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THE PRINCIPLES OF CLASSIFICATION AND A CLASSIFICATION OF MAMMALS

GEORGE GAYLORD SIMPSON
Curator of Fossil Mammals and Birds

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PREFACE

IT IS NATURAL to reach the end of a long and difficult task with feelings of congratulation toward oneself and of apology toward others. This mingling of satisfaction and apprehension, of conceit and abasement, has nowhere been better expressed than by Dr. Johnson, whose introduction to his dictionary needs only the substitution of a few words (bracketed to protect his prose from contamination) in order to serve equally well as an introduction to this work:

"I look with pleasure on my book, however defective, and deliver it to the world with the spirit of a man who has endeavored well. That it will immediately become popular I have not promised to myself: a few wild blunders, and risible absurdities, from which no work of such multiplicity was ever free, may for a time furnish folly with laughter, and harden ignorance into contempt, but useful diligence will at last prevail, and there never can be wanting some to distinguish desert; who will consider that no [classification] ever can be perfect, since while it is hastening to publication, some [discoveries] are budding and some [theories] falling away; that a whole life cannot be spent upon [one classification], and that even a whole life would not be sufficient; that he, whose design includes whatever [classification] can express, must often speak of what he does not understand; that a writer will sometimes be hurried by eagerness to the end, and sometimes faint with weariness under a task, which Scaliger [might well have compared, as he did dictionary-making,] to the labors of the anvil and the mine; that what is obvious is not always known, and what is known is not always present; that sudden fits of inadvertency will surprise vigilance, slight avocations will seduce attention, and casual eclipses of the mind will darken learning; and that the writer shall often in vain trace his memory at the moment of need, for that which yesterday he knew with intuitive readiness, and which will come uncalled into his thoughts tomorrow."

This work, as such, was begun in 1927 when I came to the American Museum to follow, at a great distance, in the footsteps of W. D. Matthew, who then left the Museum to go to the University of California. The classification began as a simple list of orders and families for use in the systematic catalogue of our collections. It soon appeared that there was a more general demand for such a list, and an outline of the classification was published in 1931. This carried the classification only to families, without bibliographic citations for the names and with only the briefest of notes. During the following years as much time as could be spared from other work was devoted to revision and expansion and to filling in the grades below families. Aside from the initial task of compilation, these have been years of exceptionally rapid discovery and intensive study, so that ideas of classification have had to be revised constantly not only for the inclusion of new groups but also in accordance with new theories of affinities. The whole classification was rewritten three times from beginning to end, and lesser changes have been made constantly right up to the time of going to press. Despite this labor, it has been impossible to keep the revision absolutely uniform or to have all parts completely up to date, as will be well understood and charitably excused by anyone who has ever attempted a similar task.

Of course my own knowledge, experience, and, I hope, judgment have increased during the many years while this classification was in work. This is reflected in numerous changes from the preliminary form published in 1931, in addition to those due to the discoveries of the intervening period. Doubtless waiting another 10 years would have resulted in further desirable changes, but, as Dr. Johnson found, a whole life cannot be spent on one task and a whole life would not suffice. In the meantime the classification is needed.

The practical purpose that underlay the beginning of this task has been kept in mind to the end. It is intended as a working classification. But the best practical work, in classification as in all parts of science, depends on theory and in its turn assists the rise and revision of theories. As the actual classification grew and as it was used in and modified by extensive first-hand researches, a large mass of notes and of ideas regarding

principles and theories also accumulated. These appear to be no less useful and no less interesting to zoologists than the classification itself, and they have also been incorporated in the present work. They bear, first, on the principles of taxonomy with special reference to the classification and nomenclature of large groups and, second, on the general history and affinities of the various groups of mammals and their integration with the classification of the Mammalia. The first subject is treated in an introductory essay, part 1, and the second in what amounts to a series of notes on the classification, part 3, which can hardly be called brief but are really succinct in comparison with the magnitude and complexity of the material treated. Finally a large bibliography is provided and serves a triple purpose: to give original citations of names, to document conclusions, and to assist the reader to broaden and bring up to date his knowledge of particular groups of mammals.

Thanks to the continuous availability of one of the best existing libraries of mammalogy, both palaeo- and neo-, almost all the publications cited have been seen, although inevitably a few, mostly of quite minor importance, have not been directly available. Of course some thousands of books and papers not here cited have also been read. The work is not entirely one of compilation but also involved, as any classification must to merit attention, the examination of original specimens of almost all the families and the majority of the genera, made possible by having at hand great collections of both fossil and recent mammals as well as by visits to other museums. Original research has also been done on some members of most of the orders of mammals. The exceptions in this respect are Chiroptera, Cetacea, Tubulidentata, Embrithopoda, and Hyracoidea (two of which are nearly monotypic orders), carefully studied with specimens but not the subjects of any important original research by me. This statement is not made in order to claim exceptional authority—probably no one is an outstanding first-hand authority on all mammals, living and fossil, and certainly I am not—but only to present credentials for the important fact that this classification is not the result of book knowledge alone.

No regular research assistance has been available, and for the most part the work has been done single-handed, a serious defect both from the point of view of time consumed and of probable failure to minimize idiosyncrasies and personal shortcomings. During the last stages of the work, however, much help was received from Mrs. Rachel Husband Nichols and Miss Jannette M. Lucas, both of whom spent many months at the laborious task of checking references and compiling much of the bibliography. It is a pleasure to acknowledge the help received from both of these people.

In addition, aid was given to the author from many other sources. Dr. T. S. Palmer aided very materially in tracing the original publications of many names. After the appearance of the first outline of the classification (Simpson, 1931a), Dr. W. Dwight Pierce made suggestions regarding bibliographic citations and some other details of nomenclature, most of which have been adopted here.

The working outline for this classification was examined as a whole, and its principles, as well as many of the more concrete problems, were discussed at length some years ago by the late Dr. W. D. Matthew, Dr. Henry Fairfield Osborn, and Dr. Walter Granger. Dr. W. K. Gregory, Dr. Childs Frick, Dr. Barnum Brown, and Dr. R. T. Hatt similarly assisted. Since then these colleagues and many others have helped further with various parts of the classification. Dr. A. E. Wood checked much of the Lagomorpha and Rodentia. Dr. H. E. Wood, 2nd, went over the Perissodactyla in detail, and Dr. E. H. Colbert did the same for the Artiodactyla and part of the Cetacea, besides giving assistance on numerous other points throughout the classification. Information and ideas have been gleaned on a smaller scale or in a less definite way from so many others that it is impossible to list them formally, and I can extend only blanket thanks to all the zoologists who have helped to instruct me. It must be added that my mistakes are my own and that none of the specialists consulted endorses all details of my arrangement of his group.

This manuscript was completed late in the

year of 1942, and only a few minor emendations have been possible since that time.

GEORGE GAYLORD SIMPSON
The American Museum of Natural History
December 1, 1942

Dr. Simpson left the Museum for service in the Army of the United States on December 2, 1942. After his departure, the manuscript was transcribed from his original handwriting to typescript under my direction. It was after the manuscript had been fully transcribed that the final, detailed checking of dates, references, and the like was undertaken by Mrs. Nichols. This proved to be a long and difficult task, occupying many months of Mrs. Nichols' time. At the same time the typescript was critically read by Dr. John Eric Hill, who made various corrections and numerous helpful suggestions. I wish to express at this place the appreciation of Dr. Simpson and of the American Museum of Natural History that is due Mrs. Nichols and Dr. Hill for their successful completion of this phase of the work.

During this final check of the manuscript any discrepancies or unsettled problems were submitted to various workers for decisions, particularly to Drs. John Eric Hill, G. H. H. Tate and Edwin H. Colbert, upon whom the responsibility for such decisions must rest.

EDWIN HARRIS COLBERT
The American Museum of Natural History
March 24, 1944

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PART 1. PRINCIPLES OF TAXONOMY

IT IS IMPOSSIBLE to speak of the objects of any study, or to think lucidly about them, unless they are named. It is impossible to examine their relationships to each other and their places among the vast, incredibly complex phenomena of the universe, in short to treat them scientifically, without putting them into some sort of formal arrangement. The science of arranging the myriad forms of life is taxonomy (from τάξις, arrangement, and νόμος, ordinance). A formal classification of animals is a part of taxonomy, but only a part when "taxonomy" is used in its full sense, and it is also a practical application of some particular set of taxonomic principles, of which many different sets are possible and useful.

Taxonomy is at the same time the most elementary and the most inclusive part of zoology, most elementary because animals cannot be discussed or treated in a scientific way until some taxonomy has been achieved, and most inclusive because taxonomy in its various guises and branches eventually gathers together, utilizes, summarizes, and implements everything that is known about animals, whether morphological, physiological, psychological, or ecological.

In this inclusive sense taxonomy embraces a great many different fields of endeavor, each involving its own data and each demanding some differences of approach, but all inseparably related. Emphasis of a particular one of these lines of approach has often obscured the existence of a common goal, and a myopic viewpoint has hidden from many students the final unity of the field of taxonomy. A generation or so ago taxonomy had fallen into disrepute. It was believed to be a blind alley, a pursuit for hack workers only, or a phase happily outgrown. "Taxonomist" was a term of reproach, and the bright young men and the older students who had, or thought they had, a truly broad, scientific, and modern viewpoint carefully avoided the subject. They were, in fact, frequently engaged in work that may properly be called taxonomic, but they did not recognize this and they scorned the name, because "taxonomy" seemed to them to mean little more than sorting dead specimens according to a few rather superficial morphological characters, writing out labels, and then stowing the specimens away in drawers.

Sorting and labeling are necessary, difficult, and important activities, not deserving scorn, but they can be done in better or in worse ways, and they are only one quite limited aspect of the systematic arrangement of knowledge and theories of animal relationships, in other words, of taxonomy. A revival of taxonomy is now occurring as these facts are being recognized—or, one should say, as they are being more widely and again recognized, for there have always been some taxonomists with a broader viewpoint, and few of the early naturalists had the narrow concept of taxonomy that finally brought it into disrepute. For instance, one of the most fundamental goals of modern biological research is comprehension of the way in which species arise, and we now find classifiers, experimental biologists, geneticists, ecologists, physiologists, statisticians—even sociologists, psychoanalysts, and many other apparently most non-taxonomic students—working together on this subject with full recognition of the fact that the common element in their problem is fundamentally taxonomic.[1]

The aspect of taxonomy involved in sorting and labeling, zoological classification in a particular and limited sense, has also profited by this broadening of interests and shows signs of rejuvenation and improvement. The classification of recent mammals (to limit the scope to a field included in the present work) had, indeed, become mostly hack work. In earlier times, when quite novel sorts of mammals were constantly being discovered, such work was so exciting, new, and important as to evoke the keenest interst and to reward the highest skill. Now no living zoologist has seen the discovery of any major groups of recent mammals (perhaps three or four families, at most, all rather closely related to some already known), and the discovery of really new genera and species has slowed to such an extent that it is clear that almost all existing kinds of mammals have been found. Thus after some two centuries classification tended

[1] The rise of this viewpoint is well demonstrated and exemplified by "The new systematics," edited by Julian Huxley, Oxford, 1940.

to degenerate into either the routine identification of collections belonging to known groups or the resorting of such known groups and the splitting up of their families, genera, and species to make two (or 10) names bloom where only one had been before. Neither activity can be said to constitute a particularly useful contribution to science.

From this sterile stage where the final degradation of mediocrity seemed to have been reached, classification is turning into two other main directions under the stimulus and within the framework of the new taxonomy. Neither of these trends is really new; on the contrary, both have been involved in taxonomy from the earliest times, but they are beginning to have a new fruitfulness and a new, richer promise. The first concerns mainly the lower levels of classification, species and smaller units. Its formal result may be no more than new definitions of these units in particular genera or families, but the important point is that these definitions are reached in the light of group criteria for variation and with genetic controls or analogues. Breeding structure, population size, ecological conditions, and many other non-morphological factors are also taken into consideration. The aim is not merely to define populations in a better way than by the older, entirely morphological rules of thumb, but also to explain their differences and resemblances and to correlate these with all the factors of organic evolution.

In spite of the fact that all studied mammals have been placed in species, the definition and study of species in this more modern way have barely been begun and involve, beneath the surface of apparently conservative Linnaean classification, a real revolution. It will provide the taxonomists with work of most fundamental importance and will give the once supposedly moribund classifiers a new lease on life for another two centuries or so. Because of the nature of materials and methods, such work is mainly in the province of the student of recent animals, the neozoologist, but the palaeozoologist also contributes significantly to it and derives much from it.

The second great task and promising field comprise the study of phylogeny and the reconstruction of classification in accordance with it. This work necessarily extends to all levels of classification, but it is more important and, at present, more fruitful on higher levels. Species and smaller groups can often be adequately distinguished and interpreted on the basis of their present condition, but genera and higher units can be ideally understood only in the light of a longer phylogenetic history. Moreover the history of individual species is commonly obscure and must remain so until much more groundwork has been completed, but the broader outlines of animal history are becoming increasingly clear and can profitably be studied in the light of present knowledge.

The data of neozoology are highly pertinent to the problems of phylogeny and major classification, but this work has fallen more and more into the field of the palaeozoologist who should, for this purpose, be a competent general zoologist as well as a palaeontologist. The reasons for this shift of interests are partly historical and partly inherent in the subject. Neozoologists have tended to concentrate on minor units as the discovery of major living groups slackened. They have to some extent lost sight of broader relationships, and only a few of them have acquired adequate knowledge of the fossil evidence pertinent to their problems. The quantity and variety of palaeontological discovery, on the other hand, are still increasing rapidly, and palaeozoologists not only have necessarily retained a broader viewpoint as regards their own materials but also have been forced to acquire working knowledge of the living animals related to their fossil forms. A second reason for the greater concern of palaeozoologists with major classification is that most animals are extinct. At present two-thirds of the known genera of mammals are known only from fossils, and the proportion is increasing rapidly because the discovery of new genera and larger units (really new, not just the elevation of a known group to higher rank) is still a commonplace in palaeozoology but has become an extraordinary and rare event in neozoology. Finally, phylogeny is a historical subject, and the palaeozoologist's point of view is primarily historical and his is the more direct approach to animal history.

The renewed vigor of phylogenetic studies and of the taxonomic investigation of larger

groups may be attributed in part to the great accumulation of fossils from all parts of the world and in part to the revival of interest in taxonomy as a whole and to the broadening of its basis and the growth of new methods and data in all fields of biology. The classification presented in the present work is a summary of only a very small part of taxonomy and a contribution of very limited scope within this broad science. Regarding this particular classification, the rapid advance of taxonomy makes both inevitable and desirable that it should quickly become outmoded. Such more durable value as it may have must probably lie in its relationship to the development of some parts of taxonomic theory, sketched briefly and partially in this introductory essay.

The following remarks may also, to some extent, serve another purpose, which demands some indulgence from the more experienced and sophisticated taxonomists who may read it. The former disrepute of taxonomy in general and classification in particular had as one result that these subjects were not, and in many cases still are not, taught to biologists and zoologists in training. Many of them have gone on to do taxonomic work of various kinds without ever having learned how. Some have remained virtually illiterate in this field, and their work has been a serious trial to their colleagues. Others have learned by experience but may still have occasional gaps in knowledge. A contribution, however small, to training in classification may not, then, be unwelcome.

PHYLOGENY

THE BASIS OF CLASSIFICATION

Classification consists of grouping things according to their characteristics or properties, placing them in a system of categories, and applying a designation to each group thus established. In zoology, the categorical system used is a hierarchy inherited from Linnaeus, with some modification, and the method of designation, although still chaotic in some parts and in others dependent on a sort of zoological common law, has been incompletely codified in a set of international rules. Before discussing the hierarchy and nomenclature, attention will be directed to the problem of the basis on which the groups to be systematized and named are to be recognized and defined.

The oldest and most obvious system of classifying animals is according to their mode of life, environmental adaptations, and associations. In such classifications whales might be grouped with fishes, bats with birds, and moles with voles. Classifications using these and analogous criteria still have practical value and they are still used in less naive form, for instance, in the ecological classification of plants and animals into biocenoses. Such a basis has, however, long been abandoned for purposes of primary zoological classification or formal nomenclature.

The second important system of classification is commonly called morphological, but all practical classifications involve morphological criteria, and this particular method may more distinctively be called archetypal. Its basis is the grouping of animals according to the number, and to some extent the kind, of structural characteristics that they have in common. Each grade in a hierarchy corresponds with certain fixed characters possessed by all the animals included under a given rubric at that level. The lower the hierarchic rank, the more characters held in common by the included forms. At one end the highest category is organic creation, with only life common to all its members, and at the other end are minimum units, each including individuals alike in all their hundreds or thousands of characters except for incidental, random fluctuation. Each group of the system has a fixed model, an archetype, consisting of a given set of morphological characteristics, and any animal that agrees, in this set of peculiarities, with the archetype belongs in that group.

