orders have been worked out and the probable (or possible) lines of evolution of these and of still existing groups of plants have been placed on a firmer foundation. In addition, the study of the fossil materials has had a considerable influence on new or modified interpretations of the structures, vegetative and reproductive, proposed for vascular plants in recent years. This is not the place to give details regarding new morphogenetic theories, because to do so would take us far beyond the confines of the gymnosperms. However, the difficulties of interpreting the morphology of the reproductive parts in various gymnospermous phyla and the increasing acceptance of telome theories in some form or another make it desirable to say a little about the concepts of "telomes."

Descriptive botany, in so far as it involves the Spermatophyta, and particularly the angiosperms, has long been based on acceptance of three major categories of plant organs: roots, stems, and leaves. On the whole, this

division of the plant body has been, and is, satisfactory. The vast majority of vegetative organs can be unequivocally referred to one or other of the three categories. Indeed, it is usually essential to do this. The classification by Goethe of the parts of the flower of angiosperms as metamorphosed leaves has also, in theory, been widely accepted, though in practice they have been given their own terminology as sepals, petals, stamens, carpels, etc., and little concern has been expressed as to their ultimate morphogenesis by the vast majority of taxonomists and other botanists describing flowers and flower-parts in the angiosperms. That there are some structures in both vegetative and reproductive parts, even of the angiosperms, that are difficult to place definitely into one or other of the categories roots, stems, leaves, is acknowledged but these have usually been considered as "outgrowths" or special developments (organs *sui generis*) and are so explained as to avoid the breakdown of the orthodox morphological scheme. However, even during the last century doubts were expressed as to the possibility of interpreting all the structures of vascular plants under the three recognized morphological groupings and without essentially curtailing if not destroying the scheme. One may quote the structure of the pine cone as a concrete example. Bower, in 1884, suggested that the stems and leaves of vascular plants had had a common origin from branch systems. Pontonié, in 1912, published his "overtopping theory" according to which from primitive equal dichotomies there originated unequal dichotomous branching and leaves were differentiated as weak overtopped branches or branch systems of finite growth. The discovery of the Psilophyta and of many more kinds of fossil vascular plants increased the difficulties of clearly separating "stems" and "leaves" morphogenetically.

The various more or less isolated data and explanations regarding the morphological nature of plant organs were brought together and elaborated by Zimmermann[101] and developed into a "telome theory." This has been modified and enlarged from time to time and some of the extensions attached to it are complicated and highly hypothetical, if not fanciful. The basic principles, however, seem to be gaining ground and may be briefly summarized as follows. The vascular land plants originated from seaweeds with a dichotomously branched plant body. The undifferentiated uniform branchings were composed of segments (telomes) and of parts (mesomes) between the points of forking. Diverse functions allowed distinction between vegetative telomes (phylloids) and fertile telomes (sporangia). All vascular plants evolved their organs along a few main organogenetic trends more or less independently by overtopping, planation, fusion, recurvation, and reduction. Overtopping of a uniform group of telomes and mesomes leads to a differentiation into an axis and lateral organs. Planation alters the symmetry of an organ and is characteristic especially of leaves. Reproductive

organs were similarly transformed from uniform telomes or telome systems especially by aggregation and recurvation (unequal development of opposite sides) often shifting sporangia to the abaxial sides of leaves.

It is particularly important to note that the acceptance of the principles of the telome theory results in the by-passing of the problem as to whether floral parts (especially stamens and carpels) in the angiosperms are "modified leaves," "modified stems," or special organs *sui generis*. They are considered telomes in origin equivalent to stem branches and to leaves, but they have never in organogenesis been "leaves," or "stems," or even "special organs" beyond their function of reproduction. A good many problems concerning the morphological nature of organs in the reproductive parts of gymnosperms can also be simplified by avoiding a classification of parts into "stems" and "leaves." However, it must be noted that there are a number of variations of the telome theory, that in some directions it is highly hypothetical, that it is not accepted by all botanists, and that for many groups of vascular plants the distinction between "roots," "stems," and "leaves" remains essential for lucid descriptions and for morphological interpretations. It may be noted, in passing, that roots are relatively neglected in telomic and other morphogenetic theories.

In dealing with gymnosperms as one vista, or group of vistas, of botany, certain limitations are deliberately accepted. There is no need to give full historical details of the development of our knowledge concerning or descriptions of the phyla. Thanks to a number of well-known and readily accessible publications this has been adequately done. It is sufficient to refer to the works of Coulter and Chamberlain[24], Chamberlain[21, 22], and Florin[53] in support of this statement. A useful introductory outline is also given by McLean and Ivimey-Cook[77]. Here, an attempt is made to supplement these accounts by reference to recently-published researches. Apart from what are considered necessary introductions and references to earlier work consideration is given mainly to results that have appeared during the past two decades.

CYCADOFILICALES

The exciting discovery by F. W. Oliver, and its subsequent working out by Oliver and Scott, that *Lagenostoma lomaxii* was the seed of *Lyginopteris* (*Lyginodendron*) *oldhamia* (*Calymmatotheca hoeninghausii*) is too well-known to need any further reference here. One result of the discovery was the establishment of a new group of "seed-ferns" or "fern-cycads" and the recognition that many of the Carboniferous fossils that had previously been accepted as ferns were seed-bearing plants with naked ovules or seeds and thus formed an extinct gymnospermous group now known as Cycadofilicales or Pteridospermae. In the first three decades of this century a great deal

of palaeobotanical research dealt with the pteridosperms and much was learnt about the vegetative anatomy and the reproductive structures of a wide range of representatives of this phylum. Even since 1930, new genera have been described, such as *Tetrastichia*, *Schopfiastrum*, and *Microspermopteris*, as well as some Mesozoic genera mentioned below. There is still some uncertainty as to the most rational classification into orders and families and it is likely that any tentative scheme will require more or less drastic modification as new discoveries are made.

The pteridosperms were first described from fossils of Carboniferous age but later it was found that the phylum extended into the Mesozoic. Thus, Thomas[99] described three genera, *Umkomasia*, *Pilophorosperma*, and *Spermatocodon* from rocks, probably of Middle Triassic age, in Natal. The gymnospermous seeds are borne in cupules on the ends of branches forming an inflorescence and larger branches are borne in the axils of bracts, with bracteoles also present in some forms. The isolated seeds of this Mesozoic group can be distinguished by their curved bifid micropyles and were probably platyspermic. The three genera named above were grouped together as a new family, the Corystospermaceae. A new species of *Lepidopteris*, related to *L. ottonis* previously known from Greenland and other Triassic localities in Europe, was described and the family Peltaspermaceae instituted for the genus. Partly as a result of the study of these Triassic pteridosperms, Thomas suggested that gymnospermous seeds must be regarded as terminal structures formed at the ends of branches, and not as marginal structures borne on a typical foliar organ. He regards the frequent use of the term sporophyll as applied to seed plants as misleading and holds that the seed-bearing organs of all other gymnosperms can be considered as derived from structures somewhat similar to those of the Corystospermaceae and that traces of a cupule can be detected in all the major groups. This telomic theory is further elaborated by Thomas in more recent papers and is extended to the angiosperms, but to consider the details and implications involved would take us beyond the scope of this article.

Andrews[1] discusses some evolutionary trends in the pteridosperms. He notes that the most serious gap in our knowledge of the group is our ignorance of "what lies within the nucellus of the seeds." Many seeds have been found and described but without embryos and with only fragments of the gametophyte. One may, indeed, doubt if the use of the term "seed" be strictly correct, or if it be used the definition of a seed as "the fertilized and matured ovule of a phanerogamous plant" may require modification. Andrews accepts three groups of Mesozoic pteridosperms for which he accepts the names: Caytoniales (see later), Triassic corystosperms, and Peltaspermaceae. In connection with the remarks just made as to how little is known of the internal structure of the nucellus in pteridosperms, Long's

account[76A] of prothallus structure in *Lagenostoma ovoides* is important because he had well-preserved material showing more internal structure than is usual in pteridosperm seeds. Three archegonial egg-cells were present. They were ovoid in shape and possessed a distinct layer of jacket cells but no neck cells could be distinguished. A "tent-pole" prolongation of the prothallus was present.

Our knowledge of the medullosan pteridosperms has recently been summarized by Stewart and Delevoryas[95] with a bibliography. *Medullosa* and the stem genera *Sutcliffia* and *Colpoxylon* are assigned to the Medullosaceae and are characterized by several steles running axially through the stem and thus distinguishing the family from the Lyginopteridaceae and the Calamopityaceae the other two families of the Palaeozoic pteridosperms. Petioles (*Myeloxylon*), various leaf genera, probable male organs (*Dolerotheca*), and seeds, "Trigonocarpales," are often, with more or less sound evidence, referred to the Medullosae. New American material has recently been described and is referred to in the paper mentioned. Hoskins and Cross[65A] described a new species of *Pachytesta* and dealt with the nomenclature of *Trigonocarpus* and *Pachytesta*. Apparently these constitute one genus but the authors retain both names, the former for seeds determinable by superficial features only and the latter for seeds with structure preserved. Presumably this procedure has some convenience in palaeobotany but it appears to be peculiar to a botanist dealing with existing floras. Baxter[9A] described a new unique plant based on a stem with pteridosperm characters and named *Microspermopteris aphyllum*. It is claimed that because of its very small size and leafless condition it offers evidence for the origin of the seed-ferns from the Psilophytales. Three new species of *Medullosa* are recognized and evidence for a climbing or creeping habit for the group is given and the idea for a bilateral dorsiventral habit is presented.

CAYTONIALES

In 1921, H. Hamshaw Thomas[97] gave a preliminary account of some fossils from the Middle Jurassic of Yorkshire which he then supposed constituted two genera, *Caytonia* and *Gristhorpia*, and which he referred to as a new group of angiospermous fruits. The material was fully described by him in a paper published in 1925[98]. Since then further investigations, especially by Harris[61, 62, 63, 64, 65], and including new material, has not only greatly extended our knowledge of this peculiar group but has resulted in its general acceptance as gymnospermous and related to the pteridosperms. There are now linked together leaves (*Sagenopteris*), microsporophylls (*Caytonanthus*), and megasporophylls (*Caytonia*, in which genus *Gristhorpia* is included). The group extends in age at least from Upper Triassic to Upper Cretaceous, on the evidence especially of *Sagenopteris* leaves.

The leaves are compound with four leaflets terminal to a slender petiole. The microsporophyll consists of a rhachis of dorsiventral structure bearing opposite pinnae which are branched and whose end branches bear single sporangia with four pollen sacs. The megasporophyll has a strongly dorsiventral rhachis bearing lateral bodies (the fruits). An individual fruit has a short stalk expanding into a closed pouch. There is a conspicuous outgrowth just above the stalk that was formerly termed a stigma but is now designated "lip." The crack (mouth) between the lip and the stalk is the only discontinuity in the fruit wall. The discovery of pollen grains within fruits, at the base of the micropyle, shows that the mouth of the fruit was open at pollination time though closure became complete later. Several seeds occur in a fruit and seven to eight probably matured. It is to be noted that, so far as the published evidence shows, the "fruits" are immature and the "seeds" are pollinated ovules with no embryos demonstrated inside them.

A great deal has been written about the possible relationships of this interesting extinct group of plants. Thomas, while considering them angiospermous, from the first pointed out their resemblances to the pteridosperms. It is now generally held that they be either classed with the pteridosperms or as a group near to them and presumably derived from them. Their interest is enhanced by the recent speculations (or recently revived speculations) regarding the possible origin of angiosperms from pteridosperms.

BENNETTITALES

The work of Wieland in the first two decades of the 20th century resulted in this phylum being amongst the best known groups of extinct plants. That some of them have bisexual reproductive structures led to the theory that the angiosperms originated from a bennettitalean or bennettitalean-like group. We are not here concerned with the problems of angiosperm phylogeny and it must suffice to refer to a paper by Just[68] in which many of the hypotheses are discussed. We may, however, note that the structure of the female part of the bennettitalean "flowers" has always been a difficulty in accepting such an ancestry for existing angiosperms.

Amongst recent publications on the group, Florin[53] reports those of Kräusel on *Sturiella*, a new type of inflorescence made up of small bisexual flowers, and on *Westersheimia*, which is unique in having pinnately branched female inflorescences, the lateral parts of which form strobili with numerous seeds and interseminal scales. Sahni[87] investigated the Jurassic Pentoxyleae. *Pentoxylon sahnii* was a branched shrub, or possibly small tree, of xeromorphic habit with unisexual "flowers" borne at the ends of lateral dwarf shoots which in appearance resembled the stem of a miniature cycad, with an armour of persistent rhomboid leaf bases. The seed attachment is, in Sahni's interpretation, stachyospermous and the secondary wood is of coniferous type,

the stomatal structure is fundamentally bennettitalean, the vascular anatomy of the leaves is cycadean, and the general anatomy of the stem is unique. The Pentoxyleae form an isolated group, as at present known, with a combination of characters hitherto accepted as more or less diagnostic of several phyla, and can only be tentatively assigned to the Bennettitales.

A good deal of descriptive work has been published on the epidermal structure of different kinds of sterile leaves and on the anatomy of roots assigned to the Bennettitales or at least to the "cycadophytes." Harris[63A] in his revision of *Williamsoniella*, based largely on new material, had shown that the flower possessed a perianth, that the microsporophylls are pinnately branched, and that the pollen is contained in two-valved capsules. The seed is shown to have various internal cutinized membranes which are interpreted as indicating a free nucellus. It is concluded that *Williamsoniella* is nearer taxonomically to *Cycadeoidea* than had been realized.

CYCADALES

The existing members of this phylum are usually classified into nine genera grouped in the one family, Cycadaceae. The researches of many botanists have resulted in their being amongst the best known groups of plants. Earlier work on them is adequately summarized by Chamberlain[21] who had himself done more than any single worker to investigate the problems of their structure and life histories. Some additions to the account given by Chamberlain may be briefly mentioned.

Baird[4] records the occurrence of polyembryony in *Macrozamia reidlei*. It is suggested that *Macrozamia* is one of the more primitive cycads as shown by the high spore output per sporangium, the large number of nuclei in the free nuclear stages, the advanced condition of the female prothallus at the time of pollination, the undifferentiated proembryo, the immature state of the embryo when the seed is shed, and the comparatively small sperm. The affinities appear to be with *Encephalartos* and *Cycas*, and especially with the former, which it resembles in general habit and structure of cones and seeds. It is thus useful to have an account of *Macrozamia hopeites*, as an early Tertiary (Oligocene) cycad from Victoria, Australia, as given by Cookson[23] The material consisted of leaf fragments from which the lower and upper epidermis, including stomata, were described.

La Rue[72] experimented with gametophytes removed from the ovules of *Zamia floridana* and obtained growths that included sporophytic characters such as cork development, roots, buds, leaves, and bundles of tracheids. This study extended to the gymnosperms the principle that, in plants possessing an alternation of generations, one generation may be derived from the other by regeneration. Shapiro[90] has recorded the occurrence of stomata on the nucellus and integument of *Zamia floridana*. It is noted that the fossil

members of the Psilophytales, ancient ferns, and pteridosperms are not reported to have stomata on the sporangia and modern ferns also lack stomata as a sporangial character. *Beania*, often considered a fossil cycad, contains integumentary stomata, but no fossil has been described with nucellar stomata.

De Silva and Tambiah[91] describe in some detail the structure and life history of *Cycas rumphii*. Schaede[89] investigated the coralloid roots of various cycads and their symbiosis with blue-green algae. It was found that, in the species investigated, the coralloid roots, whether inhabited by Cyanophyceae or not, contain no bacteria and Schaede suggests that those observed by previous authors were probably introduced from the outside by an imperfect technique. The mucus in the intercellular spaces occupied by algae is a secretion of the host plant and is evidently of importance for the nutrition of the algae which are regarded as innocuous parasites of the cycads. The conditions for free nitrogen assimilation by Cyanophyceae are not present in the coralloid roots, so the host cannot profit in nitrogen by them. Since these results in part contradict the work of other authors it would be desirable to have the whole matter re-investigated. Chrysler[22B] explains certain anatomical features found in *Zamia* and *Stangeria* as persistence of juvenile features. Sax and Beal[88] record the haploid chromosome numbers of the nine genera of existing cycads as follows: *Cycas* 11, *Bowenia* 9, *Macrozamia* 9, *Stangeria* 8, *Encephalartos* 8, *Dioon* 9, *Microcycas* 13, *Ceratozmia* 8, and *Zamia* 8. Different genera may vary considerably in chromosome morphology but species within each genus have similar chromosomes.

Arnold[3] has discussed the origin and relationships of the cycads in a recent paper. The modern cycads are the remnant of a much larger vascular plant group that during the past ranged far beyond its present limits. Every genus probably evolved within or near its present general range and none arose from any of the others. *Cycas* has been considered the most primitive, because of the lack of definite ovulate strobili, but *Stangeria* bears the largest number of fern-like characters. The modern cycads are probably not closely related to the Bennettitales because of important differences in form of the stomatal apparatus and the inflorescences, regardless of resemblances in habit and internal structure. The Cycadales are believed to have evolved from pteridospermous ancestors during the latter part of the Carboniferous period, but the particular pteridosperm that served as the ancestor has not been identified. They were much better adapted to adverse conditions and survived the Permian better than did the pteridosperms and rapidly spread over the earth in the early Mesozoic.

NILSSONIALES

Separated by Johansen as an order distinct from, though placed next to, the Cycadales, the Nilssoniales are often referred to "the cycads." Harris[64A]

has given a useful summary of "*Nilssonia* and its reproductive organs." *Nilssonia* is known to occur in strata from the Rhaetic to the Cretaceous. Leaves, of various species, are known so far as concerns their form, anatomy of the lamina, and cuticle. The stem is not certainly known though a possible stem has been found in Yorkshire bearing scars suitable for the leaves. The male cones (*Androstrobus*) have been studied for their form, shape of the microsporophyll, and some details of sporangia and pollen. The female cone (*Beania*) is likewise known by the whole cone and the form and cuticles of the sporophyll and something of the external structure and internal anatomy of the seed has been deciphered. Harris suggests that the loose construction of *Beania* (even when immature) indicates a pendulous amentum-like organ, and this implies a fairly tall stem, perhaps of tree form. The reproductive organs agree closely with those of the *Zamia* group of Cycadales, except in the loose construction of *Beania*. It may well be that the Nilssoniales are better classified as a taxon within the Cycadales.

CORDAITALES

The group of plants classified as the Cordaitales is entirely extinct. Various estimates of their extension in time have been made, depending largely on acceptance or rejection of determinations of wood and leaves. No reproductive organs of the cordaitean type have apparently been found for certain outside Palaeozoic deposits and the claim that the Cordaitales survived into the Mesozoic era is a doubtful one. It is most probable that they died out in the Permian, perhaps owing to increasing aridity of the climate and to competition with other gymnospermous groups that were better adapted to the climatic changes. Our knowledge of them is mainly based on material from the Carboniferous and Lower Permian and especially on the earlier studies of Grand 'Eury, Renault, and Bertrand, and these have been well summarized in various palaeontological text-books.

It need only be recalled that the researches of the French palaeobotanists showed that the Cordaitales were trees with branched stems and simple leaves. The stems show pith (often large), a zone of wood (usually without but sometimes with growth rings), and a cortex which is frequently a wide belt. The leaves vary considerably in size and shape and were apparently leathery in texture, with xeromorphic structure and dichotomous venation. Needle-like leaves have been recorded for *Pitys*.

Some of the Cordaitales are reported to be monoecious and others dioecious but none is known to be bisporangiate. The male and female reproductive organs have been termed *Cordaianthus*. There has been some dispute as to the exact morphological interpretation of the parts of the reproductive organs. Florin[47, 48] has re-examined the material studied by Renault and has also investigated new specimens. He concluded that the male dwarf

shoots are not partial inflorescences but are microstrobili or flowers placed in two opposite rows axillary to bracts on the axis of an inflorescence. The male flower axis carries numerous spirally disposed scales, some of which are simple and sterile while others are dichotomized at the apex and terminated by a cluster of usually 4 to 6 erect microsporangia. The microsporophylls either occur along almost the whole secondary shoot or are confined to its apex and are primitive organs that appear to have developed, parallel with the foliage leaves, from morphologically little differentiated branches. The female organs, according to Florin's interpretation, have a morphological structure comparable with that of the male. They are inflorescences with a long main axis (up to 3 dm in length) carrying usually alternating bracts in two opposite rows. Bud-like bodies, the female flowers, arise in the axils of these bracts. Two main types of female inflorescences are recorded: an earlier more primitive type has elongated megasporophylls projecting from the apical region of the flower, and repeatedly forked carrying more than one ovule (or seed); a later reduced type with short unbranched and uniovulate megasporophylls concealed among the sterile scales of the flower axis. The bud-like fertile bodies on the main axis of the cordaitean female inflorescences are interpreted as simple strobili or flowers, that is, the fertile dwarf shoots are built up of an unbranched secondary axis and numerous spirally disposed and homologous scales. Most of these scales are sterile and simple or forked. The other scales on the flower axis are megasporophylls. The ovules and seeds are bilaterally symmetrical and atropous. In the older forms they correspond to the platyspermic *Samaropsis* type of broad-winged detached seeds of Palaeozoic deposits, while in the younger type they belong to the *Cordaicarpus* form with narrow wings.

As in the pteridosperms the "seeds" of the Cordaitales so far described in detail have no embryos. Darrah[26] has briefly recorded, under the heading "the embryo of *Cordaites*," small samaropsoid seeds several of which "contain well-preserved dicotyledonous embryos." He notes that "This is the first Palaeozoic embryo thus far recognized."

GINKGOALES

The only existing member of this phylum is the well-known maiden-hair tree, *Ginkgo biloba*. This is now cultivated in many parts of the world and occurs as a native in a restricted area in southern Anhwei and northern Chekiang, in eastern China. Its horticultural and botanical history has been given in some detail in an account by Hui-Lin Li[75]. Li notes that *Ginkgo* was unknown to ancient Chinese writers and that its records in literature cannot be traced back definitely for more than a thousand years. He corrects various statements made by Wilson and other writers. *Ginkgo* was first

introduced into Europe at the botanical garden at Utrecht and reached England about 1754. The majority of the cultivated trees are male.

Since it is unique amongst existing plants *Ginkgo* has received a great deal of attention from botanists and the main features of its structure and life-history are well summarized by Chamberlain[21]. Recent investigations include studies of the origin and development of the long and short shoots[59], the growing of embryos under experimental conditions[8], and the study of the karyology[84, 72A]. The chromosome number is stated to be $2n = 24$, with almost identical chromosome morphology in both ovulate and staminate trees. The only difference is that in the ovulate plant four chromosomes of the somatic complement bear satellites while in the staminate tree only three chromosomes show satellites. It is believed that the pair of short sub-telocentric chromosomes in the male plant, only one of which bears a satellite, are sex chromosomes. Thus, an XY-type of sex determination is assumed, since the heteromorphic pair of chromosomes in the male is the only karyological feature differing from the condition in the female. Details of fertilization and the cytology of pollen grains and ovules have also been described recently[72B]. The structure of the reproductive organs and the morphological interpretation of the various parts have been much discussed, especially for the female plant. Thus, the female organ of *Ginkgo* has been variously termed an axillary inflorescence, an axillary flower, a modified megasporophyll, a dichotomized placenta, the fertile lobe of a trophosporophyll, and an axillary sporangial truss bearing terminal ovules. The collar at the base of the ovule has been interpreted as two fused prophylls of a flower, as the vestige of an aril, as a megasporophyll, and as an outgrowth on the sporophyll, and the integument as the fused segments of a perianth, as two fused megasprophylls, as a single megasporophyll, or as the lamina or part of the lamina of a megasporophyll. Gaussen[56] regarded the "flower" as composed of a much reduced axis carrying one single or two-to-several fused uniovular petioles (carpellary leaves). It is interesting to note that *Ginkgo biloba* shows great variability in the female reproductive organs, as described by Emberger[39A] and Karsten[70] and the latter comments on so ancient a plant showing this. Seward[89A] gives an account of fossils referred to the Ginkgoales and more recently Florin[46] described the morphology of *Trichopitys heteromorpha* from Palaeozoic rocks in southern France. He concluded that *Trichopitys* was a primitive member of the Ginkgoales (Ginkgoinae). From his studies of the fossil he reached the conclusion that the *Ginkgo* female flower is a branched axis with one or two to several ovules but is without sporophylls, i.e. it is a wholly fertile, dichotomized sporangial truss (syntelome) bearing terminal ovules without relation to leaves. It thus corresponds to the axillary female flowers or seed-scale complexes of *Cordaites* and early conifers, but is not an inflorescence.

The fossil *Czekanowskia* was reconsidered by Harris[63B]. The name is applied to Mesozoic leaves which are abundant and widely spread in certain deposits. He describes *Leptostrobus cancer* from the Yorkshire Inferior Oolite (Middle Deltaic). Its fruiting appendages proved to be two-valved capsules, each valve having a row of small seeds, probably with inverted orientation and with apical archegonia. Evidence is given for attributing *Leptostrobus* to *Czekanowskia*. Harris states that on leaf characters *Czekanowskia* is either a member of the Ginkgoales or is a member of another order with leaves almost exactly like those of the Ginkgoales. On the other hand, *Leptostrobus* is remote from the female fructifications of the Ginkgoales. "For reasons of convenience no new family is at present instituted."

TAXALES

Until recently, though sometimes with expressions of doubt as to the best course to follow, the Taxales have been included in the Coniferales s.l. Florin[44] has shown clearly that the taxads stand apart from the true conifers. The position of the ovule is the most important character. In the taxads it is always a direct continuation of the flower axis, while in the conifers (and Cordaitales) it is essentially terminal on more or less stalk-like lateral appendages (macrosporophylls) of the flower axis, which were distinctly produced in the oldest known genera. Further, the conifers (and Cordaitales) have well-developed or more or less reduced cone-like (biaxial) inflorescences composed of female flowers placed in the axils of bracts. The taxads have uniaxial female flowers placed singly and axillary on vegetative shoots (sometimes greatly reduced) and bear erect ovules, every one enclosed in an aril arising as an outgrowth from the flower axis. The male flowers of taxads are particularly remarkable for the radially symmetrical, perisporangiate sporophylls found in certain genera and for the gradual change from this to a dorsiventral structure in others. The recently described genus *Nothotaxus*[45] is remarkable for the sterile scales between the microsporophylls, a supposedly primitive feature unknown amongst the true conifers.

Living taxads are classified into five genera: *Taxus*, *Torreya*, *Nothotaxus*, *Austrotaxus*, and *Amentotaxus* with a total of about nineteen species. Fossils have been described as belonging to *Taxus* and *Palaeotaxus*. The genus *Cephalotaxus* belongs to the conifers but occupies an isolated position among the recent representatives of the phylum. Sterling[93] has described the proembryos and early embryogeny in *Taxus cuspidata*.

CONIFERALES

According to Buchholz[19] the existing Coniferales (s.l. including the Taxales) have fifty genera and about 550 species, thirty of the genera being confined to the Northern and fourteen to the Southern Hemisphere.

Buchholz, and also Li[74], have summarized the present ranges of the conifers and have emphasized the clear differentiation into a northern and a southern group. This separation, according to Li, has been shown by palaeobotanical records to have existed since the Palaeozoic. Nearly all of the considerable number of monotypic and oligotypic genera, most of which show restricted or disjunct ranges, thrive best in a damp mesophytic habitat and are now practically all confined to lands bordering the Pacific Ocean. This is considered by some botanists to support a theory of continental drift, particularly that of Du Toit who believed in two ancient land masses, Gondwana in the south and Laurasia in the north, separated by the Tethys Sea.