The ideal of archetypal classification would be reached if the series of descending units including a given animal defined all its distinguishing characters and at the same time implicitly specified on each level all the animals with similar characters. For complete

convenience each step down the scale might add one diagnostic feature to the set. For instance, an excellent classification, on these premises, would be:

A. With a backbone. (Includes all vertebrates.)
I. Giving milk. (Includes all mammals.)
1. Without teeth. (Includes some edentates, whales, monotremes, etc.)
a. With claws. (Includes South American anteaters, pangolins, monotremes.)
With a plume-like hairy tail. (Includes only the animal called *Myrmecophaga tridactyla* in the neo-Linnaean system.)

This was the sort of classification adopted by almost all early naturalists, including Linnaeus and most of his successors before Darwin. The meaning read into it was either that it was a subjective and arbitrary system adopted solely for convenience or that it corresponded with a set of supernal models, archetypes in the philosophical sense, of which objective animals are more or less imperfect copies. In the first case, the attitude was that of a librarian who might place all quarto volumes together, the more easily to locate a tome that he knew to be a quarto, without any suggestion that the resemblance implied any community of origin, subject, author, or plan. The second, philosophic basis might be likened to a sort of subject classification of the works of an extraordinarily prolific author (or a divine creator) who treated a large but definite number of themes in still more numerous different books, each with many variant editions. In both cases the resulting classifications were of the same sort, although in each no two students used precisely the same criteria for their catalogues.

For aid in the easier identification of specimens, classifications wholly archetypal in principle are still in common use. They are entirely valid, are often more practical than any others, and can even be called perfectly natural in some sense of that abused word, but they are not now accepted as the standard or ideal of zoological classification. In fact, they are not, as a rule, called classifications but keys, and it is understood that a "true" or "natural" classification has, by intention, quite a different basis and expression.[1]

The change in the assumed basis of classification came with general acceptance of the theory of evolution. The belief that different animals, even very unlike animals, were actual flesh-and-blood relatives and had common ancestors suggested that it would be more natural, or philosophically preferable, to define groups by community of origin. This radical change, much the most revolutionary in the whole history of taxonomy, had extraordinarily little immediate effect on the general nature and aspect of formal classifications. From their classifications alone, it is practically impossible to tell whether zoologists of the middle decades of the nineteenth century were evolutionists or not, and classifications intended to be phylogenetic differed as much among themselves as they did from frankly archetypal classifications.

This was partly because the superficial aspects of classification do not necessarily change when the underlying meaning changes —we still use the Linnaean hierarchy and nomenclature (in essentials), although we have rearranged and multiplied his categories and give them a totally different significance. More particularly, in this transition period and, in decreasing extent, almost up to the present, the reason for so little evident change in classification was that the evolutionists and non-evolutionists followed the same procedures. The evolutionists continued to group animals by the number and kind of characters that they have in common, but they explained the possession of these characters by community of inheritance, while the non-evolutionists explained them by a subjective pattern. By substituting "common ancestor" for "archetype" the same classification could be considered phylogenetic or not, at will. The common ancestor was at first, and in most cases, just as hypothetical as the archetype, and the methods of inference were much the same for both, so that classification continued to develop with no immediate evidence of the revolution in principles.

As changes in classification did begin to result from the adoption of the phylogenetic

[1] But it will be found that some modern classifications are almost completely archetypal in fact, although not so intended by their authors in theory.

basis, they were in large part caused by simple shifts in emphasis on particular characters. In non-evolutionary theory, there were, for instance, few good reasons for not classifying whales as fish. Their living in water, their having fins, their lack of hair, and their other fish-like peculiarities might as well have been emphasized as their warm blood, their mammary glands, their lungs, and their other mammal-like characters. But in evolutionary theory it becomes apparent that whales had terrestrial ancestors and that their mammal-like characters were derived from those ancestors and their fish-like characters were not. Hence whales are mammals phylogenetically. Such changes of emphasis eventually did produce profound changes in the substance, to much less extent in the form, of classification. The change would have been more immediate and still more radical were it not that the non-evolutionary taxonomists did weight characters, sometimes in accord with later evolutionists. Thus Linnaeus did class whales as mammals because he felt that some characters later found to be phylogenetically significant were somehow of extra importance.[1]

The long struggle away from archetypal and toward truly phylogenetic interpretation of animal relationships, not yet wholly completed, has involved these main phases: first, the effort to determine in individual cases which characters in common were really derived from a common ancestor and which were not, and second, the realization that phylogeny is kinetic and that this aspect is primary while the static concept of characters in common is a useful tool but is not a final criterion and may lead to erroneous results.

Acceptance of phylogeny as the basis for classification, not because it is the only valid basis but because it is agreed upon as the most desirable, is merely a preliminary. It leaves two enormous, almost inconceivably complex problems to be solved. Phylogeny must itself be determined before classification can be based on it. A phylogeny, even when perfectly known and universally accepted (which none is in detail), is not a classification, and the intricate relationship between phylogeny and classification leaves more than ample room for the exercise of skill and judgment and for differences of opinion.

THE DATA OF PHYLOGENY

Phylogeny cannot be observed. It is necessarily an inference from observations that bear on it, sometimes rather distantly, and that can usually be interpreted in more than one way. These data may be more or less direct results of phylogeny, or they may be phenomena that have been indirectly modified by phylogenetic history. Since that history has some influence on everything that an animal is or does, the data for phylogenetic inference may, and as far as practicable should, include everything that can be known about an animal. But no animal is completely known, and all that is known cannot always be used in practice, so that the data actually used are in many cases very limited.

The most direct, but unfortunately not the most useful, approach to the phylogeny of recent animals is through their genetics. The stream of heredity makes phylogeny; in a sense, it is phylogeny. Complete genetic analysis would provide the most priceless data for the mapping of this stream, although it would only exceptionally provide unequivocal and conclusive criteria (as in the case of certain chromosomal inversions that must, for mechanical reasons, have risen in a fixed sequence[2]). Aside from such rare cases, genotypic similarities and dissimilarities have to be interpreted phylogenetically in much the same way as phenotypic likenesses and differences, and the advantage of genetics lies rather in the fact that the genes (and some other genetic factors) are the immediate physical continuants of phylogeny, while morphology is less direct, a result of these hereditary factors as modified by other influences.

[1] The "insight" often attributed for such reasons to Linnaeus and some other early naturalists may nevertheless be false praise. On his own premises Linnaeus produced an almost perfect classification, which is true enough and praise enough. Some of his successors did not—indeed some of the points on which they "anticipated" evolutionary classification seem almost to be illogical or erroneous on their own grounds, not ours. On points where good archetypal and good phylogenetic classifications tend definitely to differ, Linnaeus anticipated phylogenetic classification very seldom and only by chance, as would be expected.

[2] See Dobzhansky, 1939, pp. 339–368.

Within their present scope, the importance of genetic data for phylogenetic studies cannot be overemphasized, but that scope is so limited that such data are not in themselves adequate for the reconstruction of more than a very few, sharply isolated, and quite minor parts of the general phylogeny of animals. They are not particularly important in this way, but are irreplaceable as examples and as the foundation for theories and limitations that must be taken into account in the phylogenetic interpretation of other sorts of data. The limitations arise in part from the physical impossibility of making a really complete genetic analysis for any animal or of making a useful partial analysis for more than a very few laboratory animals. Obviously, extinct animals, so much more numerous than recent animals, are excluded; so, from sheer limitations of time and facilities, are 999 recent species out of 1000—to be conservative. At best, such direct analysis is possible only within single species or, in relatively rare cases, between very closely allied species. Although (probably) homologous genes can occasionally be recognized in distantly related animals by their phenotypic expressions, the homologization of genetic structure throughout any considerable generic or higher taxonomic unit appears at present to be an impossible goal. Despite these inherent boundaries of experimental genetics, developments like theoretical and observational population genetics, which is as much a branch of taxonomy as of genetics, greatly extend the usefulness of this subject and tend to make its applications more general, but still, in the main, on low taxonomic levels.

Physiology is another field that supplies essential data for phylogeny and that is, like genetics, confined to living animals and to a small percentage (but larger than for genetics) of those as regards direct observation. Such physiological characters as homothermy and poikilothermy have long been used in classification and now seem rather obvious in that respect. That particular character and many others like it are so broadly distributed and so completely correlated with structure, which is more easily observed, that they cannot be said to be of much immediate use in classification, interesting as they are as phylogenetic phenomena. More recently various biochemical characters have been investigated, such as the primate blood groups (which, however, as yet appear to have very limited value for taxonomy). Of greater promise in this field is the mostly very recent work on systematic serology.[1] It still suffers from paucity of observations, only a few animal species having been studied in this way, and from a consequent deficiency of well-founded general theory and interpretive principles. Some students seem to believe that serological reactions are directly proportional to phylogenetic relationship, which surely is not true, and others, that there is no correlation, which is equally surely untrue. "Comparative serology, like comparative morphology, is no simple guide to animal relationship . . . the two methods of analysis should be considered complementary to each other" (Boyden). It is probably an exaggeration to compare serology, which has an unknown but possibly limited hereditary repertory, with the whole field of morphology, which may have an incomparably larger repertory, and the domain of serology is much smaller, but systematic serology seems likely to become a powerful adjunct in the study of phylogeny. At present its data are too few and of too dubious significance to have had a particularly noticeable effect on classification.

In the latter part of the nineteenth century some evolutionists believed that they had discovered the golden key to phylogenetic problems in the study of embryology according to the recapitulation theory, formulated and publicized by Haeckel on the basis of von Baer's theory of ontogenetic differentiation. In its crude form, the principle was that "ontogeny repeats phylogeny," therefore to reconstruct phylogeny one has only to observe ontogeny, a relatively easy and direct approach. This dream has vanished, but embryology retains a place, far less simple than was hoped, in the study of phylogeny.[2] On-

[1] Excellently reviewed by Boyden, 1942, pp. 109–145.

[2] The collapse of the recapitulation theory was noted and accelerated by Garstang, 1922, pp. 81–101. The place of embryology in modern taxonomy is well reviewed by De Beer, 1940, in "The new systematics," pp. 365–393.

togeny does not repeat phylogeny. It is inherited, just as adult structure is inherited, or, from another point of view, it is inherited and adult structure results from it. Embryonic structure is no more free from the effects of new mutations, from adaptation, convergence, divergence, and the like than is structure in any other phase of the life cycle. Embryos are often more similar than adults in related animals but they may actually be less similar. Special features held in common with other embryos may be evidence of common origin or may not. Embryological data add to the other morphological data available for the study of phylogeny, but they are not essentially different in kind. The real point is not a division into embryological and morphological fields but consideration of the whole animal, which includes its kinetic structure throughout the life cycle and not merely the static condition at an instant in time. As a rule, taxonomic groups based on any one embryonic stage agree closely with those based on any one adult stage. This happens to be particularly true among mammals, in most of which the embryonic adaptations and environments are closely similar. In other cases the two disagree (notably among some invertebrates) and then the conflict must be resolved on the merits of each case; sometimes the embryos and sometimes the adults seem to give the more valid taxonomic grouping.

Some classifiers deny that geography has any useful bearing on phylogeny—in fact, some classifiers deny that anything but individual morphology has any valid use in this connection, but we need not take them seriously. It is self evident that geography is related to taxonomy, and in so difficult a study it is inexcusable to reject offhand any line of evidence that might give light. It is true that zoogeographic facts are often hard to interpret phylogenetically and sometimes seriously misleading, but the same can be said of any other sort of data. Similar animals living in adjacent areas are likely to be more closely related than animals, even equally similar animals, widely separated. Animals of similar immediate geographic origin are more likely to be related than animals whose immediate ancestors lived in different regions—in fact, animals clearly cannot have common ancestry without also having common geographic origin. These and other principles are highly pertinent in interpreting phylogeny, and they deserve equal weight with morphological data unless the latter unequivocally contradict them. For instance, there are in South America many rat-like rodents, all rather similar in basic characters, all known to have had North American ancestors not earlier than the Pliocene, and many closely related to forms now living in North America. It is possible that some of these Neotropical genera are of quite different phyletic origin from others and, concurrently or alternately, that some have their closest living relatives in distant parts of the Old World, and this has been claimed on morphological grounds, but the geographic situation makes this possibility most improbable and throws the burden of proof on this claim. Zoogeographic and phylogenetic theories must be concordant if both are true, and a stated phylogeny cannot be considered well established unless it can be reconciled, at least, with any equally probable zoogeographic deductions.

Genetical, physiological, embryological, and geographical data have been mentioned first, mainly because the orthodox classifier is likely to think of them last, but morphological data and palaeontological data (also largely, but not exclusively, morphological) always have been and (barring some wholly unheralded and most improbable achievement in some other field) always will be the principal basis for the study of phylogeny.

The postulate of archetypal classification was that structural similarity is proportional to natural affinity, leaving "affinity" as an undefined or metaphysical concept. The same postulate was accepted in phylogenetic classification, restated in more or less this form: structural similarity is indicative of common phyletic origin, and as a rule its degree is proportional to the nearness of the common ancestry. There is still little doubt that this tends to be true, or is true on an average, but it is now recognized that this criterion is insufficient for the determination of probable phylogeny and that it may be misleading in individual cases.

As a somewhat crude but striking example, an exhaustive comparative list of the morphological characters of a thylacine and a kangaroo would probably show that the thylacine has a greater absolute number of such characters in common with a wolf than with the kangaroo. (In fact no such list has ever been, or is likely to be, made; another reason why simple tabulation of "characters in common" is not a practical means of classification.) Similarly it would probably be found that the kangaroo has more characters in common with a jerboa than with the thylacine.[1] Now no one has any doubt that the thylacine and kangaroo are phylogenetically much closer together than either one is to either wolves or jerboas. The first two are classified in one order, Marsupialia, and the last two in two different and distant orders. It is not correct to say that this arrangement is still morphological in principle because the Order Marsupialia is commonly defined in morphological terms, and the collocation is supported by regarding the characters common to thylacines and kangaroos more basic, or important, or essential, than those common to thylacines and wolves or to kangaroos and jerboas. That would beg the question, because the selection and weighting of these characters are not in accordance with their number, magnitude, or any other purely morphological criterion but in accordance with their phylogenetic significance as determined on other grounds. The great majority of characters used in the study of phylogeny and in classification are indeed strictly morphological, but their interpretation is not.

Much the best data for the phylogenetic interpretation of morphology are provided by palaeontology. Fossils are documents that free us from the limitation of studying history only by its results at one given time, a time purely accidental from the standpoint of phylogeny as a whole, which has no useful relationship to the fact that we happen to be living now, and a time that is for many groups, including the mammals, one of the worst that could be chosen for such a purpose. In some cases (a large absolute number of cases but very few in comparison with the diversity of forms of life) intergrading sequences show how one group of animals arose from another. These sequences are not phylogenies in the flesh (or bone) and are seldom so obvious as to permit no possible misunderstanding, but they are the nearest thing to seeing phylogeny. In many more cases the sequences, as now known, are broken by considerable gaps but still show trends that point to phylogenetic connections by extrapolation, or intermediate types that suggest or support a common origin for otherwise sharply distinct groups. Finally, fossils give examples of the operation of evolution on a large scale and over a long period. From these examples general principles can be deduced, and these principles, together with those derived from genetics, embryology, and all the other fields of taxonomic studies, serve as an increasingly secure basis for the phylogenetic interpretation of morphology.

[1] In fact, when kangaroos were discovered, Erxleben, Blumenbach, and other highly competent taxonomists did classify them as jerboas on these grounds, entirely valid in archetypal classification.

MORPHOLOGY AND PHYLOGENY

In that part of taxonomy that is directed toward the production of a formal classification, the observational data used in practice are almost wholly morphological. The principles of selection and interpretation of these data are, as a rule, phylogenetic and are drawn from the much larger field of taxonomy as a whole. Phylogeny may, however, be implicit rather than explicit in the work of classification, and this is particularly true of the classification of the great numbers of contemporaneous species, subspecies, or other small taxonomic units in the recent fauna of the world.