Earlier work on the cytology of the conifers, as by Flory[55], has been extended by Methra and Khoshoo[80] who include data from fifty-one species of fourteen genera of the Abietaceae, Taxodiaceae, and Cupressaceae. Families and genera they find are essentially homoploid and a basic karyotype is characteristic of almost every genus. Species within a genus either differ in the number and nature of secondary constrictions and satellites (*Pinus* and *Cupressus*) or resemble one another even in these details (*Callitris*). The mechanisms of evolution have been gain or loss of a chromosome, structural rearrangements, and gene mutations. Polyploidy has played but a small part. Chromosome numbers (n) have been found in Abietaceae: 12, 13, 22, 24; Taxodiaceae: 10, 11, 33; Cupressaceae: 11, 22; Araucariaceae: 13. The general uniformity within a genus does not hold for *Podocarpus* where values for n of 11, 12, and 19 have been found.

A great deal of research on fossil conifers has been carried out by Florin[46A, 48] and only a few recent papers need be mentioned here. The female cone of the Rhaetic *Cycadocarpidium* and foliage of *Podozamites* pertaining to it are considered true conifers[50, 52]. The cone scale is not a compound carpellary leaf carrying ovuliferous pinnae at its base, but is composed of a bract with an axillary fertile shoot or seed-scale complex. The "ovuliferous scale" was not formed by fusion of ovuliferous folioles, but corresponds to the sterile portion of the seed-scale complex. A species named *Pityostrobus jacksonii* from the Lower Greensand of the Isle of Wight has the general characters of the modern genus *Pinus*. The seed-scale complexes possess much inflated apophyses and definite bract scales are also present[25]. Three new species of coniferous woods from Cretaceous deposits in the Canadian Arctic have been referred[7] to species of *Cedroxylon* and *Piceoxylon*. Fossils attributed to the Araucariaceae are known from early Mesozoic times onwards but only become really common in Middle Jurassic strata. Kendall[71] has described araucarian remains from the mid-Jurassic Estuarine Series of North Yorkshire. Shoots and cone-scales and male cones were examined. Endô[40] records a *Sequoia* branchlet from Jurassic deposits in Manchuria.

The separation of the Voltziales from the Coniferales, as proposed by Johansen, may be justified but the full diagnosis and contents of the group require further investigation and taxonomic consideration. Florin[48] and others retain the Triassic *Voltzia* and other genera, such as *Pseudovoltzia, Ullmannia, Glyptolepis, Schizolepis, Cheirolepis*, etc., under the general heading of "conifers" or "fossil conifers." Florin[48] has given a very clear series of diagrams of the female flowers of these and other Permian and Mesozoic gymnosperms, with references to literature. Zimmermann[101] (pp. 289–92) also deals with the macrosporangia of the Voltziales.

The interesting researches by Doyle and his colleagues on pollination mechanisms in existing conifers [29, 31, 33, 34, 35] have permitted a consideration of developmental lines in the Coniferales from this point of view. In the basic type as shown by the Upper Carboniferous and Lower Permian genera such as *Lebachia* and *Ernestiodendron* an erect ovule receives, in a fluid exudate from a simple micropyle, a pollen grain entirely covered by a large air-sac except for a small distal area. In the Upper Permian there developed, as in *Ullmannia* and *Walchia*, inverted ovules associated with grains of a modern type. This type is basal in the Pinaceae, Podocarpaceae, and Araucariaceae. The air-spaces are flotation devices which float the grains up through the pollination fluid in the micropylar canal of an inverted ovule, and tend to orientate them with the germinal furrow in contact with the nucellus. From this, two lines appear in the Pinaceae, both ultimately showing loss of the exudate, stigmatic development of the micropylar area, suppression of air-sacs from the grains, and pollen germination elsewhere that on the nucellus. In *Pinus, Picea, Larix*, and *Pseudotsuga* the ovular exudate is ultimately replaced by an increasing dominance of the stigmatic tendency. In *Abies, Cedrus, Tsuga*, and (?) *Pseudolarix* the exudate is early suppressed and the stigmatic function of the micropyle, never very marked, is ultimately replaced in *Tsuga* by pollen reception on the cone scales, over which long tubes grow from the wingless grains. *Podocarpus* has a simple micropyle with no stigmatic tendency. In *Saxegothaea* scale reception and the germination thereon of wingless pollen has been achieved as in *Tsuga*. The Araucariaceae show scale reception and germination thereon of wingless grains. Cupressaceae and Taxodiaceae (and Taxaceae) show the simple pollination-drop type with wingless grains.

The Araucariaceae (*Araucaria* and *Agathis*) have long attracted the attention of botanists and have been involved in various phylogenetic and morphogenetic hypotheses. An investigation of the ovule and "seed" of *Araucaria bidwillii* by Wilde and Eames[100] led to a reaffirmation of the axillary nature of the fertile scale in the female reproductive structure in araucarians and to a new classification of the species of *Araucaria*. Gaussen[57] analysed the various characters of *Araucaria*, cotyledons, germination, leaves,

tracheids, and male and female reproductive parts, and concluded that the total of characters of the sporophyte of the genus "surevolved" in the parts situated far removed from sexual influences. The idea of "surevolution" appears to be that evolution leads to a simpler but specialized structure on which are then superimposed diversifications which more or less resemble the primitive type. This surevolved type may then become the relatively primitive type of a new cycle of evolution. In *Araucaria*, parts situated near the sex organs are subjected to retarding action which are more marked under female influence. Licitis-Lindbergs[76] has dealt with branch abscission and disintegration of the female cones of *Agathis australis*.

A considerable amount of work has been done on the Podocarpaceae in recent years. Hair and Beuzenberg[60] have given a preliminary account of chromosomal evolution in the family. *Podocarpus* and *Dacrydium*, in particular, form an exception to "the correlation between the stability of chromosome numbers and the length of the reproductive cycle, reaching an extreme in the unvarying basic number of most families of slow-growing, long-lived trees composing the gymnosperms." This statement is itself open to criticism additional to that of Hair and Beuzenberg. The $2n$ chromosome numbers found are, in *Podocarpus*: 38, 36, 34, 26, 20, 24, 22, 37, 35, 33; in *Microcachrys*: 30; in *Dacrydium*: 30, 24, 22, 18, 20; in *Acmopyle*: 20; in *Pherosphaera*: 26; in *Saxegothaea*: 24, and in *Phyllocladus*: 18. There is a regular numerical relationship between two classes of chromosomes, V's and I's, such that with each successive change in basic number a V replaces or is replaced by two I's. The evidence suggests that a progressive reduction in basic number has been a major factor in chromosomal evolution in the Podocarpaceae and if so that the process began at a higher level, $n = 20$ I, giving a continuous progress towards an economy of centromeres and stability of chromosomes. Doyle and Looby[36] studied the embryogeny of *Saxegothaea* and showed its relationship to other podocarps. Simple embryogeny seems primitive in the podocarps and from it two distinct types of polyembryony have arisen. Polyembryony is probably derivative in the other conifers also. Buchholz[18] gave details of embryogeny in several species of *Podocarpus* and in *Phyllocladus* and showed that in the former genus there are several more or less distinct types of embryogeny. Brownlie[16] claims that in New Zealand species of *Podocarpus* embryogeny seems to be the simplest in the genus. Boyle and Doyle[12] still further extended our knowledge of gemetophytes, fertilization, and embryogeny in podocarps. The great range of variation in developmental features shown in the family can apparently be accounted for by the operation of about a dozen evolutionary developmental tendencies, some effective in one line, some in another. The microstructure of the wood has been examined in seventy-four species of *Podocarpus* by Kaeiser[69] who shows that there are features which, on

the characters of the xylem parenchyma, pits, and rays, separate most of the sections.

The Cupressaceae is, in several modern classifications, a family with a rather large number of genera. Li[73] has given us a reclassification of *Libocedrus* and of the family as a whole. Boutelje[11] has described the wood anatomy of *Libocedrus* and *Fitzroya* and Florin and Boutelje[54] the external morphology and epidermal structure of the leaves of *Libocedrus*. Kaeiser[68A] studied the microstructure of the wood of species of *Juniperus* and obtained data supporting the separation of the genus into at least two groups. Bannan[6] described the microscopic wood structure of North American species of *Chamaecyparis* and showed that while there are slight differences in mean values between homologous wood samples of the three species, intraspecific variability is usually so extensive that the specific ranges overlap widely. The life-history of *Callitris* has been worked out by Baird[5] and it is concluded that *Callitris* is a natural genus of closely related species, in which *C. robusta* is probably primitive and *C. roei* and *C. macleayana* are relatively advanced. Wóycicki[100A] on the basis of series of experiments reaches the conclusion that the so-called "juvenile forms" (*Retinospora*) of *Thuja*, *Biota*, and *Chamaecyparis*, often cultivated in gardens and propagated by cuttings arose as "sports" and are not, as stated by Beissner and other authors, permanently juvenile forms obtained by cuttings of seedlings of normal plants. *Fitzroya* and *Diselma* have been investigated by Doyle and his associates[28, 32, 37]. *Fitzroya* is, in general, in features of its life-history intermediate between cupressinean and callitrinean life-histories. *Diselma* is characterized by a central columella in the cone.

In the Taxodiaceae, the morphology and embryogeny of *Sequoia gigantea* (now often placed in the genus *Sequoiadendron*) was worked out by Buchholz[17] who found that it resembled that of *Sciadopitys* more nearly than that of any other conifer so far investigated and differed in many important features from the embryogeny of *Sequoia sempervirens*. The "living fossil," *Metasequoia glyptostroboides*, has attracted a great deal of attention in recent years. It grows to a tall tree and is restricted in natural range to a small area on the border of the Chinese provinces of Szechuan and Hupeh. The genus was first described by Miki (in *Jap. J. Bot.*, 1941, 11, 237–303) from fossils and the existing tree by Hu and Cheng (in *Bull. Fan. Mem. Inst. Biol.* N.S. 1, 1948, 153–61). It is remarkable in having a decussate arrangement of foliage leaves and cataphylls, male strobili, and cone scales, thus differing from all other known members of the Taxodiaceae and recalling the Cupressaceae. An interesting account of living and fossil *Metasequoia* has been published by Florin[49]. It is to be expected that more detailed research will be done on *Metasequoia glyptostroboides* as the many trees now in cultivation in Europe and America attain maturity. The gametophytes and embryogeny of

Athrotaxis have been very fully investigated by Brennan and Doyle[13] and the results support the view that the genus has developed in the south independently of the northern members of the family since early times.

Larix leptolepis of the Pinaceae was studied by Doyle[27] as regards its reproductive system. There is a distinct natural affinity between *Larix* and *Pseudotsuga*. Sterling[94] cultivated larch embryos in synthetic media and showed that by artificial treatment cleavage of the first embryonal tubes could be induced. He suggested that since the intrinsic behaviour of the embryo can be altered by environmental conditions it may perhaps not be assigned the definite phylogenetic significance proposed by Buchholz. An interesting flat-leaved pine, from Annam, Indo-China, has been described by Buchholz[20]. Hybrids between *Pinus contorta* and *P. banksiana* showed[81] that in F_1 the bicyclic terpenes in the turpentine of the latter dominate over the simpler monocyclic terpene of the former. The time scale of morphogenesis at the stem apex of *Pinus resinosa* was investigated by Duff and Nolan[38] and seasonal changes in metabolism in the leaves of species of spruce (*Picea*) were worked out by Neish[83].

GNETALES

The three genera, *Gnetum*, *Ephedra*, and *Welwitschia*, are often nowadays placed in three separate families and some authors even raise them to generically monotypic orders or even phyla. Most usually, and probably with our present knowledge most satisfactorily, they are kept in one order, the Gnetales or Chlamydospermae. The structure of the vegetative and reproductive parts has been much studied and the earlier work was well summarized by Pearson[85]. Only some of the more recent investigations and conclusions will, therefore, be considered here. The diversity of opinions expressed as to morphological interpretation of reproductive parts, relationships of the three genera among themselves, their past histories, and their possible connections with the angiosperms, is very great.

Johnson[67] studied the growth and development of the shoot of *Gnetum gnemon*. The superficial layer has attained the status of a true tunica. It is discrete at the summit but contributes to the inner tissues of the foliar buttress and rarely may show periclinal divisions on the flanks. In the possession of a distinct tunica and corpus, *Gnetum*, it is concluded, has attained angiospermous level but a gymnospermous trend is reflected in the organization of the central mother cell zone recalling the condition seen in cyads and *Ginkgo*.

Fagerlind[40A] investigated the structure and development of the gametophyte in several species of *Gnetum*. The wall layer of the pollen chamber recalls the situation found in angiosperms in its mode of formation. A pollen chamber is barely recognizable. The cells of the inner integument

"stretch" to create the prolonged neck. In *Gnetum gnemon* the 2*n* chromosome number is 22. Two types of megasporophytes may be recognized with reference to "flask-necks": a short, broad type in *G. gnemon* and long, slender type in *G. latifolium*. In a consideration of the phylogeny of the angiosperms from a gymnospermous prototype, the long slender flask-neck, together with a large number of nuclei at the free nuclear stage, renders such species as *G. latifolium* possible candidates for the role of transitional forms standing between the "typical gymnosperm" and such species as *G. gnemon* which are more like an angiosperm in these characters than are other species of *Gnetum*. In another paper Fagerlind[41] considered the strobilus and flower of *Gnetum* and the possibility of the light his conclusions throw on the make-up of the angiosperm flower. He regarded the strobilus as an axis with whorls of bracts in whose axils are swellings on which the male and female flowers are formed. The axis of the female flower produces three integument-like appendages and its apex develops a typical nucellus. The male flower has an integument-like envelope and a stamen that is often dichotomously branched. The strobilus and the male and female flowers are regarded as homologous, differing only in the different development of their axes and axile appendages. Thus the *Gnetum* nucellus is a shoot apex with suspended growth activities and the envelopes of the male and female flowers are homologous with leaf whorls. This explanation is reconciled with the telome theory by regarding the stem as a columnar syntelome composed of radial, parallel telomes or telome sympodia. Negi and Lata[82] describe the male gametophyte and megasporogenesis in *Gnetum ula* and *G. gnemon*. The 3-nucleate pollen-grains consists of a single prothallial cell, a tube nucleus, and a generative cell. The last divides in the pollen tube to give rise to two equal male cells. The female gametophyte is of the tetrasporic type. Bharadwaja[10] has given a taxonomic account of *Gnetum* in India, Pakistan, and Burma.

Mehra[78] records the occurrence of hermaphrodite flowers in *Ephedra intermedia* and describes the development of the female gametophyte of the same species. The hermaphrodite flowers are built on the same plan as the pseudohermaphrodite male flowers of *Welwitschia*. Some plants are strictly male or strictly female, while others bear male, female, and bisexual cones. Since *E. intermedia* is tetraploid it is suggested that "sex" may be governed in the individual by the ratio between X chromosomes and autosomes. In another paper Mehra[79] notes that the two male nuclei are of the same size in *E. foliata* and *E. sinica*, equal or unequal in *E. likiagensis*, and markedly unequal in *E. altissima*, *E. intermedia*, and *E. saxatilis*, particularly in the last. Cutler[25A] monographed the North American species of *Ephedra* and gave many structural and anatomical details.

Rodin[86] has investigated the anatomy of both the young and mature

leaves of *Welwitschia*. The absence of definite and reliable fossils of the Gnetales that are of use in tracing their phylogeny is one cause of the isolation of the group generally accepted in modern schemes of classification. The discovery of pollen grains of *Ephedra* in Quaternary deposits is of interest in showing that the genus formerly ranged in areas where it is now absent. The reported discovery by Chiguryayeva[22A] of a pollen grain of *Welwitschia* in Tertiary beds in Western Kazakhstan needs confirmation.

Florin[43] gives the chromosome number of *Welwitschia* as $n = 21$ and of four species of Ephedra as $n = 7$. Tschigouriaeva[96] says that the pollen of *Gnetum* is spherical with spines, while that of *Ephedra* and *Welwitschia* has furrows on the sides thanks to which the grain can change its form and dimensions without lacerating the envelope. Fagerlind[42] deals with the apical embryo-meristem and shoot-meristem in *Gnetum*, *Ephedra*, and other gymnosperms and concludes that the tendency to transform the original meristem type into a tunica-corpus differentiated one is pronounced only in *Gnetum*, *Ephedra*, and a few other genera.

Eames[39] considers the relationships of the Ephedrales and to some extent of the Gnetales s.l. The group as a whole is gymnosperm-like in that the ovules are naked and borne in cones, and angiosperm-like in that the ovules and microsporangia are borne on somewhat flower-like fertile shoots and their xylem possesses vessels. That Ephedraceae stand much farther from Welwitschiaceae and Gnetaceae than the last two families do from one another is suggested by recent studies. The stomatal apparatus of *Ephedra* belongs to a primitive basic type different from that of *Welwitschia* and *Gnetum*, and characters of the cones, nodal anatomy, primary structure of the stem, and wood structure point in the same direction. In *Ephedra*, the two kinds of fertile shoots are homologous, the ovule is terminal on a lateral appendage of the fertile shoot, as are the microsporangia, and not cauline (terminal on the shoot apex) as it has usually been considered to be and as it apparently is in *Gnetum* and *Welwitschia*. It is urged that terms like inflorescence, flower, perianth, stamen, anther, etc., used for angiosperms should not be used for the Gnetales s.l. There are reasons for considering close resemblance to the Cordaitales, where the ovule has recently been stated to be appendicular.

GYMNOSPERMAE, CONCLUDING REMARKS

A number of recently-published papers dealing with aspects of structure and life histories of gymnospermous phyla remain to be briefly mentioned. Camefort[20A] studied the structure of the vegetative growing point in a number of gymnosperms. He accepted the "initial ring "interpretation of L. Plantefol and, applying it to the gymnosperms examined, showed the importance of the absence of a tunica in this group of phyla as compared with

its presence in the angiosperms. A fine work by Gregus[58] of 236 pages with 350 plates, with the title *Identification of Living Gymnosperms on the Basis of Xylotomy* has recently been published in Budapest. A general conclusion is reached that, on the basis mainly of wood anatomy, the existing families (phyla, etc.) of gymnosperms can be divided into three fairly well circumscribed evolutionary series, showing correlations with the three types of the Pteridophyta: 1. *Cycas*, *Ginkgo*, Araucariaceae, Podocarpales, and probably Taxales with the Pteropsida; 2. Cupressaceae with the Sphenopsida; 3. Taxodiaceae and Pinaceae with the Lycopsida. Thus it is probable that the gymnosperms are, like the Pteridophyta, not of monophyletic but at least of triphyletic origin. A consideration of compression wood, particularly in conifers, is given by Spur and Hyvärinen[92]. The vexed question of the morphology of the female reproductive organs, especially in conifers and taxads, has been dealt with in detail by Florin[51]. After prolonged study of fossil forms, especially of Cordaitales and Coniferales, he explained that the primitive fertile seed-complex in the axil of each bract was a radially symmetrical short shoot (strobilus) with several sterile scales and one to a few univoluate megasporophylls, the ovules being terminal in position. Later types of cones have arisen by the reduction and transformation of this primitive organization. Most often there was a differentiation of the strobilus into a proximal fertile part facing the cone axis and a distal sterile part (ovuliferous scale), while its anterior sector facing the bract became totally suppressed. Exceptionally, no "ovuliferous scale" at all was developed and the strobilus became wholly fertile. The ovular integument is a continuation of the megasporophyll, and appears to arise out of two transversal primordia at its apex. The taxads differ from the true conifers by their simple strobili being placed axillary on reduced vegetative shoots. Their ovules are seated terminally on the strobillar axis itself; megasporophylls are accordingly absent.

Arnold[2] considered the classification of the gymnosperms from the viewpoint of palaeobotany. The conclusion is reached that the Cycadophyta and Coniferophyta (Cycadales and Coniferales) are separate developmental lines that are distinct from each other as far into the past as they can be traced. In the classification Arnold proposed the Gymnospermae are not considered a taxon and the term is dropped.

The relationship of angiosperms to the presumably older gymnosperms has been much considered. On this subject papers by Just[68] and Battaglia[9] may be consulted.

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PLANT PHYSIOLOGY

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PLANT physiology is the study of the life processes of plants. It tries to analyse and explain the processes of growth, development, chemical change inside the cell and organism, and the responses of the plant to its environment. Since we are dealing with living plants, one would assume that there must be a very close connection between botanical gardens and plant physiologists, since both are concerned primarily with living and growing plants.

There are several reasons why this is not so. One reason lies in the development of the early, sixteenth-century, botanical garden, which was used entirely for teaching and as a repository of the known plants, to a display garden with largely horticultural interest. The botanical garden did not follow the development of botany during the eighteenth, and especially the nineteenth century, into an experimental science. Another reason is that most of the early work in plant physiology was carried out by non-academic people, who had only their private gardens or estates at their disposal. Thus Stephen Hales, Duhamel du Monceau, Ingenhousz, Senebier, de Saussure, Knight, Dutrochet, and Darwin did all their experimental work at home or at their country places, and it was not until the second half of the nineteenth century that important physiological work was carried out at universities or in university botanical gardens. Even then it was usually the poorest greenhouses which were made available for the experiments of the plant physiologist. It is no wonder, therefore, that at present we see everywhere experimental greenhouses and experimental gardens spring up, but not in our traditional botanical gardens. It will take much time and convincing, before plant physiologists will become an important part of every botanical garden, experimenting with the priceless materials present in those gardens, and supplying much useful information to the grower of plants. The new knowledge about plant nutrition, plant hormones, plant responses to their environment, all is of great importance for the growing of plants and for the horticulturists in our botanical gardens. Let us see the extent of this knowledge, and how it affects plant growers. Let us first see where we stand with our chemical knowledge of plants, and what we know about the chemical reactions which are going on inside the plant.

In the middle of last century protoplasm, one of the major constituents of the cell, became recognized as such and shortly thereafter a special constituent of protoplasm occurring in each cell, the nucleus, was found. The

evidence the geneticists gathered made it soon clear, that whereas the various life processes had their seat mainly in the protoplasm, the hereditary potentialities of the cell were localized in the nucleus. The material which carries the hereditary characters, the chromosomes, can be stained with special dyes, and this material has now been identified with deoxyribonucleic acid, a very complex chemical of high molecular weight, in which phosphorus, a five-carbon sugar (deoxyribose), and four different purine bases: thymidine, adenine, guanidine and cytosine, are all linked together into a long chain, which is coiled up into a spring-like structure.

The protoplasm is a complex mixture of a number of substances, of which proteins are the main component. Proteins are also long chain-molecules, with molecular weights much over 10,000, but these chains are built up out of a series of amino acids, which are tied together by peptide linkages. About 14 amino acids make up all proteins, and all of them are characterized by the molecular grouping —NH—CHR—COOH, with R standing for a benzene or indole nucleus, an aliphatic chain or a sulphur-carrying group. Other important constituents of protoplasm are lipoids—fat-like substances such as lecithin and cholesterol—carbohydrates such as sugars, and a whole host of other substances.

The pigments which occur in so many plant cells either occur dissolved in the cell sap—these are mostly anthocyanins, giving the red and blue colours of flowers and the purple colour of foliage—or in special bodies inside the protoplasm, the so-called plastids. The chloroplasts are the most important among the latter, and they carry all chlorophyll and most carotenoids, the yellow and orange water-insoluble plant pigments. When a beet is cooked, the red anthocyanim diffuses out of the killed cells into the surrounding water, but the water-insoluble carotene of carrots and tomatoes does not come out into the water in which these are boiled. When they are stewed with some fat, this fat will absorb the carotene, and the fat droplets which are floating on the stew may become bright orange by absorbing carotene in them.

The green plant pigment, chlorophyll, was almost 200 years ago recognized as being necessary for the process of photosynthesis, and 80 years ago Engelmann gave rigid proof that in the higher plants, only the light absorbed by chlorophyll is active in CO_2 reduction. In recent years this picture has changed somewhat by the recognition that light absorbed by carotenoids can also contribute towards photosynthesis, but usually to a minor extent only. An important advance in our knowledge about photosynthesis is that more has become known about the structure of the chloroplast, the body which contains the chlorophyll. This chlorophyll is not evenly distributed throughout the chloroplast, which usually is several μ in diameter, but it is localized in grana. The electron microscope has shown that the

chlorophyll is present in layers (in lamellae), and that the grana are places where these lamellae are massed.

Our knowledge about the chemistry of the process of photosynthesis has increased enormously during the last years, particularly since the chain of reactions through which the reduction of CO_2 passes into carbohydrates could be followed by radio-active tracer techniques. When radio-active C^{14} is offered to a plant in the form of $C^{14}O_2$, then a small amount of it is absorbed in darkness, and becomes incorporated in the bicarboxylic acids of the Krebs-cycle. But the moment such a plant is exposed to strong light, actually within only a few seconds, radioactive phospho-sugars, especially phosphotrioses, are formed, and a few seconds later the first sucrose with C^{14} can be found. Within a fraction of a minute many other chemicals inside the cell, notably amino acids, have incorporated C^{14} in them, but the first stable chemical formed as a result of photosynthesis is sucrose.

The pathway of CO_2 reduction is only one aspect of photosynthesis. For we now know that the light energy, absorbed by the chlorophyll, is not directly transferred to the CO_2 molecule, but that this energy is used for the hydrolysis of water (splitting H_2O into H and OH). Details about the processes involved in this water hydrolysis are still very much in debate, but it is now agreed that both high-energy phosphates, such as adenosine triphosphate, and molecular oxygen are formed as products of this hydrolysis of water. This means that the oxygen liberated by a photosynthesizing cell is not derived from the reduced CO_2 molecule, according to the formulation

$$CO_2 + H_2O + \text{light energy} \rightarrow (CH_2O) + O_2$$

but that this should be:

$$CO_2 + 2H_2A + \text{light energy} \rightarrow (CH_2O) + A_2 + H_2O$$

in which in the case of the higher plants and the green algae H_2A stands for H_2O, and in the case of the photosynthetic sulphur bacteria H_2A stands for H_2S; in the latter organism no oxygen but sulphur is liberated during photosynthesis.

We can expect in the next few years further important advances in our knowledge about the chemistry of photosynthesis, about the relationships between the CO_2 reduction and photolysis of water, of the path of light energy from the moment that this is absorbed by chlorophyll until it is transformed into chemical energy, but at present these subjects are still too much in a state of flux, with important new discoveries made every year, tending to change the details of the picture considerably, to present them in a general review. There is just one fact which should be mentioned. Even under the most favourable conditions one could not expect to have *all* light energy transformed into chemical energy during photosynthesis. But most

investigators now agree that approximately 30 per cent of the light energy can be transformed into the chemical energy of the sugars produced. Since light comes in definite small packages of energy, so-called quanta, we can express the efficiency of light utilization in terms of quanta. For the reduction of one CO_2 molecule a minimum of 8 light quanta are required.

The light energy which is captured in a few bold chemical steps, and stored in the form of carbohydrates, is used by the plant for all its further growth and metabolism. This means that thousands of different chemical reactions and syntheses have to be powered by the energy contained in the sugars. It is as if the big silver guineas of sugar energy now have to be changed into shillings and even pence for the powering of protein synthesis (where each peptide bond needs *some* energy), of growth, of the hundreds of metabolic steps taking place every minute in the living cell, and where each sugar molecule must aid in driving many different steps. This apportioning of the sugar energy is taking place in the glycolytic cycle, where the sugar molecule is gradually broken down to CO_2 and H_2O in a large number of steps, each yielding a small amount of the energy originally present in this sugar molecule.