The procedures of reconstruction of phylogeny from comparisons of contemporaneous animals are in some respects different from procedures involving sequences of faunas, although the two approaches are complementary, have the same goal, and involve many of the same data and methods. In the study of sequences there is a visible, dynamic flow in which the direction and rate of structural change can be directly observed, at least in part. In the study of contemporaneous faunas, only some of the results of phylogeny at a given instant are observed.

All animals resemble each other in some respects, but no two are exactly alike. The

basic postulate of phylogeny is that all animals had a common origin[1] and that in a given group, such as the Mammalia, all its members are genetically continuous through their ancestry. In comparing two animals, the phylogenetic interpretation of morphology seeks to estimate how far back in their history the latest genetic continuity (interchange) existed between their ancestors. This datum point may be near the time of origin of life or it may be only a generation in the past, and its reference to anything approaching a definite, absolute scale is very seldom practicable in the present state of taxonomy. The more general sort of inference is relative. It involves three or more groups of animals and seeks by cross comparisons of two at a time, or equivalent procedure, to establish the sequence of the origin of the two or more discontinuities that have arisen in their phylogeny.[2] As will be seen, this sequence cannot directly be translated into formal classification, but it is the most essential point in phylogenetic morphology, which is the basis of classification.

Animals may resemble one another because they have inherited like characters, homology, or because they have independently acquired like characters, convergence. On the average, two animals with more homologous characters in common are more nearly related, their ancestral continuity is relatively more recent, than two animals with fewer. There is no theoretical reason why this should always be true, and there certainly are many cases in which it is not true, particularly among abundant, small units, like species, and between other groups whose discontinuities arose within a relatively short span of time. Such groups are, however, related in approximately the same degree, and any errors in inferring the exact sequence among them are rather unimportant and do not essentially falsify the general picture of phylogeny. It is not possible and it is not particularly desirable from a practical point of view that phylogeny should be so exact a science that it could establish any difference in degrees of affinity, however slight. The rule that degree of homology is directly proportional to degree of affinity is true within limits narrow enough for most purposes and is a valid working principle. For larger groups, particularly, greater discrimination of degrees of affinity can frequently be obtained from palaeontological data, and such determinations are, of course, preferable when they are obtainable.

It is a complication that a third sort of process also produces similarities: parallelism. The term is descriptive rather than explanatory and refers to the fact that distinct groups of common origin frequently evolve in much the same direction after the discontinuity between them has arisen, so that at a later stage the phyla may have characters in common that were not visible in the common ancestry but that tend, nevertheless, to be more or less in proportion to the nearness of that ancestry. This proportional tendency distinguishes parallelism from convergence, but the distinction is far from absolute. The two phenomena intergrade continuously and are often indistinguishable in practice.

In the most restricted sense virtually all evolution involves parallelism. Homologous genes tend to mutate in the same way. The chances of survival of a single mutation are extremely small, and a mutation must usually occur in parallel (in different animals) many times before it becomes permanently established and sufficiently widespread to be characteristic of a population. This process is not immediately affected by a discontinuity in the breeding structure of the population. The separate and now discontinuous groups still carry homologous genes, and these still will tend to have the same mutations. Thus such groups may and, in all probability, frequently do develop the same characters, not typical of their ancestry or directly inherited but nevertheless due to inheritance: the inheritance of genes prone to mutate in the same way.

A distinctly different genetic process may

[1] It is not an absolutely necessary postulate that all forms of life had one ultimate ancestry, but the postulate is accepted for almost any defined subdivision of the Animalia, and particularly for higher metazoans such as Chordata or Mammalia.

[2] Between subspecies, a literal genetic discontinuity does not necessarily exist. It may be said either that they have no phylogeny, among themselves, or that phylogeny as applied to them has different implications and principles. (This is not to say that the origin of a subspecies must involve any evolutionary process different in kind from those involved in the origin of species.)

produce morphological phenomena hard to distinguish from those of mutational parallelism and also described as parallelism. Proportions and some other characters (for instance, bony processes and perhaps horns in some cases) are commonly the result of relative growth rates that are genetically controlled. That is, an animal does not inherit these proportions as such, but inherits factors that determine what the proportions will be at any particular gross size that the animal happens to attain. Then if two distinct lines of descent both evolve in the direction of greater adult size—and this is so common as to be an established rule (with the usual exceptions)—they may develop characters of proportion that are the same in both and that are quite different from those of the common ancestry but that were, nevertheless, inherited from that ancestry. Relative growth has been most thoroughly studied, but there appear to be many genetic controls, the phenotypic expression of which depends on other factors and which can, therefore, produce this sort of morphological parallelism.

There is still another sort of parallelism that does not arise primarily from common inheritance, like the two sorts just mentioned, but that has the same sort of morphological results and the potentialities of which are also approximately proportional to degree of affinity. Groups of common origin inherit many homologous characters, and they frequently also retain or develop similar habits and environmental preferences. Then convergence that is strictly such and not attributable to an ancestral genetic factor is likely to occur in them, and if it does, it acts in the same direction as the conservative element of homology. The coincidence of convergence and homology produces particularly close morphological parallelism. (For instance I so interpret the resemblance of †borhyaenids and dasyurids, although some students think that this is more strictly homologous.)

Homology is always valid evidence of affinity. Parallelism is less direct and reliable, but it is also valid evidence within somewhat broader limits. It may lead to overestimates of degree of affinity, but it is not likely to induce belief in wholly false affinity. Convergence, however, may be wholly misleading, and a principal problem of morphological classification on a phylogenetic basis is the selection of characters that are homologous or parallel and not convergent. The greater part of the difference between phylogenetic and archetypal classification has arisen from the difficult and still incomplete task of distinguishing convergent resemblances from others, a task ranging from such gross and easy cases as the thylacine-wolf resemblance to most subtle and difficult, perhaps really insoluble, cases such as may be involved in shades of pelage among rodents. It cannot be hoped that important errors in this respect have been or are likely to be completely eliminated, but there is reason for confidence that such errors, in the main outlines of mammalian phylogeny particularly, are now few. Their elimination has been, not solely but largely, due to palaeontological discoveries and studies. These studies have also established and confirmed the reassuring empirical rule that convergence also has fairly definite limits and that these limits become narrower the more sharply convergence is distinguishable from parallelism. In other words, the maximum possible effects of convergence also tend, although much less closely, to be in proportion to nearness of affinity.

These limits are set by the retention of ancestral dissimilarities in convergent groups, and the phylogenetic interpretation of differences is as important as that of likeness. As similarities must be divided into those that do and those that do not indicate the proximity of ancestral continuity, so dissimilarities must be divided into those that do and those that do not indicate remoteness of such continuity. All heritable dissimilarities are to some degree indicative of phylogenetic separation, but the differences that develop after discontinuity appears in an ancestral group are not to be weighed against the evidence for the former continuity. They indicate the remoteness of a particular dichotomy, but do not speak against the reality of previous uniformity at a given level. Thus the differences between thylacine and kangaroo are divergent on a subordinal level and are not inherited from different proto-marsupial ancestors. On the same level, the differences be-

tween thylacine and wolf are inherited from different ancestors, and they illustrate the descriptive principle of conservation, not of divergence, although they arose by divergence at a still more remote time, or on a still higher level of classification.

The principle of irreversibility, which is an extension and a special case of the principle of conservation, is one of those most widely used (under one name or another) in phylogenetic morphology, but few principles have been more confused or ill applied. Originally propounded by Dollo, the so-called law of irreversibility in its broadest form is that morphological structure in phylogeny does not wholly return to a markedly different ancestral condition. This has been interpreted to mean (and Dollo's epigrammatic style permitted the misunderstanding) that a specialized character never returns to a more primitive stage and that a lost character is never regained. In this form, the principle is not literally true, and adherence to it has seriously misled students and has been used to support theories of undeviating phylogeny that seem almost to deny the reality of evolution as a sufficient explanation of animal diversity. In fact there is no real doubt that the direction of evolution has changed very markedly within phyla, that single characters do sometimes return to an ancestral condition, and that lost characters can be regained.

The more general principle of which irreversibility is a special case is that the morphology of an organism has evolved through all the distinguishably different morphological stages in the phyletic ancestry of this organism and that the given structure would be different had any of those steps been different. This principle is not theoretically demonstrable: complete reversion and complete convergence are not wholly excluded by present genetical or general evolutionary theories, but they are highly improbable in the light of those theories. Empirically, the principle seems to have no exceptions if only higher structural grades or hierarchic categories are taken into account. Whether exceptions occur on a generic or specific level is a matter of opinion. At least none seems ever to have been clearly demonstrated. In application, the principle means that no degree of convergence has produced identity of structure and that a homogeneous morphological group does not arise from two or more different groups. In the closest and most striking instances of convergence known, the groups are still readily distinguishable, and animals do not become so modified that no perceptible evidence of their broader affinities remains.[1]

Thus the conservation of ancestral characters, or of less immediate effects of ancestral structural stages, sets limits to the degree of divergence of lines of common origin and to the degree of convergence of lines of different origin. An analogy among dissimilarities to parallelism in similarities would be the inheritance of different morphological characters in two lines from the same ancestry. Such a phenomenon is theoretically possible, but it appears to be rare and of no great importance. Of course, variants in an ancestral population are very commonly segregated in descendent lines, but the morphological peculiarities do then visibly exist in the ancestry as a group.

These are the most important principles that validate and guide phylogenetic grouping by morphological characters-in-common, the modern equivalent of archetypal grouping, sometimes so similar to the latter in appearance as to be mistaken for it[2] but fundamentally different in principle. These methods of interpretation can never be wholly discarded, but they are importantly and increasingly supplemented by palaeontological sequences which afford a more direct and certain approach to phylogeny. In the ideal case, in such a sequence the morphological variation of each population overlaps that of the next. It is then assumed that the populations are genetically continuous in a vertical, time, sense and that they are the physical expres-

[1] It may be said in opposition that this is arguing in a circle and that when structurally identical animals arise they are accepted *ipso facto* as of the same ancestry, or when all trace of affinity is lost the affinity is said *ipso facto* to be non-existent. This is true of the application of the principle, but it is based on numerous proved examples, as far as such things can be proved, and no contradictory case has been similarly proved.

[2] Some modern classifications are really quite indistinguishable from archetypal classification, but these are either failures or they are individual refusals to accept the conventional basis of modern classification.

sion of a true phylogeny. It has been pointed out that this assumption is not always justified in the most strict, exact sense, but it must in all such cases be so nearly true that it is merely quibbling to refuse to accept it.

More often there are gaps in the sequence, and any sequence sometime reaches an end, as far as our available record of it goes. The gaps can be filled by inference without much doubt when no marked change in the direction of evolution seems to have occurred. The almost universal absence of continuous record of the earliest stages of branching between important phyla constitutes a more serious difficulty, but the problems can usually be solved with reasonable probability because of the fairly obvious and simple criteria for convergence, divergence, homology, and conservation provided by the preserved sequences. If the early members of two groups are more alike than the later, their later dissimilarities are divergent. If the early members are less alike, their later similarities are convergent. If the early members are much alike and the later members have further likenesses, these are parallel. Characters shared by early and late members of one group are conservative. Those shared by early members of two groups are likely to be true homologues. Intermediate early groups, often appearing isolated in the record, tend to establish the affinities of the two and the nature of the common ancestry if, as frequently happens, the intermediate group has some characters common to the other two and some peculiar to each.

The concept of structural, rather than directly phylogenetic, ancestry is also indispensable in the useful interpretation of palaeontological data. The term may imply that a known early form, the structural ancestor, is such that it might be ancestral to a later group but that the lack of annectant types makes it impossible to assert direct descent with reasonable security. "Structural ancestry" may also mean that the known sequence is not believed to be completely linked by actual genetic continuity but that its various stages belong to the larger units (such as genera) through which genetic continuity ran, without necessarily involving the individual members or species of one genetic sequence throughout. From the point of view of superspecific groups, such structural sequences are legitimate and extremely useful approximations of phylogeny despite the fact that they cannot precisely be said to be phyletic. In the nature of things, structural sequences must be more numerous in palaeontology than phyletic sequences. For any one time in the past, fossils are obtainable only from limited areas and never from the same area for a continuous and major part of geological time. Thus the collecting area almost never includes the whole range of the group in question and usually excludes important variants, races, or species distributed elsewhere. If the center of phyletic evolution remained in one place for a long time, the centers of fossil preservation are likely to shift, and while deposition remained constant, the centers of evolution were likely to move. The fossil mammalian fauna known from a continent at any given time is frequently richer in genera of a given group than the recent fauna but is almost always poorer in species, and it cannot reveal the exact phyletic origin of all recent species.

CLASSIFICATION

PHYLOGENY AND CLASSIFICATION

It is often stated that the purpose of classification is or should be to express phylogenetic relationships, but, in the first place, no one has ever devised a method of classification that could express phylogeny sufficiently or consistently, and, in the second place, the system that is actually used in zoology was not devised for that purpose and is notably incapable of serving it. The basis of this system is phylogenetic, as has been strongly emphasized here, and this means that the groups to be recognized in classification should be as nearly as possible valid phylogenetic entities and that the criteria of definition are to have phylogenetic implications, but this is quite different from expressing phylogeny. The categories and nomenclature of classification are also used to dis-

cuss phylogeny and so to express it in quite a different sense, in much the sense in which a dictionary might be said to express the English language.

This is, as I see it, the primary purpose of classification: simply to provide a convenient, practical means by which zoologists may know what they are talking about and others may find out. It is helpful for this purpose and it is also a secondary but still essential aim that classification should be consistent with the most important thing that evolutionary taxonomists have to talk about, that is, with animal affinities.

Any subdivision of a general phylogeny that includes only series of populations genetically continuous in any direction (not excluding the time dimension) and through any included intermediaries is a valid and consistent phylogenetic group. Such groups are to be made the units of classification, but there is an enormous number of such possible groups, vastly more than can possibly be used in any one practical classification. If there were no disagreement as to the phylogeny of mammals—and few suppositions are more contrary to fact!—it still would be possible to base on that phylogeny a variety of classifications not literally infinite in number but certainly running into many millions, all different and all valid and natural in the sense of being consistent with phylogeny.

The particular classification that is to be used depends, first of all, on historical factors. It is possible, as some modern writers have shown, to invent a syntactic system and a vocabulary that more efficiently express the emotions of a particular individual than does orthodox English, but if language is to be used as a general medium of communication such experiments are not particularly helpful. Similarly almost any student of zoology might invent for the particular animals with which he is concerned a wholly new classification that would serve his individual purposes better than the orthodox system. Classification, however, like speech, is a means of communication and it requires a consensus and a certain degree of historical continuity in order to function. Good classification is conservative. A given group and name may originally have been defined on quite different grounds from those now employed and their limits may be largely accidental, yet they should be retained as long as they continue to be useful and do not definitely contravene the principles of modern taxonomy and the accepted theories of phylogeny.

Yet classification is and should be in a state of constant flux, and conservatism does not mean simply accepting a given arrangement because it is in use. There is an operative consensus that sets limits to reasonable choice, but there are also many alternatives with historical precedent and usage and these allow considerable latitude for selection. Beyond this matter of selection, which is guided by taste, experience, and authority (and authority is the taste and experience of others), classification changes mainly for two reasons: because new knowledge and theories make established arrangements inconsistent with the current understanding of phylogeny, and because increase in number of known groups and in how much is known about each may make desirable readjustment and subdivision of the scale of classification.

The framework of classification is a system of categories on a hierarchic scale, such that a group in any one hierarchic position is broader than any below it and includes one or more groups on the next lower level of the scale. The process of classification is to equate phylogenetically consistent groups of animals with the categories of the hierarchy in accordance with a series of historical and taxonomic principles, some of the more important of which will be discussed on following pages.

The actual practice of classification is less direct than might appear from so simple a statement of the relationship of phylogeny to classification and is not always clearly understood even by those most actively and proficiently engaged in it. A category of classification is theoretically defined, at least by implication, in phylogenetic and genetic terms. The thing thus defined is a group or population in which the objective units are individuals (but it is not the individuals as such that are defined). This group is real, natural, and absolute, since it consists of a finite number of real individuals with definite characteristics and related in a stated way. But the

thing actually available and studied by the classifier is not this group, but only a series of specimens, constituting, by hypothesis, a sample drawn from such a group. And the group boundaries and differences as drawn in practice are not established on genetic data but on morphological data. The theory is that there also exists in nature a morphologically definable unit that tends to correspond with the practically undefinable genetic unit. Thus the actual procedure, in almost all cases, is this: from a series of concrete specimens in hand an inference is made as to the nature of a morphological group from which the sample came, and an endeavor is made to frame the morphological concept in such a way that the inferred morphological group will approximate a genetic group. The thing that is actually classified is an inference, a purely subjective concept, which approximates a real, but unobservable, morphological unit, which in turn approximates an equally real but even less observable genetic unit.

THE HIERARCHY

Any practical system of classifying a large number of things, like animals, involves a hierarchy by which minor units are progressively gathered into groups of increasingly greater scope. The particular hierarchy that is now used in zoology has been adopted from Linnaeus. The method used by Linnaeus was based on the work of still earlier writers, and it has been considerably expanded and modified since, but it was first consistently used, in what is basically the accepted form, in the tenth edition of the "Systema naturae," 1758, which is universally taken as the starting point of modern classification and nomenclature.

In that work the hierarchy was as follows:

Empire ("Imperium"). The phenomenal world.
Kingdom ("Regnum"). Three in number: mineral, vegetable, animal.
Class ("Classis"). Six were recognized in the animal kingdom; example, Mammalia.
Order ("Ordo"). Eight were recognized in the Mammalia; example, Primates.
Genus. A very different unit from that now bearing this name, with only four in the Primates (*Homo*, *Simia*, *Lemur*, *Vespertilio*) and only 39 among mammals; example, *Homo*.
Species. Example, *Homo sapiens*.
Variety ("Varietas"). Example, *Homo sapiens europaeus*.

No need is now felt for the category "empire," and "variety" is now used in several ways, rather ambiguously, and is not usually considered a formal part of the hierarchy. The other Linnaean categories are still retained, but usually designated in the vernacular rather than in Latin, as in Linnaeus. Two other categories are now universally inserted: phylum, between kingdom and class, and family, between order and genus. The complete basic hierarchy has thus become:

Kingdom
Phylum
Class
Order
Family
Genus
Species

In theory, these categories, and these alone, are obligatory. If an animal is classified, it must belong explicitly or implicitly to a defined group at each of these seven levels. In practice, some doubt as to the proper placing at some level may exist, for instance it may be impossible to put a genus in a defined family, and it is then designated as *incertae sedis* (or *inc. sed.*, "of uncertain position") as to family.

Use of the basic or obligatory categories alone has, however, become inconvenient. The number of known, definable groups has become so enormous and there are so many different degrees of recognizable relationships between them that more subdivisions are needed in the hierarchy. This need has been met in part by decreasing the scope of the lower categories, especially the genus, and by inserting new categories throughout the hierarchy. Most of these are designated by the Linnaean names with the prefixes "super-," "sub-," and "infra-," a convenient expedient because the rank relative to the obligatory categories is obvious. Other categories with root names have often been proposed, but none is in universal use. The most commonly employed, and the only ones used

in the present classification, are cohort, between class and order, and tribe, between family and genus. Some other names for categories occasionally used are: branch, division, forma, gens, legion, nation, phalanx, phratry, proles, race, section, and series. "Division" and "section" are conveniently used as noncommittal terms for groups of undefined or intermediate categorical rank, but the other terms do not seem useful in formal classification at present.

The complete hierarchy in most common use, and to be used here, is as follows:

Kingdom
Phylum
Subphylum
Superclass
Class
Subclass
Infraclass
Cohort
Superorder
Order
Suborder
Infraorder
Superfamily
Family
Subfamily
Tribe
Subtribe
Genus
Subgenus
Species
Subspecies

The obviously omitted possible categories like infrafamily, supertribe, or supergenus may be inserted if needed, and some of them are in use, but they are not employed in the following classification of mammals. It may also be noted that there is increasing use of a category "species group" or simply "group" between subgenus and species or between genus and species (and then nearly the same unit as subgenus).

The obligatory categories are, of course, used throughout a classification.[1] The others are used only when needed or desired, and then introduction into one part of a general classification does not necessitate their employment throughout. Thus in the following classification of mammals, the great Order Rodentia is divided into suborders, but the relatively small and little-differentiated Order Lagomorpha is not. If, however, an optional category is introduced, it should be used consistently throughout the limits of the next higher category (except for groups specified as *incertae sedis*). Thus in the Order Edentata the Suborder Xenarthra is divided into infraorders and all Xenarthra are placed in one designated infraorder or another (but in the Suborder †Palaeanodonta infraorders are not used).

It is an extraordinary peculiarity of classification as a science that not one of the ranks in this hierarchy can be satisfactorily defined in absolute terms. The basic unit in theory and the most nearly definable rank in practice is the species, but very little acquaintance with taxonomic literature is needed to show that its definition is one of the most discussed of all problems in this field and that the species of different authors are not of equal rank. The central idea of most genetic definitions of a species is that this is a group in nature so constituted and so situated that a hereditary character of any one member of the population could be passed on to a descendant of any other member. Such a definition has exceptions and necessary qualifica-

[1] Which may, however, be too summary to include lower categories and which may leave superior categories as understood; for instance, the following classification omits species, at the bottom, and leaves Kingdom Animalia and Phylum Chordata understood at the top.

tions even within the field in which it is applicable, and it is not applicable at all to many groups that are, nevertheless, called species. It cannot, for instance, be applied to animals that do not reproduce sexually, nor can it be applied to the species of a lineage in time. Moreover, as has been amply pointed out, species are not definable genetically in practice. Nevertheless the definition and the relatively few cases to which it has been strictly applied provide the best and most nearly general available criterion. It may be said that a morphological species is a natural population such that the extent and nature of its variation and of its distinctions from other known populations are analogous to those of known genetic species. This definition is applicable to any group that is called a species. The species of actual classification is, of course, an inference from a sample as to the nature and limits of such a morphological species.

Since species have an element of continuity, both genetical and morphological, subspecies are subdivisions of a continuum and are necessarily more or less arbitrary. It does happen at times that part of a species is nearly uniform in nature and intergrades steeply and along narrow lines with other parts of the species. Then the subspecies has real, though blurred, limits. In other cases, intergradation is so gradual and widespread that subspecies are purely arbitrary. The tendency has been for classifiers to place in a supposedly distinctive subspecies any sample that they happen to have and that they think they can distinguish from all samples of different origin. The result is often unsatisfactory, and great improvement is possible, but more space will not be taken here for this subject, of great importance but outside the main theme of the present work.

All categories above the species have in common that they may include groups discontinuous, genetically and morphologically, between themselves. A genus with only one known species (called a monotypic genus) does not, in fact, include such a discontinuity, and there are many such genera. Here again the criterion that is used in practice is not that provided by theory but is related to the latter. The practical classifier grants to a genus a certain "size," by which is meant, as a rule, a certain morphological scope, with the implication that this scope tends to approximate a certain degree of phylogenetic differentiation, to include all animals related to each other within certain limits. This morphological scope may be almost entirely filled or exploited by known species if the genus has many (is polytypic), or only one or a few species may be known, leaving much of the assigned scope blank. The same considerations apply to all units above the specific level, which differ mainly in the assignment to them of increasingly larger scope as the hierarchy is ascended.

The question, Precisely how large is the scope of a genus, a family, or an order? is not much more determinate than the question, Precisely how far is up? An effort is made to give approximately the same scope to groups of the same rank and to grade different ranks more or less evenly from species to kingdom. Nevertheless, this ideal is never fully attained even by one student within one group, and there is great variation between different students and different groups. This variation rises in part from current custom or fashion; genera are now much smaller units than they were a century ago, and most of Linnaeus' genera have become families, some of them orders. Extent of knowledge also has an influence; little-studied families have, as a rule, larger genera than those known in more detail. Students have a strong tendency to use smaller genera in the groups of their specialty than in those less well known to them personally. The number of known forms has a similar and in part an inevitable and necessary tendency; in a family with many species the genera are likely to be smaller than in one with few species. Finally, personal taste is profoundly effective in this respect; some authors, like Thomas, have used almost irreducibly small genera, and others, like Winge, have used almost impractically large genera. This subject of splitting and lumping will be mentioned again when something more has been said of the practical use of the hierarchy and its relationship to phylogenetic principles.

MONOPHYLY AND POLYPHYLY

The condition that classification must be consistent with phylogeny has as its most

important corollary the requirement that all the animals within a given group, whatever its rank, must have had a common origin. A second and scarcely less important corollary is that the animals assigned to a given group are more closely related to each other than they are to the members of other groups of the same rank. Both requirements demand exceptions and qualifications; practical classification can be achieved only by compromise.

The principle that the units of classification must have a unified origin, or be monophyletic, easily leads to absurdity if not reasonably interpreted. Its complete *reductio ad absurdum* is the suggestion that each group must have originated from a single pair of animals, a requirement that has perhaps never been fulfilled in the history of life and that certainly cannot be demonstrated in any case. The rule that a group, to be considered monophyletic, must be derived from a single species of a preceding group is more reasonable and can sometimes be met in practice, but it also requires qualification. It is not at all clear that practical classification could consistently meet this requirement if phylogenetic knowledge were complete. In fact, knowledge is so far from complete that adherence to such a rule would lay classification open, to an unnecessary and undesirable degree, to the caprices of shifting theory and individual opinion. It is not useful to set up a classification in which groups with different names cannot be distinguished morphologically, but this does happen if theoretical monophyly is too strictly demanded. For instance, Abel has placed the Old World and New World horses usually referred to *Equus* in different genera because he believes (rightly or wrongly) that they did not arise from a single preceding species or genus, and yet no consistent structural definition serves to distinguish the two "genera." It is, again, probable that the mid-Tertiary horses called †*Merychippus* arose from more than one species of †*Parahippus* (and whether they did or not, some students think they did), but no practical and experienced taxonomist has thought it advisable on this account to split up the well-defined genus †*Merychippus* into several different genera difficult or impossible to distinguish clearly. Aside from the obvious practical disadvantage of such a course, it is not really evident that such a procedure would assist the clear and valid expression of a phylogenetic fact.

Given a group that is composed of related animals and defined by morphological and related data, the most practical and, at least for the present, the most desirable additional requirement seems to be not that it should be derived from one immediately antecedent genus or species, but, with intentional vagueness, that its immediate ancestry should be included within a group of lower rank than itself. For instance, it is not probable on the basis of present knowledge that all the animals here included in the Mammalia arose from the Reptilia as a single species, genus, or even family, but it is not suggested on this account that some of them should be returned to the Reptilia or that another class should be created for them.[1] They certainly arose from a unified group of reptiles of much smaller scope than a class, perhaps a family or perhaps a superfamily, and for practical purposes this is an adequate fulfillment of the requirement of monophyly.

Classification is, above all, a practical problem.

VERTICAL AND HORIZONTAL CLASSIFICATION

The existence of groups that are ancestral to two or more ultimately quite different phyla and the implication in classification that members of one group are more nearly related to each other than to members of other groups of the same rank give rise to the most difficult problems of classification of fossils. When the ancestral group is known, how is it to be classified? Can it be more nearly related to one than to the other of its descendent lines? In a sequence, is a group more nearly related to its ancestors, its descendants, or its contemporaries of like origin; in the human family analogy, is a man more nearly related to his father, son, or brother?

In the simplest case of an ancestral unit with two descendent lines, the usual solution

[1] Just that has been suggested. The student of classification is likely to feel that almost all arrangements for which there is any reason, and a good many for which there is none, have been proposed.

in classification is either to extend the name and concept of one descendent group, the one morphologically more conservative if such a distinction is clear, to include the ancestry, or to give the ancestry a separate name and to consider it a group of the same rank as each descendant. Both systems are in common use, and it is impractical to try to use either exclusively and consistently. On lower levels of classification the second solution seems more often useful. For instance, the group immediately ancestral to the genera †*Pliohippus* and †*Hipparion* (among others) is also given generic rank and is called †*Merychippus*.

Such simple cases are not particularly confusing, but analogous problems can be very intricate. It has, for instance, frequently happened that a group of, say, about subordinal scope has included numerous phyletic lines, all rather closely related but showing incipient divergence, and that one of these lines has outlived most or all of the others and has itself eventually split up into a group of about equal scope with the first. A concrete example is provided among Mammalia by the Carnivora. The early forms are quite varied, yet they are apparently derived from an immediately antecedent common ancestry. One of these early groups, the †Miacoidea, survived and apparently gave rise to all the divergent phyla leading to our modern terrestrial carnivores. In such a case how is the principle of nearness of affinity to be applied? The †Miacoidea are certainly nearly related to the later carnivores, the Fissipeda, for they are ancestral to them. At the same time, they are certainly nearly allied to the more ancient and archaic †Creodonta in the way often or customarily expressed by inclusion in one taxonomic unit, for they are derived from the same immediate ancestry. There are two sorts of affinity here, and following either one consistently throughout a classification is a practical impossibility. If the †Miacoidea are placed in the Suborder Fissipeda, then consistency might seem to demand placing each of the other early, †creodont subfamilies in a separate suborder, since their divergence from each other is equal to that of the †Miacoidea, yet logical adherence to this method would make classification absurd by eventually separating virtually every ancient species as distinctive of a suborder or other large group. On the other hand if the †Miacoidea are placed in the †Creodonta, the implication would seem to be that they are more nearly related to, say, the †hyaenodonts than to any fissipeds, which is not the case.

There are only two practical methods of dealing with such a situation, neither one of which is a clear expression of the evolutionary affinities involved. One is to place all the early forms including the †Miacoidea in the †Creodonta, separating the descendants of the †Miacoidea as Fissipeda. The other is to place the †Miacoidea in the Fissipeda and nevertheless to lump all other early lines in the †Creodonta. These two solutions are equally valid, and both have been proposed and used in this particular example and also in dealing with numerous other analogous cases.

The choice here is between so-called horizontal and vertical classification. Horizontal classification separates ancestral from descendent groups and unites contemporaneous groups, or those in a similar stage of evolution, if they are derived from a common ancestry. Vertical classification unites ancestral and descendent groups and separates contemporaneous groups that are diverging from a common ancestry. It is sometimes stated that these are mutually exclusive principles and that classification must be based on one or the other, but in fact neither can be followed consistently and any classification necessarily combines both methods. The most ardent exponent of vertical classification finds it necessary to separate ancestral and descendent genera, for instance.

Each point of view has its advantages and its dangers. Horizontal classification is usually easier and more objective. The earlier horses and tapirs, for instance, have more in common than have the earliest and latest horses, and it would be much easier to define and to recognize a horizontal group containing both primitive horses and tapirs than a vertical group containing all the horses and excluding all the tapirs. The horizontal arrangement may also be more stable, because the relative ease of recognition makes it less likely to be disturbed by later discovery, whereas most evolutionary phyla are diffi-

cult to distinguish and require considerable material for their proper recognition. Vertical groupings often require extensive rearrangement following new discoveries or new studies that modify ideas of the details of phyletic descent.

The principal advantage of vertical, and disadvantage of horizontal, classification is that the former is more in accord with the whole conception of evolutionary descent. Its principal proponents, such as the late H. F. Osborn, therefore, sometimes speak of it as evolutionary classification, as opposed to the more static and historically pre-evolutionary, more strictly Linnaean, horizontal system. Yet the horizontal affinities are just as real and are just as evolutionary as the vertical. Horizontal classification can, therefore, be as consistent with phylogeny as vertical classification, and since neither can really express phylogeny, there is really no *a priori*, theoretical reason for preferring one to the other even if one could be employed to the exclusion of the other, which is not possible.

The practical classifier is constantly reminded of Delage's words: "Quoique l'on fasse on n'arrivera jamais à respecter toutes les affinités dans la répartition des êtres en classes, ordres, familles, etc. . . . Il n'y a là qu'un moyen d'étude qu'il faut prendre pour ce qu'il vaut."

A special and peculiarly confusing case of horizontal classification is continually presented to palaeontologists who must classify the successive stages in unified, or essentially unified, phyletic sequences. Such a sequence is formalized as a succession of species, or on a larger scale a succession of genera, each of which gives rise to those that follow. From a genetical point of view, species, genera, or other units in this sense are totally different things from the horizontal units of contemporaneous faunas to which the same categorical names are applied. The very essence of a (horizontal) species in genetic definition is that interchange of heredity is possible throughout the group, but that established discontinuities prevent transmission to any other specific group. In the species as a division of a vertical line, interchange is impossible throughout the species, if only because the later members obviously cannot breed with those already dead, and on the other hand heredity is directly transmitted to what is defined as a wholly distinct species, the descendent species. The principle of nearness of affinity is also necessarily violated in all such cases. If one genus gives rise to another, the last species of the first genus will be more closely related to the first species of the next genus than to the first species of the first genus. Thus species placed in different genera sometimes are, and must be if the system is to be used at all, more closely related than species placed in the same genus.