It is most remarkable that essentially the glycolytic cycle is the same in microorganisms, in plants, and in animals, and much of the knowledge about sugar breakdown inside the plant is derived from work with animals (e.g. the Krebs-cycle) and with yeasts (glycolysis). This is not the place to discuss in detail what is happening with a sugar molecule on its way to oxidation to CO_2 and H_2O. A sucrose (or glucose) molecule is perfectly stable inside the cell, in spite of its very high chemical energy content. But the moment these molecules become phosphorylated (combine with phosphate under the influence of enzymes), they become chemically labile. Thus phosphorylated sucrose breaks down into glucose and fructose, fructose-diphosphate splits into 2 phospho-triose molecules, these change further to phospho-pyruvic acid, at each change giving up a small portion of the chemical energy originally present in the sucrose. The pyruvic acid in turn is taken up in the Krebs cycle, where in a series of chemical transformations, all steered by enzymes, alternatingly CO_2 and electrons are given off.

There are alternative pathways for the oxidation of sugars in plants, all discovered originally in animals or micro-organisms. The first steps are again glycolysis, but then the electron transfer mechanisms are located in flavo-proteins or in cytochromes and cytochrome oxidases. Again we do not have enough space to outline these processes in detail, but each partial step in the oxidation of the sugar results in the transfer of the energy lost by the sugar to an enzyme or some chemical like adenosine triphosphate. This energy is then available for other chemical reactions or syntheses.

Most of the sugar breakdown in the cell occurs in special organs, the

mitochondria, small bodies of about 1 μ in diameter, which contain the enzymes just discussed. The rest of the cytoplasm contains also enzymes, but these are mainly involved in hydrolysis and other chemical reactions.

Much has been learned about carbohydrate, fat, and protein metabolism in the plant; this all takes place in the individual cells, and most living cells are involved in these reactions. Other chemical processes are limited to certain organs and tissues. For instance synthesis of nicotine in the tobacco plant is located in the roots; tobacco grafted on tomato roots does not contain nicotine, whereas a tomato grafted on tobacco roots will have nicotine in its cells.

Much work has been done to elucidate the synthesis of rubber in plant cells. Whereas in plants like *Parthenium argentatum* the rubber is formed in parenchyma cells, in *Hevea brasiliensis* rubber formation occurs *only* in latex vessels. The physiological role of many of these specialized chemical plant products, like alkaloids and rubber, has not been elucidated as yet, and we also have to find out much more about their synthesis. But in the future, with the enormous advances in chemistry and biochemistry, we can expect much new and important information about plant metabolism.

Plant growth has been investigated among many different lines. The phenomenon itself has been studied, and it has been found that in most plant organs it is a combination of cell division and cell enlargement, the former process predominating in young embryonic organs, cell enlargement occurring mostly during the later stages of growth. The latter process is mainly one of cell wall extension and water uptake, and after much confusion it seems that plant physiologists are once more agreeing upon cell wall extension as the primary process guiding cell elongation.

Most cell walls consist of an isotropic base material, pectin, in which cellulose fibrils are imbedded. These fibrils join into, mostly, submicroscopic micellae, which produce the amazing mechanical strength of the cell wall. Once layers of micellae have been laid down lengthwise in the secondary cell wall, such a cell is unable to elongate any more. But in the young growing cell most cellulose fibrils are laid down more or less perpendicularly to the direction of elongation of the cell. This prevents them from increasing in girth, but allows elongation.

Cell division is partly an autonomous process, controlled by the nucleus, and independent of the activities of neighbouring cells or tissues, and partly it is activated or controlled by hormones. Thus far it has been impossible to control cell divisions in the growing point of a stem or root; whatever the treatment of this growing point, its cells will give rise to a stem or a root, if they develop at all. But in other cases we can induce mature cells to divide, either by mechanical or by chemical means. Cutting a potato tuber will cause the cells near the cut surface to divide and to form a cork layer,

wounding of the parenchyma lining of a string-bean pod causes the formation of a wart, which is due to the liberation in the wounded cells of traumatic acid. Without wounding, the same wart can be produced by application of this acid. Whereas the development of a growing point into embryonic stem and leaf tissue can hardly be influenced by internal or external stimuli, the enlargement of the stems and leaves to their final size by cell elongation is under the control of both internal factors and the environment.

The seed is an embryonic plant. Temperature and light strongly influence its germination after it has taken up enough water to make growth possible. Germination is the initiation of growth; applying water alone is usually not enough to enable growth.

Much work has been carried out on the germination of seeds. The seeds of most crop plants, such as grains and vegetables, germinate immediately when they are put in the ground, or placed on moist filter paper. This is not generally true for other plants; it almost seems the rule that seeds from wild plants germinate only after considerable delay, or after specialized treatments. This is understandable, for very often seeds are the means by which plants survive unfavourable weather conditions. Many seeds ripen in autumn, and do not germinate until the following spring when the growing conditions for the seedlings are favourable. All annual plants pass at least half of each year, the cold winter or the dry summer, in the form of seeds, and they have the most diverse mechanisms to control their germination at the proper time. These mechanisms have their seat either in the seed-coat or in the embryo, or in the endosperm. In many seeds the seed-coat is very hard and cannot be penetrated by the embryo as it swells through water uptake. In such cases germination can be produced by filing off part of the seed coat, or in general by "scarification." In other cases one or more of the seed-coat layers are impermeable for water or oxygen; also here breaking of the seed coats leads to immediate germination. In other seeds the embryo is immature at the time of seed ripening; it then has to pass through a period of so-called after-ripening before it can germinate. Many seeds, which have to pass the winter in a dormant stage, are awakened from their dormancy through a cold treatment. Such seeds are stratified by subjecting them for several weeks or months to freezing temperatures; after this they will germinate readily.

Among seeds of desert annual plants we find mechanisms which delay germination until a rain of sufficient intensity has wetted the soil to such depth that the seedlings can complete their life cycle with this water. This is accomplished by water-soluble inhibitors, which are leached out of the seeds only by a sufficient amount of rain. Such inhibitors may either be ordinary salts, like NaCl, or they may be organic substances.

Not only in the seed do we find dormancy of embryonic tissue; the same occurs commonly in the buds of plants. All deciduous plants, many plants

with rhizomes or tubers, and a number of conifers go each year through a rest period, when the growing points of the stems, enclosed in buds, are dormant. This is in contrast with annual plants and a number of tropical plants, in which the growing point never gets into a resting stage, but continues to form new tissue as long as the plant lives. The dormancy of buds is usually induced by the shortening days of late summer and autumn; a peach or pear tree may be kept in continuous growth by keeping it continuously under long-day treatment. But once the buds of these plants have become dormant, only a cold treatment with temperatures close to freezing for one to several months will induce them to restart growth. In several cases, such as *Syringa*, chemical treatments (with ether vapour or nitrophenols) or hot water baths may substitute for the cold treatment.

Temperature and light have an enormous effect on growth of the different plant parts. Roots grow fastest in darkness, and for a limited period stems also elongate most when kept in the dark, giving rise to etiolated shoots. But for continued stem and leaf growth light is necessary both for photosynthesis and for normal morphogenesis.

Each plant and each plant organ has its own optimal temperature conditions for growth. These conditions were first studied for seeds, and later for bulbs and other plants. In the case of bulbs, such as tulips and hyacinths, it was found that for each stage of development a special temperature is required for optimal development. For instance, when in July the foliage of a hyacinth has died, the growing point inside the bulb has only a few leaves formed for the next year's shoot. When kept at high temperatures (30–35°C), a whole embryonic inflorescence is formed at the growing point, but to make these flowerbuds grow, the bulbs must be subjected for several months to low temperatures, first 13° and later 17°C. This means that a hyacinth can only develop normally in a climate in which a cool winter alternates with a warm summer. There are any number of plants which require such seasonal changes in temperature, like the camellia, whose flowerbuds are only formed in warm weather, and whose flowers open only at lower temperatures. Flowering in many biennial plants such as beets and carrots occurs only when a cold winter interrupts growth. This results in so-called vernalization, without which no flower initiation in the growing point is possible.

In other plants, like the peach, seasonal thermoperiodicity is still more complicated: flower buds are formed during summer in response to vernalization during the previous winter; opening of these flowerbuds occurs only in response to cold treatment during the following winter.

In practically all plants which have been investigated the phenomenon of thermoperiodicity was found. This means that for normal and optimal development most plants require a temperature change from day to night,

and usually they grow best when the night temperature is lower than the day temperature, as it is under natural conditions. Actually, the temperature range over which normal growth occurs is fairly narrow for most plants and the temperature range over which plants are able to set fruit and produce viable seeds is still narrower. For instance, most tomato varieties will not set much fruit when the night temperatures are below 15° or above 20°. The potatoes are formed most abundantly when the night temperature is about 12°, and, except under short-day conditions, no tubers are formed at all above 18°C.

Thus the successful growing of plants is very closely associated with temperature, which means that each plant has an area and a time of year where and when it will do best. This limits successful vegetable and crop production to certain regions of the world for each crop. Peas, lettuce, and potatoes are cool-climate plants, tomatoes and corn warmer-climate plants and sugarcane, rice, and many other plants are successful particularly in the tropics.

We cannot leave the subject of growth control without discussing photoperiodism. Forty years ago it was first realized that the relative length of day to night controlled the flowering behaviour of a number of plants, and now we know that flowering of most annual plants, and the vegetative growth of many shrubs and trees is controlled by day length. Those annual plants which normally flower in autumn, like chrysanthemum and cosmos, are short-day plants; that is to say that they initiate flowerbuds when the length of day is less than a critical number of hours. Spring and summer flowering plants, such as Iceland and California poppies, will produce flowers only when they are exposed to a day length longer than the critical period. It has turned out that this photoperiodic response is both a reaction to the relative length of day and night and to the periodic change of light and darkness, which has to occur on a 24 hr cycle. In most cases the plants have to be subjected to a series of light-dark-light successions before they will form flower buds.

Only when leaves are present can a plant be induced to flower by the proper photoperiodic treatment. It is in the leaves where the photoperiodic stimulus is perceived. But the reaction occurs in the buds. It has been found that the photoperiodic stimulus is transmitted through the phloem, and that it can cross a graft union. This has led to the assumption that the flowering stimulus is carried by a hormone, florigen, but all attempts to extract it have thus far failed.

Another interesting fact about photoperiodism is that the leaves of some plants, once subjected to the proper photoperiodic treatment, become induced. They will then continue to induce vegetative buds to produce flowers.

As indicated earlier, photoperiod not only causes growing points to change

from the vegetative to the flowering condition, but it may induce dormancy, it may change the leaf shape of leaves produced under a special photoperiod or it may change branching. Growth of the different parts of a plant is integrated to a very great extent. In this way the plant is always properly proportioned and one part does not develop out of line with the other parts. This proportional development is only partly due to limitations in the amount of water and nutrients taken up by the roots, and the amount of photosynthates produced in the leaves. For if we supply a plant with extra water and nutrients and sugars (by e.g. growing it in sterile culture in bottles with nutrient solution) its proportions remain the same, and it usually does not grow any faster.

If the detailed control of relative growth of the different parts and organs of the plant is not accomplished by differential nutrition, we must look for another source of such control. This is found in plant hormones, substances produced in minute quantities in one part of the plant body, controlling growth in other parts after they have been translocated there. As a first example we will consider stem growth. Usually the extreme tip of the stem is indispensable for the elongation of the stem further down. Removal of this tip greatly decreases growth, replacing the cut tip restores most of the growth. This effort of the stem tip is due to small amounts of a substance, the stem growth hormone or auxin, which are produced in this tip, and are translocated downwards to the growing region of the stem. This hormone, auxin, is responsible not only for regular growth, but also for the response of the plant to its environment. When light hits a stem from one side, such a stem usually bends towards it, which is called positive phototropism. This is caused by an effect of the unilateral light on the lateral distribution of auxin inside the stem; more auxin moves towards the shaded side, causing that side to grow faster, which results in a curvature towards the light. In the same way gravity causes auxin to be moved towards the lower half of a horizontally placed stem, resulting in faster growth of this lower half and an upward bending of it. This is negative geotropism, so common among plant stems. Many other tropistic responses of plants, such as traumatotropism, and different reactions to these stimuli, such as negative phototropism and positive geotropism of roots, can be explained by auxin behaviour too.

Although auxin is a major factor in the growth of stems and roots, it is by no means the only one. In stems it has been found that gibberellin, apparently also a hormone, is essential for growth. At present it is not clear where this substance is formed in the plant. In roots growth cannot proceed without small amounts of thiamin (vitamin B) and occasionally niacin and vitamin B_6, which are produced in the leaves, and therefore are hormones in the development of the plant.

To complete the hormonal control picture of the plant we know that many young leaves grow proportional to the extent of the surface of the old leaves since control is transmitted apparently through purines synthesized in the older leaves. At least, it was found that in several cases adenine can cause growth of young leaves *in vitro*. Several growth factors—whether they act as hormones has not been established as yet—have been recently isolated from coconut milk. Kinetin was shown to interact with auxin in regeneration of roots and shoots on tobacco stem cultures; other substances are highly effective in inducing callus growth.

This picture of chemical control of plant growth is by no means complete; there is still very much to be discovered, especially as regards problems of differentiation. We know that auxin can induce stem elongation, but it also is effective in root initiation, fruit set, dormancy, etc., and we do not know how in each case the auxin effect is steered into one direction or another. Other aspects of the chemical control of plant growth lie in the use of herbicides, which will kill plants if sprayed on them; many of these herbicides are chemically related to plant growth hormones (e.g. 2, 4-dichlorophenoxyacetic acid, a powerful herbicide, and indoleacetic acid, one of the auxins).

In one case, that of the crowngall, induced by bacteria on plant stems, the tissues can become induced by the gall-forming agent to continue independent growth, and such cells become cancer-like. In most other cases, however, gall-forming organisms, such as gall wasps and gall midges, cause only a temporary overgrowth, which stops as soon as the insect has ceased to grow.