Despite these difficulties in theory, the direct use of inferred morphological groups and the principle of analogy of scope permit workable practical solutions. Vertical lines are divided into species, genera, etc., such that the morphological scope (in the vertical direction) is comparable with those of genetic species, genera, etc. (in the horizontal direction). The horizontal lines between vertical units are necessarily arbitrary when the sequence is continuous. This does not mean that the resulting groups are unnatural or unreal; one may cut a piece of string arbitrarily at any point, but the severed pieces are still real and each has natural continuity. Decision as to just where the divisions are to be made depends on a number of factors. It may be that species do sometimes arise in a single genetic step and then there is a real and obvious division point, but this is not a universal phenomenon, it is not rigidly established as real in any given case, and it must be rare. Usually the boundary is originally drawn at a gap or offset in the sequence that might conceivably be due to sudden origin of a new group but that seems always to be caused solely by the hazards of discovery when the crucial evidence is found. The positions of boundaries are thus more often than not mere historical accidents. When a known continuous series is divided, an effort is usually made to draw the boundaries, as a matter of practical convenience, at points where striking or important new morphological characters or modifications become widespread or universal in the evolving population. Such boundaries are not, as a rule, par-

ticularly sharp because the spread of a new character usually takes a geologically perceptible period of time.

THE DIMENSIONS OF CLASSIFICATION

The problem of vertical and horizontal classification leads on to more general consideration of taxonomic dimensions, in a somewhat figurative sense. The morphology of an animal is literally three dimensional. When, for instance, two species are defined horizontally by differences in their (average) morphology they are distinguished in three-dimensional space. This is the static procedure, but morphology as used in classification also has two kinetic elements, to some extent analogous with additional dimensions.

In addition to its average, three-dimensional condition, every morphological group has variation in two directions, variation at any given time and variation between different times. These are not only essential qualities and quantities of group morphology, they are often the real crux of the problem of classification.

Variation within a group at one time is as much a character of the group as is any so-called constant characterization and may be more important and more characteristic than any demonstrable constancy. The typical statement of classifiers that, for instance, the skull in a given species is 60 mm. long, 30 mm. wide, and 15 mm. deep, aside from being untrue (for it can apply only to an average in a sample or to one individual and cannot be true of the species), is wholly inadequate and misleading. In the species, each of these dimensions or all three together have another dimension, that of variation. This is more difficult to measure and in fact cannot be measured in the real morphological or genetic species, but it can be estimated from a given sample (whatever the size of the sample), and this estimate is an integral, or even the essential, part of the inference that is the thing really classified. The techniques of such estimation are many, and the best of them are somewhat difficult. They cannot be specified in this more general dissertation on the principles of classification, but it cannot be too strongly emphasized that some estimate of variation is inherent in any valid classification. Classification is not concerned with individual animals but only with groups.

Every group has duration and exhibits morphological differences in time as well as in space. In the definition of units that are notably vertical, with a long extent in time, temporal variations or trends frequently become predominant, and definition solely by three-dimensional characters-in-common, or by these plus horizontal variation, is always inadequate in such cases and may be impossible. For instance, the linking of †*Hyracotherium* with *Equus* in the Equidae is solely on the basis of temporal variation and is flatly contradicted by any horizontal criteria.

Usage, accident, compromise, and a substratum of taxonomic theory have given rise to some tendency to use the various hierarchic grades in ways qualitatively as well as quantitatively different because of different balance between the various dimensions of classification. It is not always true, except in the most literal sense, that a genus is nothing apart from an agglomeration of species, a family of genera, and an order of families. The distinctions are not and cannot be maintained consistently or exactly defined, but there is a real and sometimes useful tendency to use categories differently. In classic taxonomy all units were three dimensional only. From species to kingdoms, organisms were arranged by a given set of characters supposedly running through every member of the given group. This is still true of some parts of classification and doubtless always will be, because we can never hope for enough data to put all of classification on the best possible basis, but the other dimensions are entering more and more into taxonomy and are affecting the various grades in somewhat different degrees.

In the great majority of cases, species in classification are essentially four dimensional. They are defined by a set of morphological characters and by the horizontal variation of these. In exceptional cases a time element also enters in, but this is usually minimized and is often absent. The genus tends more than any other unit to retain its classical, three-dimensional status and to be defined in practice as a group of species possessing certain characters in common. The elements of

horizontal and vertical variation are, of course, operative in genera as in all other units, and by some authors or in some groups these may become essential in the generic concept, but the present custom is usually to refer to a given genus variant or successive species on the basis of their possession of a minimum set of diagnostic characters.

This is a principal reason why the genus is, on the whole, the most definite and permanent unit of modern classification, to such an extent that the genus may be considered the basic unit of practical and morphological taxonomy, although the species is the basic unit of theoretical and genetical taxonomy. It requires less knowledge and skill to recognize units of a static category, especially when this is by intention a rather broad and definitely a group category, than to do the same when variables must be treated as such. This is particularly true in palaeontology for the dual reason that palaeontological classification involves more variables and that the data for dealing with them are usually less adequate.

The subfamily, or an analogous grade between genus and family, is being increasingly used as a unit whose greatest dimension is in time, and into the definition of which temporal changes or trends enter most largely. The extent to which the other taxonomic dimensions are also employed differs as greatly as possible between different authors and, to some extent, in different parts of the classification. At one extreme, the primarily phylogenetic unit, which in this case is sometimes but rather rarely designated as a subfamily, has ideally only one dimension, that of time. It is supposed to be a succession of actually ancestral and descendent individuals unified in character at any one time. However useful such a conception might be, it is in most cases unattainable. In practice it leads to an arrangement in which the theoretically different grades are actually coextensive, to genera each with one species, subfamilies and families each with one genus, etc., and thus defeats the whole purpose and use of hierarchic taxonomy.

Somewhat broader and more rational is the conception of the fundamentally temporal unit as a succession of ancestral and descendent genera, commonly with the implicit or even unconscious proviso that only one genus in any one subfamily existed at one time or at least that little or no generic branching occurs within the subfamily. Such a classification is seen in Osborn's Proboscidea or Kretzoi's "Ailuroidea," to cite only two examples of very different merit. Even this leads in practice to a great majority of monotypic subfamilies, which is certainly a drawback as there is no good reason to maintain a grade of classification and to remember a multitude of names in it if the grade usually has no greater scope than one below it in actual use.

At the opposite extreme is the classic use of the subfamily as a smaller sort of family, without conscious attention to the temporal element. Even here the time dimension does inevitably enter into the subfamily in the very nature of things, usually to greater extent than into genus and species, whether it is explicitly recognized and accounted for or not. This being true, it seems better to make such recognition and to accept the subfamily as a grade in which the time dimension is essential and is generally longer than the other dimensions (as far as such a comparison of incommensurate things can be made), one stressing phyletic relationships, although not in the sense that it must be purely monophyletic throughout. Such a grade is more subject to fluctuation, impermanence, and inconsistency than almost any other, for phyletic theory is the most subjective element in taxonomy, the most influenced by differences of opinion, and the most liable to radical change with the advance of knowledge. Hence comes another significant advantage in the tendency to lay extra stress on phylogeny in the subfamily and tribal grades. These are subsidiary grades between the genus and family, deriving their names from those of genera and capable of great flexibility and even distortion without seriously affecting the essential and obligatory grades of taxonomy. Therefore their instability is less threatening to that of classification as a whole.

Aside from such split classifications as use the family in substitution for a grade usually given lower status, the family is the lowest grade that now tends to be well rounded in all dimensions, and it belongs among the

higher units that differ little in essential character except for their being larger and larger in scope as they bracket the lower units in ascending the hierarchy. The family always[1] includes several distinct phyla, with certain characteristic structures running nearly or quite through all, with a certain characteristic sort and degree of variation embracing all, with characteristic differences in time within each, and, with some temporal differences, influenced by a common heritage, manifested in many or in all. Proponents of purely vertical, phyletic classification may apply this principle exclusively, as all do in part, to almost any unit below the family, but somewhere they have to start horizontal grouping, to bring together quite distinct (even though related) contemporaneous forms into one group. At present even the most ardent splitters and so-called phylogenetic taxonomists usually start frankly horizontal grouping at about the grade of family, so that this element of horizontality, though it be combined with and even subordinate to phyletic and temporal consideration, here becomes particularly characteristic and striking.

SPLITTING AND LUMPING

Diagnosis[2] is the art and practice of distinguishing between things. Definition[3] is the art and practice of setting limits to things. Both enter into taxonomy and it is unusual to distinguish between the two, but they are essentially different and their complementary roles should be clearly understood.

To use a broadly valid analogy, a geographer might say that Stamford is a town 35 miles east of New York and 30 miles west of Bridgeport. This is a diagnosis: he has distinguished Stamford but he has not delimited it. A second geographer might give the surveyed boundaries of Stamford: this is definition; he has established a division between all that is Stamford and all that is not. Similarly a species may be diagnosed by distinguishing it in some way from other known species, or it may be defined by giving its characters and setting limits to the range of variation included in it.

Analysis[4] is the art and practice of splitting things into their components, of separating the elements of a compound or group. Synthesis[5] is the art and practice of putting things together, of forming compounds or groups. Their opposite functions in taxonomy are relatively well differentiated, but their complementary nature in this science is not always clearly understood.

In the geographic analogy, one geographer might characterize each of the towns of Connecticut, New York, and England by diagnosis or definition (he would probably use diagnosis): this is analysis. Another might distribute them in the categories Connecticut, New York, and England, then unite Connecticut and New York with others to form a category United States, and unite England with others to form a category Great Britain. Then he would place the United States in a larger category, North America, Great Britain in Europe, and finally show that North America and Europe are parts of his major category Earth. This is synthesis. Similarly from one point of view the classifier analyzes families into genera or genera into species, and from another he synthesizes species into genera and genera into families.

Diagnosis, analysis, definition, and synthesis all are necessary in taxonomy and all are, to some extent, used by every classifier, yet in the matter of point of view and of emphasis a classifier usually leans more heavily one way or the other, toward diagnosis and analysis or toward definition and synthesis. These tend to be coupled in this way, because diagnosis and analysis both exclude and separate, while definition and synthesis both include and unite. The diagnostician-analyst must to some extent know what is included in each of the things he separates, and the definer-synthesist must have some

[1] That is, theoretically. Usually it does so also in practice, but even in a broad classification some monotypic families occur. In such cases the assumption is that other phyla existed but are not known. It is not safe to assume, and it probably rarely happened, that a single phylum in the most limited sense ever became so unlike its parent stock and its relatives as to be classed as a separate family without itself splitting up into more than one minor phylum.

[2] Ultimately from the Greek διαγιγνώσκω, to distinguish between two (things).

[3] Ultimately from the Latin *dēfinio*, to enclose within limits.

[4] Greek ἀνάλῦσις, dissolution.

[5] Greek σύνθεσις, compounding.

conception of the components of the regions that he defines, so that the two are not truly independent, but they have opposite tendencies. In less formal, more expressive language, the former is a splitter, the latter a lumper.

Splitters make very small units—their opponents say that if they can tell two animals apart, they place them in different genera, and if they cannot tell them apart, they place them in different species. Lumpers make large units—their opponents say that if a carnivore is neither a dog nor a bear they call it a cat.

Over the generations that separate us from Linnaeus, there has been slow oscillation between splitting and lumping, although each has had its practitioners in every generation. Linnaeus started modern classification in a highly lumped condition, and there was then an accelerating swing toward splitting that culminated toward the middle of the nineteenth century in a first peak of exaggerated emphasis on analysis. Later in that century some prominent lumpers appeared and the balance tended to swing in their direction, although even the most extreme lumpers did not return to the Linnaean magnitudes. Around the turn of the century and since then, splitting again was predominant. Classifiers revived most of the units proposed earlier and added thousands more. This phase was inevitable in the history of zoological discovery. When many novelties are being found, the more striking problem is synthesis, determination of the affinities of these new forms with the old. With discovery becoming rare, the tendency is to go back over the known materials and to split them into smaller and smaller bits.

Simply distinguishing between things belongs on a low level of intellectual pursuits and degenerates into hackwork. It was no coincidence that this extreme splitting phase coincided with the growing disrepute of taxonomy and a strong movement away from this division of biology and toward others, particularly experimental and ecological studies. These studies are now being redirected into the field of taxonomy where they will assist in achieving a better balance between analysis and synthesis.

It is sufficiently obvious that both analysis and synthesis are necessary in classification and that both splitting and lumping have a place, or, to the extent that the terms involve antithesis, that neither one is correct. It is desirable that all distinguishable groups should be distinguished (although it is not necessary that all enter into formal classification and receive names). It is also desirable that they should all be gathered into larger units of increasing magnitude with grades, each of which has practical value and which are numerous enough to suggest the degrees of affinity that can be and need to be specified. No consideration can exactly fix the number of species to be recognized, but the application of modern definitions, principles, and methods (an application still very far from completion) will set fairly close limits to possible disagreement between competent classifiers. Even now among students of high ability the one most inclined to splitting seldom recognizes twice as many species as his most lumping colleague, although he might recognize five times as many families.

It is in the superspecific categories that splitting now most requires attention and correctives. In theory it is possible to say that the number of animal species is fixed and objective, or nearly so, but the number of higher units is subject to no limitations other than that they cannot, at any one level, be more numerous than the species. What is deplorable in splitting is the tendency to raise the ranks of groups without need, that is, without gaining any practical advantage. One of the more evident symptoms of this tendency is the appearance of many monotypic groups in classification. If a classifier makes mostly monotypic families, genera, etc., it is a fair statement that he is giving family rank to what should be called genera, generic rank to species, etc.

To the extent that it is inconvenient and should be corrected, superspecific splitting arises mainly from two causes. Specialists on particular groups almost always have a tendency to exaggerate ranks within their specialty, unless this is consciously perceived and corrected. They see differences more clearly, and their main occupation is likely to be analysis. Having special knowledge, the multiplicity of names is more helpful than difficult for them within a given

field, and they do not always appreciate the great inconvenience experienced by the more general student to whom this field is only one of many. Treating one group as a special case they have no occasion to coordinate ranks with those in other groups and, often, little comprehension of the necessities of higher levels and the broader problems of classification.

The second principal cause of excessive superspecific splitting is related but distinct: classifiers sometimes try to include in classification the designation of too many degrees of affinity in comparison with the number of hierarchic grades used. Since they are usually concerned with relatively low levels of affinity, they will extend these far up the hierarchy, without particularly noting or caring that this deprives the system of grades that should be available to distinguish higher levels of affinity. They usually exaggerate this by abbreviating the hierarchy; for instance, many splitters do not use subgenera. In fact all degrees of affinity cannot be formally recognized in classification, and the steps in the whole scale of affinity must be equal in number to those in the hierarchy.

The remedies are, first, appreciation of the most general aspects of the problem on all levels of classification, second, recognition of the fact that in classification "on n'arrivera jamais à respecter toutes les affinités," and third, in each case where it seems really desirable to recognize an intermediate grade of affinity, consideration of the possibility of doing so by an intermediate grade in the hierarchy instead of elevating the group to the next major grade. In this last respect, the subgenus is perhaps the most notably neglected rank. When students recognize a definable group of species within what has been called a genus, they too often propose calling the group a separate genus when it could perfectly well and far more conveniently be called a subgenus if it really needs formal designation within the hierarchy.

NOMENCLATURE

THE LINNAEAN SYSTEM

Many biologists and even some taxonomists seem to feel rather pride than shame in their ignorance of the principles of zoological nomenclature. The same men would be quick to condemn a solecism in the use of their native languages, and nomenclature is the grammar and vocabulary of zoology. Neither nomenclature nor grammar is an end in itself, but they are not less important on that account. The comparison can be extended to point out that literate men do make mistakes in grammar and literate zoologists do make mistakes in nomenclature, but that only dolts see in this an excuse for illiteracy.

It is a requirement of classification that every group have a distinctive name, and one of the principal purposes of classification is to supply these names. Like the hierarchy, the currently accepted system of nomenclature is adapted from Linnaeus and its zero point is 1758; no names published before that date can be considered but all names published since then must be (provided that they are definitely Linnaean names). The essence of the system is simple, although its application often becomes complicated. Supergeneric names are single words that are to be considered Latin plurals (whatever the actual etymological derivation).[1] Generic names are single words that are considered Latin singulars. Specific names are two words, of which the first is the name of the genus and the second is a word treated as a Latin noun in apposition with the generic name, a noun in the genitive, or an adjective modifying the generic name.[2] Subspecific names consist of

[1] It is not always remembered that these names are plural, and errors in grammar sometimes result. One can say "the Order Proboscidea is . . . ," because the subject is "Order," but one must say "the Proboscidea are . . . ," because the word "Proboscidea" is plural.

[2] Occasionally only the second word of a specific name is used and the generic name is understood. For instance, if a species *Felis concolor* is repeatedly mentioned, it may be called *concolor* after the first mention of it. In such cases *concolor* is sometimes loosely called the specific name, but it is not so by definition. Sometimes this part of the specific name is called the trivial name. It is more frequent and better usage never to employ a trivial name alone but, if desired, to abbreviate the generic part of the specific name if no possible confusion can arise, e.g., *F. concolor*.

three words, of which the first two are the name of a species and the third is an additional word treated in the same way as the second.

Names of genera and higher groups are always capitalized. The second words in specific names and the third in subspecific names are never capitalized.[1] Names of genera, species, and subspecies are distinguished in print by the use of a different type face, almost always italics, but names of supergeneric groups usually are not distinguished in this way, and if they are distinguished this should be in a different way from generic and lower names. Names of subgenera have the same form and are printed in the same way as generic names, but if they are cited in connection with the name of a genus or species they are placed in parentheses after the generic name; e.g., *Sciurus* (*Parasciurus*) *niger* is a species of the subgenus *Parasciurus* in the genus *Sciurus*.[2] Insertion of the subgeneric name is optional; *Sciurus niger* is also a valid name for the same species as *Sciurus* (*Parasciurus*) *niger*.

The name of the author and the year of first publication may be, but are not necessarily, added to any zoological name. If used, the author's name is in text type (not italics as in the case of genera or species) and follows without intervening punctuation. A comma is placed between author's name and date. Example: *Sciurus niger* Linnaeus, 1758. When a species is transferred to a genus other than that to which its author originally referred it, author's name and date are commonly placed in parentheses.[3]

When a genus is divided into subgenera, one subgenus (that with the same type as the genus, as explained later) must have the same name as the genus: e.g., *Sciurus* (*Sciurus*) *vulgaris* belongs to one subgenus of *Sciurus*, *Sciurus* (*Parasciurus*) *niger* to another. Similarly, when a species is divided into subspecies, one (with the same type as the species) repeats the same name; e.g., *Sciurus niger niger* and *Sciurus niger neglectus* are subspecies of *Sciurus niger*.

Names of superfamilies, families, subfamilies, tribes, and subtribes are derived from names of valid, included genera by adding the following terminations to a stem form of the given generic name:

RANK	ENDING	EXAMPLE (FROM *Sciurus*)
Superfamily	-oidea	Sciuroidea
Family	-idae	Sciuridae
Subfamily	-inae	Sciurinae
Tribe	-ini	Sciurini
Subtribe	-ina	Sciurina (this possible subtribe is not used in the present classification)

Selection of the stem to be used sometimes involves difficulties and cannot be fully discussed here, where the aim is to provide a summary explanation of nomenclature rather than an exhaustive manual for nomenclaturists. It is amply exemplified in the following classification. A few authors use the ending -oidae for superfamilies, but this is contrary to the widest usage and is not recommended.

There is no standard termination for names of groups higher than superfamilies, and these may be but do not need to be derived from names of included genera. It is best to avoid using for these groups names with the set endings listed above, but some names in -oidea, the superfamily ending, are in common use for groups higher than superfamilies and are not rejected on that account.[4]

[1] It was formerly customary to capitalize these words if they were derived from the name of a person, and this is still occasionally done by conservative Europeans, but the custom is everywhere dying out and is considered definitely bad usage by American zoologists.

[2] This rule is one of the most frequently violated by those half educated in nomenclature, who commonly put in parentheses in this way a name considered synonymous with the generic name or the name of a supposedly distinct genus to which the species is sometimes referred. Thus they might perpetrate such an absurdity as *Parasciurus* (*Sciurus*) *niger*, which means on the face of it that they consider *Sciurus* a subgenus of *Parasciurus* (a nomenclatural impossibility, as it happens), but which they think means that *niger* is commonly placed in *Sciurus* rather than in *Parasciurus*.

[3] This rather unimportant rule is as often honored in the breach as in the observance and several zoologists have signified their intention of abandoning it. Failure to follow it is justified, if desired.

[4] Poche, 1936–1938, has recently proposed a new hierarchy with 41 grades between kingdom and genus (exclusive), each with a standard suffix. If zoological nomenclature were starting afresh, rather than dating from Linnaeus, some such fully standard and stereo-

A technical zoological name may have any derivation, and the tracing of these names to their origins is an interesting and frequently amusing bypath of zoology. An effort is usually made to propose a name that has some degree of appropriateness, and this is a convenience to the student, but once a name has been applied in zoology it means, simply and solely, the defined group of animals and its intrinsic or etymological meaning has no bearing on the matter. For instance some Ungulata (literally "hoofed [mammals]") have claws, not hoofs, some Carnivora (literally "flesh-eaters") are strict vegetarians, most Edentata (literally "toothless [mammals]") have teeth, and †*Basilosaurus* (literally "royal lizard") is a mammal, not a reptile.

A few names are simply Latin or Greek words adopted without significant change of meaning, such as the generic names *Homo* for man, *Felis* for cats, or *Bos* for cattle. Such words are relatively few, however, and compounds from Greek or Latin roots are most common, such as the generic name †*Homalodotherium* (Greek ὁμάλός, of like degree, ὀδούς, tooth, θηρίον, beast, i.e., a mammal with the teeth in a continuous series) or the ordinal name †Multituberculata (Latin *multi*, many, *tubercula*, tubercles, and the termination *-ata*, i.e., animals with many cusps [on the teeth]). The gods have lent their names, often in strange company; *Diana* is a monkey and *Venus* is a clam. Place names are not uncommon; for instance, †*Uintatherium*, the beast of the Uinta Mountains, and personal names, such as †*Leontinia* for a lady named Leontine who was married to a zoologist, or †*Henricosbornia* for the late Professor Osborn, are numerous. *Lama* (Peruvian), *Tenrec* (Malagasy), *Dugong* (Malay), *Conepatus* (Aztec), and many others are derived from native languages spoken in the regions where the animals live. A few names, such as *Kogia* and †*Degonia*, are bad puns; some, like †*Decastis*, are anagrams, and some, like *Tatera*, are frankly invented, without intrinsic meaning.

typed system might be desirable, although even in such a case the irregularity of the particular terminations proposed by Poche would make learning them a great and unnecessary feat of memory and their adoption would be inadvisable. In the actual, realistic situation the proposal is simply fantastic and merits no consideration from unregimented zoologists. Aside from his hierarchy and nomenclature, Poche's intention to clarify the rules and to extend them to higher groups is praiseworthy, although his conclusions are not definitive or desirable as a whole.

PRIORITY AND THE INTERNATIONAL RULES

Early naturalists were quick to adopt the Linnaean system of nomenclature, which has been in almost universal use since the latter part of the eighteenth century, but within this framework they often used whatever names they pleased, sometimes modifying names or proposing new names for what now appear the most trivial reasons. As a result of this capricious behavior, of ignorance of names already proposed for the same groups, and of the proposal of names for groups afterwards found to be inseparable from those provided with other names, there were soon a large number of synonyms in existence, and usage differed widely. Repeated efforts were made to work out some sort of code for selecting a single, distinctive, valid name for each group, and these culminated in the adoption and promulgation of the "International Rules for Zoological Nomenclature" by the International Zoological Congress.[1] The Rules also provide for an International Commission on Zoological Nomenclature empowered, with certain cumbersome restrictions, to suspend the Rules in specific cases in the interests of stability. This Commission has issued Opinions from time to time (published in this country by the Smithsonian Institution). The Opinions have sometimes gone beyond the powers explicitly granted to the Commission and have undertaken the interpretation and to some extent the amendment of some provisions in the Rules. These Rules and Opinions are at present the most widely accepted authority in nomenclature, and it goes without saying that every literate zoologist must be thoroughly familiar with them, even if he does not personally adhere to them in every respect. No attempt will be made here to summarize the Rules and Opinions or to discuss their details, but their

[1] The Rules have been repeatedly printed. At present they are readily obtainable in Schenck, E. T., and J. H. McMasters, 1936, "Procedure in taxonomy," Stanford University, California.

basic provisions will be briefly mentioned, and some of the important points not adequately treated by them will be discussed. The Rules mention the formation of family and subfamily names, but they are otherwise solely concerned with names of genera, subgenera, species, and subspecies.

The first 24 articles of the Rules are essentially a codification of much of neo-Linnaean usage already summarized in the preceding section of the present study. Article 25 of the Rules is the famous Law of Priority, which is the basic principle and the storm center of technical nomenclature, and the rest of the 36 articles are taken up mainly by the application and interpretation of this law. In essence, the law says simply that the valid name of a genus (or subgenus) or species (or subspecies) is the binary (i.e., Linnaean)[1] name under which it was first designated in a publication accompanied by some sort of indication of what group was intended. Prior to 1931 almost any sort of indication was sufficient to validate a name, but subsequent to 1930 the Rules require more definite differentiation and, for a genus, designation of type (see below). Once a name is published, no change can be made in it by anyone unless it can be definitely established that an error in copying or printing made the name as it appeared in the publication different from what its author certainly intended at the time.

There is no provision for completely deleting names except by suspension of the Rules, but a name can be invalidated because it is antedated or preoccupied. A name is antedated, or is a synonym, if another name applicable to the same group was published at an earlier date. Such names can be revived and become valid if it is later decided that the names do, after all, refer to distinguishable groups. A preoccupied name or homonym is one that is exactly the same as a name previously published for a different group.[2] A homonym is completely dead and can never be used again in zoological nomenclature. The Law of Priority as stated also authorized rejection of non-Linnaean ("non-binary") names and those published without the required characterization of the group of animals intended—these last are called *nomina nuda* (sometimes, but incorrectly, applied to a name invalid for some other reason). There is no requirement that this characterization be adequate, objectively correct, or zoologically valid, but only that the author thought it was or intended it to be a characterization of some sort. There are many names the proper application of which cannot now be determined although they fulfill the requirements of the Rules, and no provision is made for invalidating these useless and annoying relics, which I call *nomina vana*, singular *nomen vanum*. In practice, they are and can only be either ignored or listed as indeterminate and without known significance. All these requirements apply within the limits of the animal kingdom. The name of a plant cannot preoccupy that of any animal, but the name of a protozoan can preoccupy that of a mammal.

These requirements seem simple, fair, and well calculated to promote standardization and stability of nomenclature. They do so more often than not in practice, but it is an open secret that the Rules are inadequate and ambiguous in some respects and that their application sometimes has made for instability and has contravened common sense, according to the consensus of zoologists. The mechanism of the Commission has proved slow and incapable of coping fully with the problems raised by the attempted rigid application of the Rules. Widespread dissatisfaction has been caused, some eminent zoologists have refused to follow the Rules in particular cases or in general, and a great deal of confusion still exists. The situation plainly calls for revision, expansion, and clarification of the Rules and for providing a more rapid, flexible, and authoritative means of passing on particular cases and designating names to be given official priority. Nevertheless, until such action is taken, the Rules are the only widely recognized standard, and deliberate contravention of them by individuals can lead only to still worse confusion. While fully

[1] The Rules call Linnaean nomenclature "binary," because names for species are double, but the system is equally concerned with the names of subspecies, which are triple, and of genera, which are single.

[2] Even a difference in one letter is sufficient to prevent homonymy except for five specified sorts of one-letter differences in specific names, listed in Article 35 of the Rules.

agreeing that the Rules badly need revision and that their results are occasionally absurd, I have attempted to follow their letter exactly in the following classification of mammals. Where the letter is ambiguous, I have taken the spirit to be that choice should promote stability and perpetuate common usage as far as possible.

The chief difficulty inadequately met by the Rules and requiring some further action arises from the facts that many obscure names fell into disuse during the period preceding adoption of the Rules and that many names (especially those of fossils) were, and still are being, based on imperfect evidence or incompetent work and are of doubtful application or prove eventually to apply to a group subsequently known under a different name. When the synonymy is discovered, or is claimed by a worker who may himself be mistaken, obscure and sometimes quite forgotten names may take technical priority over names universally understood and invariably used over a long period. Such occurrences promote instability because of the very Rules that were adopted for the sake of stability. Often they invalidate the names that are used in classic and standard studies and have the effect of requiring students to remember two names for one group: the name long standard but technically invalid and the technically prior name. If, upon notice of priority, the change were made once and for all, stability would eventually be achieved and even the great inconvenience just mentioned would not be an excessive price for this happy result. Sometimes this has happened, but it is not the invariable or perhaps even the usual outcome in such cases. Often the discovery of a prior name merely puts an end to what was essentially stable nomenclature. Someone may find a still older, still more obscure name—a generation has not sufficed to dig them all out. Someone may find grounds for questioning or disproving the applicability in the given case of the name claimed as prior. Many zoologists may continue to use the familiar but invalid name.

Despite the disadvantages and annoyances of such cases, it is to be remembered and emphasized that they are not in a majority, that the Rules do tend on the average to promote stability, and that the only promising remedy is amendment, not rejection of the Rules.

TYPES AND HYPODIGMS

It is one of the peculiar shortcomings of the International Rules that they nowhere mention types of species and that they give elaborate rules for determination of the types of genera (Article 30) without ever saying exactly what the type of a genus is, what it is for, or how it functions. Since the operation of the Law of Priority, which is the most important theme of the International Rules, depends very largely on the system of types, this reticence is a serious fault. Few subjects in taxonomy are understood in more different ways or are more misunderstood than the nature and use of types despite the fact, or perhaps in part because of the fact, that most taxonomists have occasion to use types directly or indirectly all the time.[1]

The type of a species or subspecies is a specimen designated when the species or subspecies is first named, or subsequently selected from the specimens used as a basis for the original description, if more than one specimen was used and none was designated as the sole type. The type of a genus or subgenus is a species (not a specimen) similarly designated or selected. Subtribes, tribes, subfamilies, families, and superfamilies also have types which are genera in all these cases. These will be mentioned further in connection with the nomenclature of groups not covered by the Rules, and in the meantime most of what is here said about types of genera applies to types of these higher units, *mutatis mutandis*. Units of higher rank than superfamilies do not have types.

A very complex nomenclature of types has been proposed with more than 50 different terms in all, but most of these are useless and misleading from the present point of view and only the following are recognized as useful and necessary:

[1] Students unfamiliar with the subject are warned that the views to be summarized here are not strictly orthodox. They do not contradict good common usage in essential respects, but they restrict usage in some directions and extend it in others. These views are more fully expounded and defended in Simpson, G. G., 1940b, pp. 413–431. Space is not taken in the present work to mention all opinions or to argue points of disagreement.

TYPE: A single specimen or species as mentioned above.

SYNTYPE: One of several coordinate specimens or species given equal value as types in the original proposal of a specific or generic name. In new work, syntypes should never be used and only one type should be designated, but syntypes were widely used in the past and so must still be dealt with.

LECTOTYPE: A syntype selected by a subsequent reviser to serve as (sole) type. Once such a selection has been made it cannot be altered by still later revisers.

NEOTYPE: A substitute proposed, under certain definite conditions, for a type (or syntypes or lectotypes) that fails to serve its purpose.

The principal, and in the usage here recommended the sole, purpose of types is to serve as name-bearers. Every specific and subspecific name is attached once and for all to a certain concrete, objective specimen, an individual animal, usually a preserved dead animal or a part thereof collected, prepared, and stored in a museum. (Designated types do not, however, cease to be types if they are not successfully preserved or if they are subsequently lost or destroyed.) Similarly every generic and subgeneric name is attached once and for all to a certain species, not to the name of a species, not to the animals that constitute a species, nor to the particular animal that is type of the species, but to the classificatory species itself, which is a subjective inference. There is no logical or practical reason why generic and subgeneric types should not be specimens, like the types of species. In fact this is quite illogical and in practice it is a rich source of confusion and disagreement, but the usage is universal and of long standing and unfortunately this is one of the few basic things about types that is distinctly (although obliquely) endorsed by the International Rules.[1]

When specimens are transferred from one species to another or when two supposed species are merged into one, it frequently happens that two specific types are placed in one species, which thus acquires two names since the names have to follow the name-bearers, the types. (The fate and allocation of other known specimens have no bearing whatever on nomenclature.) It is then that the Law of Priority operates to designate which name is to be used for the species. If the type attached to the synonymous name is later removed and put in a species without the bearer of an older name, the formerly synonymous name goes with it and is revived. The same considerations apply when two or more generic name-bearing species are placed in a single genus.