The water balance of plants may seem a rather simple problem, but in reality it is still beset by many unknowns or doubts. A land plant is able to live only as long as it has a sufficient water content. Near the critical content the plant first wilts, and if this water stress is not soon relieved, the plant dies. Normally the plant lives in a gradient of water stress. The air is usually not saturated with water vapour, and therefore will tend to dry out any moist objects in it. A plant contains usually more than 80 per cent, and often 90 per cent of its total weight in the form of water, and this tends to transpire into the air. Against this loss the plant must have a water supply, which for most plants lies in the soil. Through a very extensive root system, often measuring miles in length, plants are able to remove even small quantities of water from a fairly dry soil. This water is moved then through tracheids and vessels in the roots, stems, and leaf veins to the leaf cells, where it is lost again towards the atmosphere. The forces which move this water from soil to air through the plant are purely physical, and depend on the saturation deficit, which increases from soil to plant to air.

The plant has a greater water saturation deficit (suction pressure, or DPD: *d*iffusion *p*ressure *d*eficit) than the soil; thus water moves from the soil into

the root cells. This water is then passed on from cell to cell in the root, to the vessels, and finally to the leaf cells, in an ever-increasing gradient of DPD. In the leaf cells DPD values of 20–40 atm are common, especially in drier conditions; under conditions of plentiful water supply leaf cells usually have DPD's between 10 and 20 atm.

Although the whole water movement through the plant is purely physical, the plant is able to control it by controlling the rate of water loss by more or less closing its leaf surface against diffusion of water vapor. This is accomplished by the opening or closing of small pores in the otherwise watertight epidermis. This is covered by a water-impermeable layer, the cuticle, which means that most water vapour must pass through these pores or stomata. When the plant transpires more water than it can absorb, the DPD of the leaf cells increases and this in turn causes a closing of the stomata.

Thus the plant is able to keep within the range of water stress which it can stand; when even under conditions of closed stomata the demand for water exceeds the supply, the plant is doomed.

One of the most baffling problems in the water balance of plants has been the question, how water stresses of more than 1 atm could exist in the vessels of stem and leaf. This problem was solved when it was shown that through the cohesion of water in water-logged vessels no vacuum or air bubbles can form inside these vessels, and thus a pull of many atmospheres can be transmitted from leaves to roots, moving the necessary quantities of water.

Another difficult problem is the water balance of plants of arid regions. During rainless periods such plants exhaust the water supply in the soil, and yet a number of them is able to survive. One type of desert plant, the succulent, has solved this problem by cutting down drastically on its water loss, and storing a large supply of water in storage tissues, usually thickened stems or leaves. In this way cacti can survive periods of many rainless months, and replenish their water supply again during the following rain. To decrease their water loss they have evolved an interesting metabolism, by which they open their stomata during night, when they absorb CO_2 which is stored in the form of dicarboxylic acids, whereas during day they keep their stomata closed losing very little water, but transform through photosynthesis the dicarboxylic acids into sugars.

Other desert plants lose their leaves during the driest part of the season, but most interesting are those plants which produce such high DPD's that they are able to keep an equilibrium between water loss and water uptake. They are the true xerophytes, and survive where other, less well adapted, plants perish.

Very real progress in the field of plant physiology has been made along the lines of the mineral nutrition of plants. The bulk of the plant is made up of water, and of the dry weight again over 90 per cent consists of the elements

carbon, hydrogen, and oxygen, which come to the plant in the form of water, and CO_2 from the air. Therefore only a small fraction of a plant consists of the other mineral elements, and of these again a few are essential for the growth and development of a plant. If any of these essential elements are lacking in the soil or in general in the medium in which the plant has its roots, it cannot grow normally.

About 100 years ago the importance of the mineral elements for the growth of plants was recognized, first in the form of mineral fertilizers, and later in special nutritional experiments, in which the plants were grown with their roots in solutions containing mixtures of salts. It became clear that unless the elements P, S, N, K, Ca, Mg, and Fe were present in the soil or in the nutrient solution in a soluble form, no plant could grow. Of these elements P and N are most often lacking in the soil, and have to be applied in the form of fertilizer, to make plants grow optimally. In a number of cases K is present in insufficient amount, but the other essential elements are usually available in normal soils.

About 40 years ago it was found, that when *only* the 7 elements enumerated above were present in highly purified form, growth of plants became abnormal; the growth rate was insufficient, necrotic spots developed on leaves or the growing point died. During the last half century it has become clear that very small amounts of B, Zn, Cu, Mn, Mo and Cl, the so-called micro-nutrients, are required as well. The same elements are essential for animal growth, but in addition mammals need I and Co, which they usually obtain from eating plants (or drinking water), but which elements are not essential for plant growth.

There are a limited number of plants, especially Leguminosae like peas and beans (also some bacteria and bluegreen algae) which can grow even when the soil or nutrient solution does not contain any nitrogenous compounds. They are able to utilize the N_2 gas from the air. Leguminous plants have the ability, in symbiosis with root nodule bacteria, to "fix" nitrogen gas into ammonia or nitrate, which they can then use for growth. This nitrogen fixation by leguminous plants and bacteria is very important in the nitrogen balance of the earth, since continuously nitrogenous compounds are broken down, partly by plants and animals, partly by fire, and partly by man in the form of explosives.

This knowledge about the mineral nutrition of plants enables us to develop the most advantageous mineral fertilizing programmes for our crop plants. The use of mineral fertilizers has not completely replaced the use of manure or of organic materials in general. The importance of these compounds does not lie in the fact that they supply organic substances to the growing plant; with only a few exceptions higher plants can synthesize *all* organic compounds they need. Organic fertilizer definitely does not

influence the plant. But it is important to keep a good soil structure. It keeps heavy soils porous, and it increases the water and nutrient holding capacity especially of light soils. Many soils lose their fertility when they lose their organic matter.

Much research has been carried out on the mechanism of uptake of inorganic compounds by plants. Most of this uptake occurs in the form of ions, and the plant cell is able to accumulate these ions inside the cell to a concentration many times higher than in the surrounding medium. This accumulation of ions against a concentration gradient requires energy, and this is supplied by respiration. Ion uptake by roots is therefore possible only when sufficient sugar is present in the roots and sufficient oxygen around the roots. We find that plants which live with their roots under oxygen-poor conditions usually have large air-channels in these roots (like the rice plant) or have knee roots which reach up into the air (as in the mangrove vegetation).

There are many other problems in connection with the life of plants which have been investigated, and they all are interesting. But there is no room to discuss these in detail. Just a few will be mentioned.

There is a strict polarity in the plant. When a piece of stem is cut off the plant, this usually will reform roots, and often shoots. These roots always are produced at the basal end of the stem, whereas the shoots develop near the apical end. This polarity in regeneration seems to be due to the polar transport of auxins in the plant cells and tissues, where it always moves from apex to base. This causes auxin accumulation at the base, which favours root formation, and a deficiency of auxin at the apex, which favours shoot initiation.

Many plant cells are sensitive to touch. The sensitive plant is the best known example of this behaviour. It shows not only a local response, but the stimulus can be transmitted to other parts of the leaf or of the plant. This transmission is by a chemical, released by the stimulated cell, which will stimulate other cells when it reaches them through the transpiration stream. This substance has not been isolated as yet in chemically pure form.

INDEX

Abies 156, 192, 508
Abutilon 291
Acacia 201
Acer 187
Acetabularia 338
acetylenic fatty acids 118
Achillea 264, 265
Achlya 352, 368
Acrasiae 321
Acrochaetium 340
Acrostichum 478
Actinomyces 321
Adoxa 93
advanced 26
Aegilops 276, 279
aeration (soil) 136
aero-aquatic fungi 369
Aerobacter 319
aerobiology 364
Aextoxicaceae 206
after-ripening 524
agameon 33
Agathis 195, 203, 508, 509
age and area 211
Aglaozonia 339
Agrostis 129
Ajuga 207
Aldanophyton 62, 442, 452, 453
Alethopteris 236
aleurone grains 108
alfalfa mosaic virus 301
Algae 328 seq.
algal cell wall 102
alkaloids 103
allantoin 110
Allomyces 352, 354, 368
Alnus 187
Alternaria 364
alternation of generations 396 seq., 436
aluminium 139
Amanita 348, 367, 368
Amaranthus 285
Amblystegium 394
Amentotaxus 506
amino-acids 103, 520
Ammophila 89
amphiploidy 276
Anabaena 335
Anabasis 190
analogy 20, 44
anatomy 14, 15
anatomy and taxonomy 91
anatomy of dicotyledons 91
anatomy of ferns 423
anatomy of monocotyledons 91
anatomy of plants 76 seq.
androkladien 55
Andropogon 201
Androstrobus 503
Anemia 473
Anemone 210
Aneura 390
Aneurophyton 453
angewandte Pflanzensoziologie 167
Angiopteris 192, 427, 468
Angiosperms 44, 52
animals 140
Anoectangium 408
Antarctic Region 206
Anthelia 413
Anthoceros 395, 396, 413, 414, 415, 466
anthocyanins 103, 520
antibiotics 359
Antirrhinum 270
antithetic theory 463
Apetalae 63
aphids 110
Aphis 308
apogamy 435
apospory 435
apple scab 365
apple varieties 126, 130
Aquilegia 271
Arachnoxylon 453
Ararat 173
Araucaria 508, 509
Arbutus 188, 207
Archaeopteris 49, 453
Archangiopteris 468
architecture of plants 105

Arctic 185
Arctostaphylos 186
Arenaria 186
Arktis 163
Armillaria 367
arochimosis 16
aromorphosis 16
arsenic 138
Artemisia 264
Artenkonkurrenz 160
Artenverbindung 154
Arthrocnemum 190
Arthrostigma 439
Ascobolus 352, 371
Ascophyllum 336
ascorbic acid 110
asparagine 110
Asparagopsis 340
Aspergillus 255, 355, 357, 365
Assoziation 148 seq.
Astelocormophyta 15
Aster 262, 263
Asterionella 371
Asteropteris 453
Asteroxylon 439, 453
aster yellows 305
Astragalus 139, 186, 191
Athrotaxis 511
Atlantic 187
atolls 199
Atrichum 394, 397, 401
Atriplex 190
Aulacomnium 401
Australian Region 204
Austrobaileya 57
Austrotaxus 506
autoradiography 253
auxins 110, 527, 531
Azolla 480, 481
Azotobacter 320, 323

Bacteria 11, 251, 313 seq.
bacteriophages 250, 295
Bacillaceae 320
Banksia 204
Baragwanthia 441, 442, 452, 453
barley 129
barriers 182
Bartramia 407
Basidiomycetae 118
Batrachosperum 329
Bauhinia 192
Bazzania 391
Beania 502, 503
beech zone 188
Bennettitales 500
Bensonites 465
Bergeria 453
Betula 186
Betulaceae 36
bihemispherical ranges 212
binom 33
biochemistry 100 seq.
biochemistry and phylogeny 120
biochemistry and taxonomy 116
biochemistry of the species 111
biometrics 53
"bios" 357
biosphere 172
biosystematics 10
biosystematy 9, 10, 30
Biota 510
biotaxonomy 9
biotic factors 178, 182, 183
Biozoenosen 145 seq.
bi(poly-)phyly 45
bipolar distribution 212
bi(poly-)rheithry 45, 63
Blackstonia 132
Blastocladia 368, 369
Blastocladiella 358, 362
Blechnum 478
blue-green algae 314 seq.
Boletus 367, 368, 378
Bordeaux mixture 372
Boreal Region 187
boron 138
botanic gardens 519
Botrychium 423, 466
Botrytis 361
Bowdichia 201
Bowenia 204, 502
Bower 414
brachymeiosis 351
Brometo-Pulsatilletum 152
Bromus 152, 274, 277, 283
Brown, R. 387
Bruchia 392, 395
Bryophyta 387 seq.
Bryum 396, 404, 407, 411

Bucheria 453
budding in bacteria 323
bulbs 525
bulliform cells 89
Byrsonima 201

Cactaceae 117
Calamaria 424
Calamophyton 453
calcium 131, 138
Callistemon 204
Callitris 507, 510
Calycanthaceae 84
Calymmatotheca 497
Calymperes 398
Calypogeia 392
calyptra 399
cambium 95
Camptothecium 410
Campylopus 397
Canarium 19
Caprifoliaceae 119
Capsella 137
carbon dioxide assimilation in fungi 362
Carex 156, 186
carotenoids 104, 520
carpel 55, 56
cartographical presentation 180
Caryophanon-Oscillospira group of bacteria 314
Casuarina 58, 62, 63, 66
catechins 103
Caulobacter 319, 323
caulobacteria 326
caulonema 402
causal plant ecology 124 seq.
Caytonanthus 499
Caytonia 499
Caytoniales 60, 62, 241, 499 seq.
Ceanothus 266
Cedroxylon 507
Cedrus 508
cell division 523
cellulose 102, 106
Centaurea 210
Central Asiatic Region 189
Central European Region 187
Centrospermae 53, 117
Cephaleuros 335
Cephalotaxus 506
Cephalotus 204
Cerastium 141, 186
Ceratodon 408
Ceratopteris 474
Ceratozamia 502
Cercidiphyllum 192
Chamaecyparis 510
Chandonanthus 413
Chara 338
characters 5, 6, 7, 20, 23, 24, 25, 47, 48
chaulmoogric acids 118
Cheiroglossa 466
Cheirolepis 508
chemotherapeutic treatment 309
Chenopodiaceae 190
chestnuts 266
Chiloscyphus 394
China 191
chitin 106
Chlaenaceae 197
Chlamydomonas 336
Chlamydospermales 62
Chlorella 336, 337
chloronema 402
Chlorophyceae 121
chlorophyll 104, 108, 109, 113, 520
chloroplasts 109, 113
Chondrophyllum 390
Chondrus 337
Chorionopteris 467
Christensenia 468
chromatids 248
chromatography 101, 104
chromomeres 252, 258 seq.
chromosomes, 14, 17, 248 seq., 393, 520
Circaeaster 44
circumpolar plants 185
citrulline 110
Cladophora 414
Cladostephus 341
Cladoxylon 453, 454
Clamydobacteria 325
Clamydomonas 121
Clarkia 266
classification 4, 5, 6, 8, 13, 36, 92
clearing agents 84
Climaciophyton 453
climatic factors 126, 178, 182
climax 141
clines 207, 208, 262