From another point of view, the system of types operates to retain some degree of uniformity in specific and generic concepts, which may otherwise be highly diverse among different students, and to facilitate comprehensible verbal communication. When a zoologist uses a generic or specific name (and throughout this discussion everything said of genera applies to subgenera and everything said of species applies to subspecies), he is giving tacit assurance that the group concept of which he is speaking includes the type that bears the name he uses. Sometimes the student in question does not really know the type and would not include it in the concept if he did know it, so that the implicit assurance is only a legal fiction. Even in such cases, however, he is understood to have given a guarantee, and for the purposes of technical nomenclature he is held to it.

It is a natural but mistaken assumption that types are somehow typical, that is, characteristic, of the groups in which they are placed. It is, of course, desirable that they should be typical because then they are less likely to be shifted about from group to group, carrying their names with them and upsetting nomenclature, but there is no requirement that a type be typical, and it frequently happens that it is quite aberrant. Types are almost never really average specimens within a species, or fully central species in a genus. Types were formerly, and still are by many students, supposed to be not only name-bearers but also the bases on which group concepts are erected and the standards of comparison for those concepts. They cannot possibly serve either function in modern taxonomy and the requirements of these functions are flatly incompatible with the re-

[1] In their strange avoidance of commitment on the subject of types, the Rules nowhere say "The type of a genus is a species," but they speak of "type species of genera" and imply throughout that genera have species as types.

quirement of name-bearing which types can and do serve.

The basis of a group concept in zoology is a series of specimens, a sample including all the specimens that are, by any one student at any one time, believed to belong in the postulated group. For this purpose every specimen in the series has equal value, and none is correctedly singled out for emphasis because it was the first specimen found, because it happens to be a name-bearer, or for any other such reason. The whole sample used as a basis for inference is called a hypodigm (*hy'podim*). The hypodigm of a genus, species, or any other taxonomic group is a series of concrete specimens, although the types of superspecific groups (such as have any) are subjective concepts. The correct procedure of practical nomenclature is to infer from a hypodigm the probable characters and limits of a natural population and then to decide the valid name of that inference by observing whether any name-bearers, types, occur in the hypodigm, using the oldest name if there are two or more types in the hypodigm. If the hypodigm does not include an established type, the group is new, technically at least, and a new name is proposed and attached to a specimen in the hypodigm. The contents of any given hypodigm naturally vary from time to time and from person to person, depending on the discovery and availability of specimens and on the criteria, skill, and taste of the procedure of inference.

A final word may be devoted to neotypes. Many zoologists do not utilize or recognize them, and those who do are far from agreed as to the proper circumstances, regulations, and implications. Neotypes are, however, frequently useful, especially in palaeozoology, and they can be assigned a helpful role in modern taxonomy. It often happens that what is known about a specific type is so ambiguous, because the specimen is fragmentary, aberrant, or lost, that the type cannot certainly be referred to one specific hypodigm and only one. If the attached name has fallen into obscurity, it is just as well to leave it there as a *nomen vanum*, but if it is in wide current use for the species corresponding with one of the hypodigms in question, the perpetuation of that usage is desirable and helps to stabilize nomenclature. This end can be accomplished by a procedure not in the Rules but not contrary to the Rules: a specimen that *does* belong to one defined hypodigm to which the type *might* belong is designated neotype and the name attached to the type is transferred to the neotype as substitute name-bearer.

NOMENCLATURE OF SUPERGENERIC GROUPS

Except for casual and unimportant mention of family and subfamily names, the International Rules say nothing about supergeneric names, and there is no generally accepted code.[1] The following list of principles is not proposed as such a code, a proposal not properly to be made by one individual, but is only an explanation of the procedure followed in selecting the supergeneric names used in the following classification of mammals. On the whole these personal principles are the expression of what has become general usage, interpreted and made more concrete on a basis intended to be that of common sense and technical convenience.

Subtribe to Superfamily Names

DERIVATION AND ORTHOGRAPHY

1. Names of the following categories are single words, capitalized, derived by adding the given termination to the stem of the name of the type genus:

Category	Termination
Superfamily	-oidea
Family	-idae
Subfamily	-inae
Tribe	-ini
Subtribe	-ina

TYPES

2. The type of any of the categories listed in 1 is a genus (the type of a superfamily is not a family; the type of a family is not a subfamily, etc.).

3. These names in themselves designate the type genus which is, without need for any other designation, the genus the name of

[1] Poche has attempted to provide one in the work mentioned in a previous note, but this is very far from being generally accepted and is here categorically rejected as completely impractical and highly undesirable.

which is used in forming the name of the supergeneric category.

4. In naming a new group in these categories the selection of name, and hence of type, follows the same principles as those for selection of new types in general. The genus selected should, other things being equal, be the best known, the most common, the most centralized within the group, or the most distinctive from other groups.

5. A type in these categories is not necessarily the included genus with the oldest name, and this criterion has no bearing whatever on the proposal of such a name and the selection of such a type.[1]

6. A name in these categories follows the type genus and can apply only to a group in which that genus is placed.

7. Names in these categories change with any change in the name of the type genus (International Rules), the type is the genus and not the name of the genus, but a new name is not automatically created by change of name of a type genus and comes into existence only when explicitly published.

PUBLICATION AND AUTHOR

8. A name in any of the categories listed in 1 comes into existence when it is published with correct derivation and orthography and with either explicit or clearly implicit designation of the category intended. In the case of an author who accepts the formal terminations given in 1, the use of the termination automatically designates the intended category.

9. Such publication is valid without any definition of the group or listing of the lesser groups that are intended to be included, but such definition and listing are highly desirable.

10. The author of a name in these categories is he who first published it with exactly the spelling adopted in the given case, except that emendations involving only the insertion or deletion of another "i" before -idae, -inae, -ini, and -ina do not affect the authorship.[2]

[1] Use of the oldest generic name has been seriously proposed, but the application of such a rule leads to extreme instability and as often as not to manifest absurdities.

SYNONYMY AND HOMONYMY

11. Names in the categories listed in 1 are synonymous if their type genera are placed in the same group at the given categorical level, regardless of whether the names were originally proposed or are commonly used for different group concepts.

12. Names in these categories are homonymous if spelled in the same way or if they differ only in the presence or absence of "-i-" before -idae, -inae, -ini, and -ina, even if they are correctly based on valid and different generic names.[3]

13. When two or more names of correct derivation and orthography are available for what is considered to be a single group in one of these categories, the name with technical priority of publication as such shall be accepted as the valid name unless there is strong contrary indication.

14. Disregard for this principle of priority is indicated and justified:

A. When the prior name is little-known and a later name has clear and great advantage on the basis of current usage;

B. When the prior name is based on a genus of doubtful pertinence to the group in question and a later name is based on a genus surely belonging to that group.

In doubtful cases the following situations may also support disregard for priority but are not in themselves sufficient to justify it:

C. When a prior name is based on a very poorly known genus and a later name on one very well known;

D. When a prior name is based on a genus excluded or unknown when the group was first recognized as a taxonomic entity and a later name is based on a genus that was included in that first recognition.

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[2] I personally find that this rule is frequently unjust and confusing, but it seems best to adopt it as a matter of bibliographic convenience. A useful corrective, adopted in the following classification, is to place in parentheses, after the name and author technically recognized, the original name and author of the group concept, when these are not the same.

[3] This odd situation can arise. For instance, the name †Didelphodontinae has been proposed for two very different groups, one with †*Didelphodus* (an insectivore) and the other with †*Didelphodon* (a marsupial) as type.

RELATIONSHIPS BETWEEN GRADES

15. A superfamily must include a family with the same genus as type, a family (if it contains subfamilies) must include one subfamily with the same genus as type, a subfamily (if it contains tribes) must include one tribe with the same genus as type, and a tribe (if it contains subtribes) must include one subtribe with the same genus as type.

16. Subtribes of one tribe belong *ipso facto* to one subfamily or family, tribes of one subfamily belong *ipso facto* to one family, subfamilies of one family belong *ipso facto* to one superfamily, suborder, or order.[1]

17. Secondary categories, such as superfamilies, subfamilies, tribes, and subtribes, are necessarily associated with and part of some higher primary category, such as order or family, and do not exist independently. A subfamily, for instance, must be part of some family.

NAMES OF CATEGORIES ABOVE SUPERFAMILIES

DERIVATION AND ORTHOGRAPHY

18. Names for infraorders and higher categories are single words, capitalized, considered as, and preferably written in, Latin plurals. They may be, but do not need to be, derived from the names of included lesser groups.

19. There are no standard or required terminations for such names. Names similar in ending and therefore liable to confusion with those of lower categories, such as names in -oidea, are to be avoided as far as convenient but are not to be rejected on this account alone.

TYPES

20. Infraorders and higher groups do not have types.

PUBLICATION AND AUTHOR

21. The name of an infraorder or higher group comes into existence when it is published with explicit or implicit indication that it is meant as the Linnaean name of a group of higher rank than a family but is not considered a superfamily.

22. Rule 9, above, also applies to these higher groups.

23. The author of the name of an infraorder or higher group is he who first published it with exactly the spelling adopted in the given case.

24. The name and author remain the same when the nominal rank of the group is changed, for instance, when a suborder is made an order or an infraorder, unless a basic change in group concept is also made, when the name and author or the author but not the name may be, but are not necessarily, changed.[2] (See also 30.)

SYNONYMY AND HOMONYMY

25. Homonyms among names for infraorders or higher groups are generally to be rejected, but may occasionally be retained when there is decisive evidence that the homonymy does not cause confusion and that retention of a homonym usefully prevents unnecessary complication. For purposes of this principle on these levels of classification, names spelled almost alike and of similar derivation are to be considered homonyms, e.g., †Toxodonta and †Toxodontia. Among permissive, but not obligatory, indications for retaining such homonyms are:

A. When the two names apply to groups with positions in the animal kingdom so distant that a reference to one can hardly be mistaken for reference to another;

[1] This rule seems too obvious to require statement, but it has been violated in recent serious and otherwise valuable work.

[2] Application of this principle requires considerable personal judgment and is open to debate, yet it seems a necessary general rule. In the construction of a large, general classification, like that of the Mammalia, uniformity, proportion, and clarity frequently demand shifting the ranks of higher groups with little or no essential change in their contents. To demand a change of name whenever such a shift is made would result in utmost confusion and duplication of terminology, and to change the author and date would be unjust and would obscure the historical origin of names and concepts. The opposite view might logically demand recognizing as author the first student to use a name in precisely its present sense. In most cases this would mean either that the technical authors of many time-hallowed names would change constantly and would tend to be the latest reviser, or that revisers were honor-bound not to change ranks of groups, which would stultify revision.

B. When the prior name has no current usage and the homonym is in general use.

C. When the prior name is used for a group of primary rank in the hierarchy (e.g., order) and the homonym is provisionally applied to the group of secondary rank (e.g., superorder, suborder) immediately including or immediately included in the group designated by the prior name.

26. In the determination of synonymy, the law of priority which operates by the use of types is not applicable to infraorders and higher groups, which do not have types, and if considered at all it is only a possible basis for judgment when other things are about equal.

27. The primary consideration in the selection of names in these higher categories is usage. In most cases the group intended, or one essentially like it, will now be found to have a name in use, and such names are to be selected and perpetuated as far as possible.

28. New names should not be proposed if old names are available and can be used with reasonable emendation, whether or not these old names are in general current use.

29. Old names and current names are, however, to be rejected if:

A. The group concept now to be recognized is essentially different from that previously understood under any name;

B. The available name in current use is not merely a reasonable emendation of the same name as originally proposed but involves a definitely contradictory concept.[1]

30. "Reasonable emendation" in the sense of 28 and 29 may include either addition or subtraction of part of the contents of the group, provided that:

A. Addition is on the basis of affinity with forms already in the given group and the added forms are numerically fewer and morphologically less varied than those already in the group;

B. Subtraction leaves in the group the forms considered most characteristic of it, those felt to be nuclear and to be the primary standard of comparison, and those used wholly or most definitely and primarily in the original definition of the group.[2]

RELATIONSHIPS BETWEEN GRADES

31. Rules 16 and 17 apply also to analogous units of grades above superfamily.

In general it is noticeable that practice as regards the higher, typeless groups and these informal principles based on practice are more flexible and depend more on individual judgment than do the rules for genera and species, rules which are supposed to work automatically and to leave little room for personal opinion. Among the smaller units, of which there are hundreds of thousands in all, no one man has knowledge of more than a small fraction, and there is no well-informed scientific consensus. Experience demonstrates that leaving nomenclature on this level at the mercy of personal judgment produces chaos. On higher levels, however, a consensus does operate fairly well, and experience suggests that complete and rigid determination by rule is not necessary in order to secure a sufficient degree of uniformity. These principles are, indeed, framed to assist the operation of scientific opinion rather than to replace it.

[1] For example, the name Menotyphla is in general use for a group including the tupaiids and their allies, but it is rejected for such a concept because it was originally proposed for the macroscelidids and their allies, and the two concepts are now believed to be contradictory or mutually exclusive.

[2] For example, addition of the tupaioids to the Primates and subtraction of the lagomorphs from the Rodentia are reasonable emendations and do not suggest or justify any change in the names of those orders.

PART 2. FORMAL CLASSIFICATION OF MAMMALIA

INTRODUCTION

THE FOLLOWING CLASSIFICATION is complete for supergeneric groups, including all such groups that are here recognized. The great majority of genera that are here considered probably valid are included, but their listing is not absolutely exhaustive. An effort has been made to include all genera that are well defined, that are widely agreed to have true generic rank, and that are in common use. Many doubtful supposed genera are included because their names are likely to be encountered in current technical literature or because, dubious as they are, they have some possibly important bearing on distribution, affinities, and the like. Nevertheless, a great number of proposed generic names that are surely or probably invalid, that are not much used at present, or that are so poorly defined or so poorly known as now to have little real meaning are deliberately omitted. The classification is thus made clearer and more succinct, and little that is probably of much value in this connection is lost. The specialist interested in tracing some obscure synonym or ill-defined or obsolete name should, in any case, turn to the excellent nomenclators that are available (notably Palmer or Neave, see p. 167), and not to a general working classifiaction.

As explained below, many names given generic rank by some specialists but here considered of lower rank are listed, but in a secondary position. These names are also indexed so that they may be found readily, and they are associated with the names of closely related, if not identical, genera. The student who does not agree in giving lesser rank to these names will thus suffer no serious inconvenience, whatever opinion he may have of my judgment in the matter.

Of course no two authorities agree exactly as to what families, genera, or other groups should be recognized. In a classification by one student, however, with reasonably consistent criteria of rank, the numbers of families and genera of mammalia and of the various orders have a certain interest. The numbers of surviving groups give some idea of present differentiation and dominance, and the numbers of known extinct groups suggest former dominance and the relative completeness of the fossil record. Because most mammalian groups have declined since the Miocene or Pliocene—probably true of all major groups except Rodentia and perhaps the higher Artiodactyla—and because all families have endured considerably longer than the average for genera, it would be expected that extinct genera would be much more numerous than living and that extinct families would tend to be somewhat more numerous than living. The extent to which this is true of each order is thus in some degree an indication of the adequacy of the known fossil record.

Of the 18 living orders of mammals, known extinct genera are more numerous than recent genera in all but four (Monotremata, Chiroptera, Rodentia, Tubulidentata), but known extinct families are more numerous than recent families in only seven (Insectivora, Edentata, Proboscidea, Hyracoidea, Sirenia, Perissodactyla, Artiodactyla).

This classification recognizes 32 orders of mammals, of which 14 are extinct, 44 per cent. Of the 18 surviving orders, 15 include known extinct families. Of the three living orders without known extinct families, all include known and surely referred extinct species (there is no order that is not known fossil), but one (Monotremata) has no known extinct genus, and the extinct genera tentatively placed in the other two (Pholidota, Tubulidentata) are of very dubious pertinence to these orders.