clovers 120, 139
coal 237
coal-balls 232
cocci 313, 320
Cochlearia 186
Code of nomenclature 10
coéfficient de communauté 159
cold-air drainage 125
Codiolum 340
cold desert 186
Colobanthus 206
Colpodexylon 453
Colpoxylon 499
Coluria 282
compatibility 353
Compositae 118, 266
Coniferales 51, 506 seq.
conifer belt 187, 188
coniferyl alcohol 102
constancy 281
constituents of plants 101 seq.
continental 187
continental drift 214 seq., 507
control of virus diseases 306, 311
Convolvulus 207
Cooksonia 453
Copernicia 201
copper 134, 138
Coprinus 353, 371
coprophilous fungi 371
Corallina 338
coralloid roots 502
Cordaicarpus 504
Cordaitales 503
Cordaites 504, 505
Cordianthus 503
Cordyceps 371
Cormophyta, lower 22, 27
Cornus 156
Corynebacterium 321, 323
Cotyledon 202
coumarin 120
coumestrol 120
Crassula 202
Crepis 18, 258
cristae 246
Crocalophyton 447
crowngall 528
Crucibulum 363
Crucifera 33
Cruciferae 57
Cryptomeria 192
cryptospecies 394
Cryptothallus 390
crystals 108
Cucurbitaceae 90, 118
Culcita 475
culture methods for algae 337
Cupressaceae 117, 119
Cupressus 507
Curatella 201
Curvuletum 163
Cutleria 339
Cyathea 192
Cyathus 363
Cycadales 54, 501
Cycadeoidales 62
Cycadeoidea 501
Cycadocarpidium 507
Cycadofilicales 497 seq.
Cycas 192, 204, 501, 502, 514
cyclopropene fatty acids 118
Cymbopogon 201
Cymopolia 338
cytology 14, 17, 177, 178, 245 seq.
cytology of algae 340 seq.
cytology of conifers 507, 509
cytoplasm 245 seq.
Czekanowskia 506

Dacrydium 509
Dactylis 279
Dahlia 115
Daldinia 363
Danaea 427, 468
data for phytogeography 177
Dauerdetermination 401
Dauerquadrat 163 seq.
Davidsonia 16
death 209
Degeneriaceae 200
deme 19
Dennstaedtia 475
deoxyribonucleic acid (desoxyribose nucleic acid) 248, 249, 250, 268, 520
Deschampsia 206
desert plants 529
desiccation 127
developmental studies 94
dew formation 128

Dicksonia 192
Dicnemon 400
Dicopsida 59
dicotyledons 18
Dicranopteris 476
Dictyostelium 358
Dictyota 414
Didiclis 458
Didieriaceae 197
differentiation 40
diffusion present deficit 528
Diluvial Period 189
Dimensionen 148
Dioon 502
Diphasium 457, 458
Dipteris 479
Dipterocarpaceae 195
Discelium 400
discontinuity 32, 35, 42
Diselma 510
dispersal 178, 181, 219, 281
dispersal of spores in fungi 362 seq.
distribution 20, 173
Dolerotheca 499
domain 181
Dorycnieto-Schoenetum 152
Draba 186
Drepanocladus 392, 393
Drepanophycus 442, 453
Drimys 203
Drosera 204
Drosophila 248, 269, 273, 395
drought tolerance 127
Dryanda 204
Dryas 282
Dryobalanops 195
Dudresnaya 340
Dumortiera 394, 416
dunes 130, 132

Eastern Asiatic Region 191
ecesis 181
"eclipse" phase 297
ecology 14, 124 seq., 173
ecospecies 37
ecotones 208
ecotypes 37, 396
Ectocarpus 339
ectohydric 407
edaphic factors 178, 182, 183
electrophoresis 101
Elymus 186
embranchement 50
embryogenesis 95
embryology 14, 95
embryology of algae 340
Empetrum 213
Empetrum-Soziationen 156
Empetrum-Vaccinium-Heide 156
Encephalartos 501, 502
endemics 208
Endogone 367
endohydric 407
entomogenous fungi 371
environment 182
enzymes 101
Eocene 184
Ephedra 42, 511, 512, 513
Ephemeropsis 400
Ephemerum 395, 400, 415
Epilobium 186
Equisetites 459
Equisetum 49, 132, 423, 424, 425, 426, 427, 459, 460
Erbstock 48
Erebus and *Terror* 176
Erica 202
Ericaceae 186
Eriophorum 186
Ernestiodendron 508
Erophila 274
Escherichia 251
establishment 181
esters 103
état préfloral 57
euanthemum 61
Eucalpytus 16, 118, 158, 204
euchromatin 269
Euphorbia 139
Eusideroxylon 195
Euterpe 201
evolution 258 seq., 434
evolution of bryophytes 412 seq.
external factors 181
extremes 126

Faeroes 187
Fagus 187
Fertilität 149

fertilization, double 60
Festuca 186
Ficus 192
Filicidae 469
Filicopsida 465
Fissidens 400
fission in bacteria 323
Fitzroya 510
Flacourtiaceae 118, 119
florigen 111, 526
floristics 262
flower 55, 56
flower buds 525
Fomes 348
Fontinalis 406
fossil plants 184
Fraxinus 187
Fritillaria 208
Fritschiella 448
frost pockets 125
Frullania 400
Funaria 394, 399, 400, 401, 402, 403, 404
Fungi 348 seq.
Fusiformis 321
fusion 496
future of phytogeography 221 seq.
future research in taxonomy 67

Gangamopteris 60
garrigues 188
Gelasinospora 355
Gelidium 337
Gemeinschaftskoeffizienten 159
gemmae 397
genealogy 42
gene pool 114, 271, 274
gene recombination 272
genes 115, 258 seq.
genetics 13
genome 23, 45
genorheithrum 41, 47
genotype 259, 268
Gentiana 210
Gentianella 211
geobotany 173
geotropism 527
germination 524
germination energy 128
Gesellschaftsdynamik 161
Gesellschaftsmerkmale 150
Gesellschaftstreue 150
Geum 210, 270
gibberellic acid 111
gibberellin 527
Gilia 266
Gondwanaland 215
Ginkgo 57, 121, 504, 505, 514
Ginkgoales 504 seq.
Glacial Epoch 184, 194
Gleichenia 192, 476
Gliodadium 380
Glomerella 352
Glossopteris 60, 61, 62
glutamine 110
Glyceria 211
glycolysis 522
glycosides 105
Glyptolepis 508
Gnetales 58, 64, 511 seq.
Gnetum 511, 512, 513
Gonapodya 368
Gosslingia 453
Gossypium 277, 278
gradations 32
gram-positive and gram-negative bacteria 318
grasses 282
grass leaves 89, 91
Grevillea 204
Gristhorpia 499
growth 523
growth factors 110
growth forms of mosses 408
Grundformen 146
gynokladien 55

Halimione 141
Haloxylon 190
Hamamelidales (-aceae) 18, 53, 61
haploidization 355
heat therapy 309
Hebe 203
Hedeia 441
Helianthus 280, 285
Helipterum 132
Helleborus 135
Helminthosporium 364
Helminthostachys 463, 466
hemispherical ranges 212
Hepaticae 387 seq.

herbarium technique 15
herbicides 528
Heterangium 235
heterochromatin 269
heteroecism 349
heterosis 274
heterospory 49, 50
heterothallism 351
Hevea 523
Hibiscus 192
Hicriopteris 476
Hippochaete 460
histology 78
historic factors 45, 124
history of pteridology 422 seq.
Holcus 129
hollow curves 38
hologeny 41, 47
homeostasis 281
Homogenität 158
homologous theory 463
homology 20, 44
homospermy 50
homospory 49, 50
Hookeria 406
Horkelia 264
hormones 527
Hornea 439
Horneophyton 415, 453
Hornia 239
hot springs 335
humidity 128
Huperzia 457, 458
hybridization 32, 273 seq., 395
hybrid vigour 274
Hydra 12
Hyenia 453
Hylocomium 390, 410, 412
Hymenophyllopsis 480
Hypnum 395, 396
hypogeal fungi 372

Iceland 185, 187
Indian Regions 194
indicator species 134
individuum (-al) 11, 12
indoleacetic acid 111
infection 297, 310
inherent factors 181
inheritance in fungi 351
insecticides 307, 308
in situ development 219
intermediates 22, 23
interrelationships of bacteria 318
introgression 275, 395
introgressive hybridization 19
intuition 23, 34
iodine 138
Iridopteris 453
Iris 277
Isoëtes 124, 424, 425, 426, 427, 429, 454, 456, 458, 459
isoflavonol 120
isolating mechanisms 284
isolation 219
isospermy 50
isospory 49, 50

Japan 192
Jodrell Laboratory 81, 91, 92, 93, 230 seq.
jordanons 33, 274
Juncus 129, 186
Juniperus 188, 192, 276, 510

karyogamy 351
Kausalität 160
Keimplasma 12
keys 35
Kingdonia 44
Klassengruppe 156
Klimax 162
Klimaxgesellschaften 163
Klimaxschwarm 163
Konstanz 150
Koompassia 195
Krebs-cycle 521, 522

Laccopteris 478
Lactarius 367, 378
Lactobacillus 321
Lagenostoma 235, 438, 497, 499
Laminaria 339
Laminariaceae 339
Larix 192, 508, 511
Laurus 188
Layia 260
leaf 56
Lebachia 508
Lebensformen 147

Leguminosae 118
Lejeunea 392
Lepidodendron 233
Lepidolaena 400
Lepidopteris 498
Lepidospermales 64
Lepidostrobus 235
Lepidotis 457, 458
Leptospermum 204
Leptostrobus 506
Leptotricha 321
Leucadendron 202
leucoanthocyanins 103
levels 47
liberation of spores in fungi 362 seq.
Libocedrus 510
lichens 11
life 15, 17, 20, 22, 23, 40, 100, 112, 245
life-cycle 12, 13
life forms 178
light 129
lignée 50
lignin 102, 107, 119
limiting factors 182
limits between taxa 32
Lindsaea 475
lines 47, 50
linguistics 30
linnaeon 32, 34
liverworts 387 seq.
Loganiaceae 119
Lolium 129
Lophosoria 477
Lophozia 392
Lotus 210
Loxogramme 479
Loxsoma 477
Loxsomopsis 477
lumpers 33
Luzula 285
Lycoperdon 363
Lycopodiidae 456
Lycopodioides 424, 458
Lycopodites 456
Lycopodium 156, 424, 425, 426, 427, 434, 454, 456, 457, 458, 463
Lycopsida 456
Lyginodendron 438, 497
Lyginopteris 235, 236, 497
Lygodium 473
macchia 188
maceration 84, 243
Macroglossum 468
Macronesian Sub-region 189
macro-recombination 261
macrostructure 106
Macrozamia 204, 501, 502
magnesium 138
Magnolia (les) 27, 28, 53, 55, 259
Maianthemum 210
Malaysian Region 195
Mallomonas 341
Malvaceae 118
man 179
manganese 138, 139
Marasmius 366
Marsilea 423, 425, 426, 480
Marattia 427, 468
Marattiidae 467
Marchantia 388, 390, 416
Marsileidae 480
Mascarene Region 197
mass-collection 19, 53, 259
matching genes 374
Matonia 478, 479
Mauritia 201
Mayanthemum 156
Medicago 281
Mediterranean Region 188
Medullosa 235, 499
meiosis 250
Melaleuca 204
Melanomma 377
Melastoma(ta)ceae 84
Melica 283
Mercurialis 137
Mesobromion 152
mesomes 496
metamorphoses 22
Metasequoia 191, 267, 510
methods of phytogeography 177
Metzgeria 394
Microcachrys 509
microclimate 126, 127, 182
Microcycas 502
Micromonospora 321
micromorphology 78
micronutrients 127, 529
microscopes 245, 246
microscope slides 93

Microseris 274
microsomes 107
microspecies 274
Microspermopteris 498, 499
microstructure 107
Mikroklimaxkomplex 163
Mimosa 201
mineral nutrition 529
mitochondria 107, 246
mitosis 248
mixohydric 407
Mnium 394, 399, 407
molybdenum 138
Monocarpus 390, 391
Monochlamydeae 27, 53, 61
monocotyledons 18
Monoklimax 162
monophyly 21, 45
Monopsida 59
monorheithry 21, 45, 61
Monoselenium 416
Montsechia 61
moraines 133
morphogenesis 14, 260
morphology, floral 14, 40, 55
mosaic 291
mosses 387 seq.
Mucor 365
Muscineae 387 seq.
mutation pressure 42
mutations 38, 48, 268
Mycena 378
Mycenoporella 378
mycorrhiza 366 seq.
Myeloxylon 499
Myosotis 210
Myosurus 274
Myrica 192
myrmecochory 283
Myrtaceae 84
Myrtus 188
myxobacteria 321, 326
Myzodendraceae 206
Myzus 306, 308

Naiadita 413
Nanobryum 400
Nanomitrium 395, 415
Nardus 89
Nathorstiana 454, 456
nattaxon 30, 32
natural selection 21, 42, 48, 262, 271, 280 seq.
Nearer East (regions) 190
Nematophyton 239
Neocalamites 459
neo-endemics 209
Neohodgsonia 390
Neomeris 338
neomorphology 9, 15
neotaxonomy 9
Neotropical Realm 200
Nephrolepis 475
Neuropteris 236
Neurospora 112, 255, 269, 352, 354, 355, 357
New Zealand Region 203
Nicotiana 18, 271
nicotinic acid 111
Nilssonia(les) 502
ninhydrin 104
Nitella 338
nitrogen 356
nitrogen fixation 529
nitrogen-fixers 320
nitrogenous anthocyanins 117
Nocardia 321
Noeggerathia 440, 455, 460
Noeggerathiopsida 460
nomenclature 10
nomtaxon 30, 32
North American Region 192
Northern Realm 185
Nothotaxus 506
Notofagus 203
Notothylas 416
nucleus 245 seq., 519
nunataks 186
nutrition of fungi 356 seq.
Nymphaea 61

oceanic 187
oceanic islands 217
Oenothera 273
Olea 188
Oleandra 475
Oligocarpia 476
Olpidium 369
Ophiobolus 375
Ophioderma 466

Ophioglossidae 465
Ophioglossum 423, 462, 466
Ophrys 281
Opuntia 140
Orbignya 201
Ordnungsprinzip 155
Orthiopteris 480
orthogenesis 283
Orthotrichum 395
Oryzopsis 277
Osmunda 124, 192
Osmundaceae 239
Osmundidae 468
overtopping theory 496
Oxalis 156
Oxycoccus 277

Pachyglossa 390
Pachytesta 499
Pachytheca 235
Pacific Region 199
Paesia 474, 475
palaeobotany 13, 92, 230 seq.
palaeo-endemics 209
palaeontology 265
Palaeotaxus 506
Palaeotropic Realm 194 seq.
Palmae 61
palynology 14, 41
Pandanales (-aceae) 61
Papaver 186
paper chromatography 101, 104
paracrinkle virus 309
Paramoecium 252
parasexuality 355
parasitism 14
Parthenium 523
pathological anatomy 94
Paxillus 378
peach yellow, 311
pectin 106
pedogenesis 132
Pelargonium 202
Penicillium 359, 360, 365, 380, 403
Penstemon 262, 275
Pentoxylon 500
Peperomia 201
permafrost 186
Pernettya 203
Peronospora 372
Personiella 390
petiole 91
Peziza 362
Pflanzensoziologie 145 seq.
Phanerosorus 478
Phascum 395, 398, 399, 402, 415
Phaseolus 115, 281
phenolic compounds 117
phenotype 259, 268
Pherosphaera 509
Phoenix 190
phloem 90
phloem necrosis of elm 311
photoperiodism 137, 212
photoreactivation 298
photosynthesis 108, 113, 520 seq.
phototropism 359, 526, 527
Phragmidium 349
phrygana 188
phycology 328 seq.
Phycomyces 357, 359, 360
Phycopeltis 335
phylad 41, 57
phyllids 391
Phyllocladus 509
Phylloglossum 434, 456, 457, 458
phylloides 496
phyllome 22
Phyllopsida 57
phyllospory 51
Phyllostachys 192
Phyllotheca 459
phylogeny 10, 41, 42, 45, 46, 47, 49, 57, 86, 87, 120
phylogeny of Pteridophyta 443 seq.
phylon 41
phylum 41
Phymatotrichum 375
Physcomitrium 399
physiological anatomy 88
physiological races 374
physiology 519
physiology of algae 336
physiology of bryophytes 406
physiology of fungi 356
phytochemistry 14
phytochoria 172, 180, 181
phytogeography 172 seq.
Phytomonas 325
phytopathology 372

Phytophthora 350, 373, 374
phytoplankton 331
phytotomy 82
phytotron 19
Picea 156, 187, 192, 508, 511
Piceoxylon 507
Pietzschia 453
pigments 109, 115
Pilobolus 359, 371
Pilophorosperma 498
Pilularia 424, 425, 426, 480
Pinaceae 117
Pinus 117, 188, 192, 195, 207, 507, 508, 511
Piptochaetium 266
Pitcairnia 217
Pityostrobus 507
Pitys 503
Plagiogyria 479
Plagiozamites 460
planation 496
plant acids 103
plant anatomy 76 seq.
plant biochemistry 100 seq.
plant disease 372
plant dyestuffs 103
plant ecology 124 seq.
plant geography 172 seq., 262
plant physiology 519
plant processes 108
Plasmodiophora 133, 375
plastids 246, 520
Platanus 61
Platoma 340
Platycerium 479
Platyzoma 476
pleiotrophy 271
Pleospora 377
Pleuridium 395
Pleuromeia 454, 456
Poa 137, 186, 207
Podocarpus 507, 508, 509
Podozamites 507
polarity 531
polar wanderings 214 seq.
pollen grains 267
pollinating insects 54
pollination 178
pollination in conifers 508
Polycarpicae 53
polyembryony 509
Polygonales 66
Polyklimax 162
polynemy 249
polyploidy 18, 220, 276, 394, 398
Polyporus 348
polyrheithry 45, 63
polysaccharides 101
Polysepta 323
Polysiphonia 340
polytopism 208
polytopy 213
Polytrichum 163, 392, 393, 395, 400, 401, 407
population samples 259
Populationsklimax 162
Populus 187, 211
Porphyra 337, 340
porphyrins 113
potassium 138, 139
potato leaf roll 306, 308
potato virus X 295, 298, 304, 305
potato virus Y 301, 306, 307
Potentilla 264, 270, 274
Phraephanerogamae 48, 50
predaceous fungi 371
primitive 26
Primofilicidae 465
Primula 281, 283
principle of extremes 126
profiles (soil) 135
propagation, vegetative 11
Prosopis 201
Protea 202
proteins 101, 520
Proteus 316, 319, 320
Protolepidodendron 453
Protomarattia 467, 468
protonema 396, 400 seq.
Protopitys 236
protoplasm 519
Protopteridium 453
Protosalvinia 447
Prototaxites 447
province 181
Prunus 117, 192
Psaronius 232
pseudanthium 62
pseudoallelism 269
pseudocarpels 56

Pseudolarix 508
Pseudomasaris 275
pseudophylogeny 45
Pseudosporochnus 453
Pseudotsuga 508, 511
pseudovicariads 210
pseudovicarism 210
Pseudovoltzia 508
Psilophytales 66
Psilophyton 239, 439, 453, 464
Psilophytopsida 464
Psilotopsida 460
Psilotum 426, 429, 431, 434, 438, 451, 455, 460, 461, 462
Pteridium 207, 474, 475
Pteridophyta 421
Pteridosperms 61, 62, 438, 497
Pteris 192
Puccinia 349, 373, 374
Puccinellia 186
Pulsatilla 19
purpose 7, 8, 20
Pyrola 156, 186
Pyronema 351
Pyrus 192

Querceto—Carpinetum 163
Quercetum ilicis gallo-provinciale 163
Quercus 187, 188, 192, 265, 266

rabbits 140
radiation 128
radio-active carbon 243
Rafflesia 195
Ramonda 207
Ranales 53, 59, 61, 118
range 173
ranges, kind of 207, 208
rare species 209
realm 181
recurvation 496
"red snow" 334
region 181
reduction 27, 496
Regnellidium 480
Reimannia 453
relationship of bacteria 315
relicts 38, 209
reproduction of bacteria 323 seq.
resins 102
Retinospora 510
R_f 104
Rhacomitrium 409, 411
Rhipsalis 217
Rhizanthes 195
Rhizobium 320, 323
Rhizoctonia 359, 367
Rhizoglossum 466
Rhizopogon 367
rhizosphere 366
Rhododendron 186, 210, 211
Rhodomicrobium 319
Rhodoreto—Vaccinietum 163
Rhodoreto—Vaccinion 156
Rhoedales 118
Rhopalocarpaceae 197
Rhynia 239, 439, 453, 455
Rhynie chert 239
Rhytidium 397
Riccardia 390
Riccia 413, 414, 416
ribonucleic acid (ribose nucleic acid) 249, 268
Rochea 202
rosebay willow-herb 140
root hairs 131
root systems 130
rubber 523
Rubiaceae 119
Russula 367, 378
rust fungi 43
Rutaceae 118

Saccharomyces 352, 356
Sagenopteris 499
Sagittaria 259
Salicaceae 28
Salicornia 132
Salix 186, 187, 192
Salmonella 255
Salsola 190
Salvinia 425, 426, 432, 480, 481
Salviniidae 480
Samaropsis 504
Saprolegnia 351, 369
Sargassum 340
Saxegothaea 508, 509
Saxifraga 186
Scapania 392, 396

scarification 524
Schizaea 473
Schizaeaceae 121
Schizolepis 508
Schizoneura 459
Schizophyllum 353
Schizopodium 453
Sciadopitys 510
Schopfiastrum 498
Scirpus 211
Scleroderma 367
Sclerotinia 361
Scorzonera 260
Scrophularia 210
Sedum 186
seed dispersal 281
seed-output 129
seeds 48, 127, 498
seed size 282
Selaginella 427, 454, 456, 458
Selaginellidae 458
Selaginellites 456
Selaginoides 424
Selago 424
selenium 139
self-incompatibility 352
semophylesis 42, 46, 63
semophyletic birheithry 50
senescence 209
Senftenbergia 473
Septobasidium 371
Sequoia 194, 267, 507, 510
Sequoiadendron 510
serial sections 79
serology 16, 59
sex in fungi 351
Shorea 195
Sieglingia 152
sieve tubes 90, 110
Silene 186, 207, 208, 211
Sisyrinchium 264
Smilax 188
sodium 138
soil algae 335
soil-borne viruses 303
soil fungi 365 seq.
soils 183
Solanum 115
Soldanella 210
Solidago 156
Sordaria 354, 358, 363, 371
South African Region 201
Southern Realm 201
Soziabilität 149
Soziationen 154
Spartina 141
Spartium 188
specialization 86
species 34, 35
speciigenesis 37
Spermatocodon 498
Spermatophyta 48
Sphaerobolus 349, 362
Sphaerocarpus 394, 413, 414
Sphagnum 392, 393, 401, 409, 410, 412
Sphenophyllum 233
Sphenopsida 459
Sphenopteris 236
Spirogyra 121, 340, 341
Splachnum 401
Sphondylophyton 453
splitters 33
sporangia 496
Sporodinia 351
spore germination (fungi) 359
Sporogonites 415
Sporormia 377
spraying 373
spread of viruses 302, 310
stachyophyll 65
stachyospory 51
Stachys 210
stamen 56
Stammgarbe 47
Stammstrauch 47
Stangeria 502
starch 102, 108
statistics 14, 53
Statistik 157
Stauropteris 465
stegophyll 56, 64, 65
Stellaria 137, 186
Stelopsida 57
Stenochlaena 478
steppe 188
Sterculiaceae 118
sterols 104
Sticherus 476
Stigmaria 233, 235, 236
Stipa 266, 267

Stipeae 266
Stratiotes 266
Streptomyces 313, 316, 319, 320, 321, 325
Stromatopteris 476
Sturiella 500
Stylites 442, 456, 459
Stypocaulon 341
swollen shoot of cacao 311
Suaeda 190
Subarctic 185
succession 141
succulents 529
suction pressure 528
Suevioxylon 61
sugars 103, 104
sugar beet yellows 308
sulphur, in rain 127
surevolution 509
Sutcliffia 499
sycamores 266
symbols 35
Sympetalae 61
syngameontic method 28
Synökologie 160 seq.
syntelome 505
synthetic method 36
synthetic taxonomy 208
Synura 341
Syringa 525
syringyl alcohol 102
systematics, definition 4, 9
Syzites 351

taiga 187, 193
Takakia 390
tangential sections 79
tannins 102, 107
Taxales 506
taxogenesis 37
taxogeny 41
taxon (a) 41, 172
taxonomy 4, 8, 14, 33, 40, 258
taxonomy of bryophytes 389
taxonomy of fungi 375 seq.
taxonomy of Pteridophyta 443 seq.
Taxus 506
Tecona 195
telome theory 51, 55, 240, 495 seq., 512
Temperate South America (regions) 205
terpenes 103
Tertiary 184
Tethys Sea 214
Tetraphis 398, 402
Tetrastichia 498
thermoperiodicity 525
Thuja 510
Thujopsis 192
Thyrsopteris 475
Tilia 187
Tilletia 351
time of development 129
Tingia 460
Tingiostachya 460
titanium 138
Tmesipteris 426, 429, 431, 434, 438, 451, 455, 460, 461
tobacco etch virus 301
tobacco mosaic 291 seq.
tomillares 188
Torreya 506
Tortella 403
Tortula 394, 396
trace elements 130, 137
Trachypogon 201
Tradescantia 248
Tragopogon 260
Trailiella 340
Transportfaktor 162
transport of growth factors 110
transport of nutrients 109 seq.
transverse sections 79
traumatotropism 527
Trichoderma 359, 365
Trichopitys 505
Tricoccae 66
Trigonocarpus 235, 499
Trifolium 129, 210, 281
Trillium 283
Trochobryum 390
tropheclexis 54
Tropical African Regions 196
Tropical and Subtropical American Regions 200
truffles 348
Tsuga 508
tundra 186
turnip yellow mosaic 295, 299
typology (typological method) 10, 27

Ullmannia 508

Ulmus 187
Ulota 398
Umbelliferae 118
Umkomasia 498
Uncinia 203
units of classification 11
uranium—lead ratio 243
urease 102
Urospora 340
Urostachys 457
Urtica 84
utilization of algae 338
Utricularia 204

Vaccinio—Piceetea japonica 156
Vaccinio—Piceetea—Klasse 156
Vaccinium 186
Vallisneria 210
varves 41
Vegetationseinheiten 155
Vegetationstypen 147
Venturia 365
vernacular names 179
vernalin 111
vernalization 525
vessels 82
Vibrio 316
vicariads 210
vicarious species 210
Vicia 281
Viola 262, 263, 264
virus composition 310
viruses 291 seq.
virus multiplication 310
Viscaria 134
vital force 82
Vitalität 149
voles 140
Volkmannia 235
Voltzia 508

Walchia 508
Waldsteinia 282
water balance 528
water fungi 368
water relations of bryophytes 406 seq.
weeds 179
Welwitschia 511, 512, 513
Westersheimia 500
Williamsoniella 501
wind 128
wood anatomy 15
wound tumour 305

Xanthorrhoea 204
Xenocladia 453
xerophytes 529

Yarravia 441, 453
yeasts 354, 361

Zamia 501, 502
Zauschneria 264, 278
zinc 138
Zostera 211
Zosterophyllum 453
Zygodon 392