The numbers of families and genera recognized by this classification within each order and within the whole class are given in the following table. For purposes of tabulation, families and genera *incertae sedis* are definitely assigned to the order which they most resemble or to which they have been referred by some authority. Since the listing of genera

ORDERS	FAMILIES			GENERA		
	Extinct	Living	Total	Extinct	Living	Total
MONOTREMATA	0	2	2	0	3	3
†MULTITUBERCULATA	5	0	5	35	0	35
†TRICONODONTA	1	0	1	8	0	8
†PANTOTHERIA	4	0	4	22	0	22
†SYMMETRODONTA	2	0	2	5	0	5
MARSUPIALIA	5	8	13	81	57	138
INSECTIVORA	12	8	20	88	71	159
DERMOPTERA	1	1	2	2	1	3
CHIROPTERA	2	17	19	16	118	134
PRIMATES	7	11	18	99	59	158
†TILLODONTIA	1	0	1	4	0	4
†TAENIODONTA	1	0	1	7	0	7
EDENTATA	7	3	10	113	19	132
PHOLIDOTA	0	1	1	3	1	4
LAGOMORPHA	1	2	3	23	10	33
RODENTIA	10	30	40	275	344	619
CETACEA	9	9	18	137	35	172
CARNIVORA	6	9	15	261	114	375
†CONDYLARTHRA	6	0	6	42	0	42
†LITOPTERNA	2	0	2	41	0	41
†NOTOUNGULATA	14	0	14	105	0	105
†ASTRAPOTHERIA	2	0	2	9	0	9
TUBULIDENTATA	0	1	1	1	1	2
†PANTODONTA	3	0	3	9	0	9
†DINOCERATA	1	0	1	8	0	8
†PYROTHERIA	1	0	1	6	0	6
PROBOSCIDEA	5	1	6	22	2	24
†EMBRITHOPODA	1	0	1	1	0	1
HYRACOIDEA	2	1	3	10	3	13
SIRENIA	3	2	5	14	2	16
PERISSODACTYLA	9	3	12	152	6	158
ARTIODACTYLA	16	9	25	333	86	419
TOTAL	139	118	257	1932	932	2864
PER CENT	54%	46%		67%	33%	

is not quite exhaustive, it may be said that about 3000 valid, named, and defined genera of mammals are known, using genera in the fairly broad sense here adopted.[1]

EXPLANATION OF THE DETAILED CLASSIFICATION

Besides the information inherent in the hierarchic arrangement, this classification gives the following data for each group, with some exceptions as noted:

1. Name of hierarchic category, order, family (written "Fam."), etc. For genera this is obvious and is omitted.

2. Technical name here considered valid and preferable for the group.

3. Author of that name and year of publication. For groups above genera this is a definite bibliographic citation and refers to the bibliography of this work, on later pages. For genera, the original publication is not necessarily cited in the accompanying bibliography. This can be found by means of the various nomenclators and indexes (see p. 167),

[1] The classification also lists about 500 generic names considered synonyms and approximately 700 believed to represent possibly valid groups but of less than generic rank. About 4000 proposed generic names are indexed; 4000 is also probably about the number of known mammalian genera that would be admitted by extreme splitters.

which the present classification is not intended to replace.

4. In some cases, as discussed below, names placed in synonymy, with their authors and dates.

5. In some cases, as discussed below, "included" names, possibly or probably designating valid groups but here considered as of lesser rank, with authors and dates.

6. For families and smaller units, the known geological and geographical distribution.

7. For many recent genera and a few families, the vernacular names.

The author and year cited for each name are for publication of the name as it is now spelled.[1] In the case of families and subfamilies, the spelling of which is by rule, this usually means the first author to give the group the rank now assigned to it. In many cases essentially the same group was earlier recognized and named but given different rank and, therefore, different spelling. In these cases and all others, an effort is made to give also the first technical name, author, and date ever applied to the group, even though that first name is not now used. These data are given in parentheses after the name now used. In this way the essential bibliographic datum of first publication in the present form is retained, but the important historical datum of first recognition under any name is also given. Both convenience to the user and justice to the author are thus served, at the expense of slight complication of the entry. It may be emphasized that authors' names are, in any case, cited primarily as a means of definition rather than as an honor to the author.

Other names are frequently also given in parentheses. There is no attempt to make these exhaustive, which would greatly complicate the classification and tend to defeat rather than to promote its purpose. The names that are cited are included because they are likely to be encountered in the literature or because they have some particular historic importance. When such names are preceded by an equal sign (=), they are believed to be essentially technical synonyms of the name given outside parentheses. Names preceded by the word "including" are not considered necessarily invalid in themselves or in concept, but are given lesser rank than was given them by their author or by some authoritative reviser. Thus the entry "*Rousettus* Gray, 1821 (=*Cynonycteris* Peters, 1852). [Including *Pterocyon* Peters, 1861.]" means that *Cynonycteris* is a name for the same thing as *Rousettus* but is invalid (in this case because it is of later date), while *Pterocyon* is a name probably or possibly designating a valid group of animals often considered a genus but here tentatively considered as of less than generic rank. The most probable inference is that it can be considered as a subgenus of *Rousettus*. Except in this way, subgenera are not included in the classification. It is impractical in a classification of the whole class, reduced to handy size, to list groups smaller than genera; for subgenera, species, and subspecies the special literature on each group must be examined.

The reason for rejecting a name is not stated when it is obvious, for instance, when it is simply a matter of priority as in "*Rousettus* Gray, 1821 (=*Cynonycteris* Peters, 1852)," a matter of rejected spelling or rejected rank, as in "Erinaceidae Bonaparte, 1838 (=Erinacidae Gray, 1821; Erinacini Fischer, 1817)," or a matter of rejected basis, as in "Tenrecoidea Simpson, 1931 (=Centetoidea Gill, 1872)," *Centetes* being shown below this to be an invalid (antedated) name equal to *Tenrec*, so that the entry shows that Tenrecoidea is the valid name for the group recognized by Gill under a name necessarily rejected now.

When the reason for rejection is less obvious, it is usually stated in a footnote or in the following discussion. The special case of preoccupation is shown by appending "*nec*" followed by the preoccupying author and date; "*Tachyglossus* Illiger, 1811 (=*Echidna* Cuvier, 1798, *nec* Forster, 1788)" means that the animal in question was first named *Echidna* by Cuvier but that Forster had already used the same name for a different animal. Cuvier's application of it to this animal must, therefore, be rejected, and the correct name

[1] An occasional slight exception is made for family and subfamily names now spelled -iidae or -iinae and originally published with a single "i." Here the author and year of this original publication are usually cited, rather than those of first publication with "ii," but this fact is stated in a footnote.

is the next oldest applied to it, which happens to be *Tachyglossus*. In some cases names have been supposed to be preoccupied when they were not so under the Rules. Thus the entry "†*Trachytherus* Ameghino, 1889, *nec Trachytherium* Gervais, 1849 (=†*Eutrachytherus* Ameghino, 1897)" sums up a complex history. Ameghino first called the animal in question "*Trachytherus*." He later discovered that the similar name "*Trachytherium*" had been used at an earlier date, so he proposed to replace "*Trachytherus*" by "*Eutrachytherus*." But this is not technical preoccupation under the Rules, and "*Trachytherus*" is still the correct name. Nevertheless "*Eutrachytherus*" is used in much of the literature, so is listed here.

The authors and dates cited for names, the spelling of which does not depend on their rank, are those of the first use of the name with its present spelling and more or less its present meaning, but not necessarily its present rank. For instance, the Subclass †Allotheria is given as of Marsh, although he originally considered the group an order, not a subclass.

The symbol † means that the name following it includes only extinct mammals. Names without the symbol always include some living mammals and in many cases also some extinct ones. For a well-rounded mammalogist, or from a theoretical point of view, the distinction is of little importance, but it involves somewhat different practical methods and attitudes, and its designation takes little extra space and may be found useful.

The geological distribution is given in broad terms, usually to within a third of a Tertiary epoch. No attempt to subdivide the Pleistocene is made, not only because of its relatively short duration but also because the published data on this point are extremely inconsistent, frequently erroneous or based on poor evidence, and not at all comparable from one author to another. Without an amount of research on each individual fauna and genus quite impossible in the preparation of such a classification as this, absolute consistency is unobtainable. Many authors, indeed, do not give any data on which independent judgment as to age could be possible, and all formations near an epoch boundary are placed sometimes in one epoch, sometimes in another. Where there is a basis for personal judgment, I have, of course, followed my own throughout for the sake of comparability. For instance, in South America I have called the Santa Cruz Beds Lower Miocene, although they may be Middle or Upper Miocene or Oligocene and have even been referred to the Eocene. The John Day in North America is called Lower Miocene, although many students have classified it as Upper Oligocene. The so-called Pontian deposits are classed as Lower Pliocene. It would require another volume and years more of labor to give the detailed world correlations and time classifications on which the geologic distributions are based, and the most that can be done is to give a reasonable idea of relative ages. Even here it cannot be doubted that inconsistencies have crept in, or have been inherited from the sources used.

As regards the Pleistocene records, these have been given as far as conveniently possible. It should, however, be noted that no effort has been made to abstract all the enormous literature on Pleistocene geology and faunas in order to record every single Pleistocene appearance of living genera. This would have doubled a task already great and would have served no useful purpose. It can be taken as a general fact that almost every genus now native to any continent also lived on that continent in some part of the Pleistocene. The absence of a Pleistocene record cannot, therefore, be taken as more than an accident of non-discovery. It has no taxonomic or historical value. The presence during the Pleistocene of recent genera in great areas that they do not now inhabit is, on the contrary, a positive fact of great importance, and these records are included as far as possible.

The following abbreviations are used for geologic occurrence:

L., Lower (or, as to time, early)
M., Middle
U., Upper (or, as to time, late)
Trias., Triassic
Juras., Jurassic
Cretac., Cretaceous
Paleoc., Paleocene
Eoc., Eocene
Olig., Oligocene
Mioc., Miocene
Plioc., Pliocene

Pleist., Pleistocene
R., Recent

With some exceptions, geographic distribution is given by continents, using the following abbreviations:

N., north, northern
N.E., northeastern
N.W., northwestern
S., south, southern
S.E., southeastern
S.W., southwestern
E., east, eastern
W., west, western
Cent., central
A., America
Eu., Europe
As., Asia
Af., Africa
Aus., Australia
U.S.A., United States of America

Particularly in the case of Australia and Asia (especially southern Asia), it is understood that a genus so designated may or does occur on adjacent islands generally similar in faunal character. If, however, a genus occurs only on islands and not on an adjacent continent, this fact is usually given.

The use of the modern continents instead of faunal realms is a compromise, especially in the case of Africa and Asia which include parts of more than one realm on one continent. It is, however, impractical to represent the exact distribution of each genus in a general summary of all mammals, and especially when fossil mammals are included and form so great a percentage of the whole. The continents have been units essentially throughout the Tertiary and Quaternary, while more strictly faunal units have fluctuated greatly and would be delimited differently for different sorts of mammals and at different times. When the limitation of a genus to a given part of a continent is clear and important, this fact is indicated geographically, e.g., by saying S.As. (=southern Asia) for an Asiatic genus notably Oriental and not Holarctic, or N.Af. for an African genus definitely Holarctic and not Ethiopian.

The last entry in the cases of many recent genera and some higher groups is the vernacular name. Care has been taken with these entries, but here, too, some compromise and generalization is necessary. Vernacular nomenclature is highly variable and unsystematic and has no exact equation with technical nomenclature, but it is certainly useful to include the equivalent vernacular and technical names as far as possible. Many genera, for instance, among rodents have no genuine, distinctive vernacular names, and no attempt is made to supply them artificially. In other cases a good, real vernacular name applies to more than one genus and is then repeated after each. Conversely, vernacular names may distinguish animals belonging to one genus. Both names are then listed here, but it has been impractical to give separate definitions of them in most cases. In cases where the vernacular name implies a false relationship it is placed in quotation marks, e.g., Tasmanian "wolf," Australian "opossum." Simple Anglicization of a technical name is generally too obvious to require explicit entry and is listed only when it really has become a common dictionary word. The few cases where invalid technical names survived as valid vernacular nomenclature merit special mention, e.g., "echidna" and "platypus" for *Tachyglossus* (=*Echidna*) and *Ornithorhynchus* (=*Platypus*). A special effort has been made to learn and record native names adopted in European vernaculars, since these are the best of common names. On the other hand, no great effort has been expended in running down all the book names invented by mammalogists as "popular" synonyms for their technical names but quite unknown to laymen who know the animals, although some of these are also mentioned if they really have much currency in the literature.

DETAILED CLASSIFICATION

Class MAMMALIA Linnaeus, 1758, p. 14.
Subclass PROTOTHERIA Gill, 1872, p. vi.
Order MONOTREMATA Bonaparte, 1838, p. 110 (=Ornithodelphia De Blainville, 1834, *fide* Palmer, 1904, p. 780). Monotremes.
Fam. Tachyglossidae Gill, 1872, p. 27 (=Echidnidae Burnett, 1830b, p. 365). Pleist.–R.; Aus. Spiny "anteaters," echidnas.
Tachyglossus Illiger, 1811 (=*Echidna* Cuvier, 1798, *nec* Forster, 1788). Pleist.–R.; Aus.
Zaglossus Gill, May 5, 1877 (=*Proechidna* Gervais, Nov. 30, 1877). R.; New Guinea.
Fam. Ornithorhynchidae Burnett, 1830b, p. 365 (=Ornithoryncina Gray, 1825, p. 343). Pleist.–R.; Aus. Duckbills, platypuses.
Ornithorhynchus Blumenbach, 1800 (=*Platypus* Shaw, 1799, *nec* Herbst, 1793). Pleist.–R.; Aus.
†Subclass ALLOTHERIA Marsh, 1880, p. 239.
†Order MULTITUBERCULATA Cope, 1884a, p. 687.
†Fam. Plagiaulacidae Gill, 1872, p. 27. [Including †Bolodontidae Osborn, 1887, p. 3.] U. Juras.; N.A. U. Juras.–L. Cretac.; Eu.
†*Plagiaulax* Falconer, 1857. U. Juras.; Eu.
†*Bolodon* Owen, 1871. U. Juras.; Eu.
†*Ctenacodon* Marsh, 1879. U. Juras.; Eu., N.A.
†*Psalodon* Simpson, 1926. U. Juras.; N.A.
†*Loxaulax* Simpson, 1928a. L. Cretac.; Eu.
†Fam. Ptilodontidae Gregory and Simpson, 1926, p. 3 (=†Chirogidae Cope, 1887a, p. 567). [Including †Cimolodontidae Marsh, 1889, p. 84; †Neoplagiaulacidae Ameghino, 1902a, p. 11.] U. Cretac.–L. Eoc.; N.A. U. Cretac.; As. U. Paleoc.; Eu.
†Subfam. Ptilodontinae Jepsen, 1940, p. 263. U. Cretac.–L. Eoc.; N.A. U. Paleoc.; Eu.
†*Cimolomys* Marsh, 1889. U. Cretac.; N.A.
†*Mesodma* Jepsen, 1940. L. Paleoc.; N.A.
†*Kimbetohia* Simpson, 1936. L. Paleoc.; N.A.
†*Ptilodus* Cope, 1881. M.–U. Paleoc.; N.A.
†*Ectypodus* Matthew and Granger, 1921. ?M., U. Paleoc.–L. Eoc.; N.A. U. Paleoc.; ?Eu.
†*Mimetodon* Jepsen, 1940. M.–U. Paleoc.; N.A.
†*Anconodon* Jepsen, 1940. M. Paleoc.; N.A.
†*Neoplagiaulax* Lemoine, 1880. U. Paleoc.; Eu.
†*Prochetodon* Jepsen, 1940. U. Paleoc.–L. Eoc.; N.A.
†Subfam. Eucosmodontinae Jepsen, 1940, p. 263. L. Paleoc.–L. Eoc.; N.A.
†*Eucosmodon* Matthew and Granger, 1921. L.–M., ?U. Paleoc.; N.A.
†*Microcosmodon* Jepsen, 1930. U. Paleoc.; N.A.
†*Pentacosmodon* Jepsen, 1940. U. Paleoc.; N.A.
†*Neoliotomus* Jepsen, 1930. U. Paleoc.–L. Eoc.; N.A.
†Ptilodontidae of uncertain subfamily:
†*Paronychodon* Cope, 1876. U. Cretac.; N.A.
†*Meniscoessus* Cope, 1882. U. Cretac.; N.A.
†*Essonodon* Simpson, 1927. U. Cretac.; N.A.

†*Djadochtatherium* Simpson, 1925. U. Cretac.; As.
†*Liotomus* Cope, 1884. U. Paleoc.; Eu.
†Fam. Taeniolabididae Granger and Simpson, 1929, p. 603 (= †Polymastodontidae Cope, 1884a, p. 687). L.–U. Paleoc.; N.A. U. Paleoc.; As.
†*Taeniolabis* Cope, 1882 (= †*Polymastodon* Cope, 1882). L. Paleoc.; N.A.
†*Catopsalis* Cope, 1882. M.–U. Paleoc.; N.A.
†*Prionessus* Matthew and Granger, 1925. U. Paleoc.; As.
†*Sphenopsalis* Matthew, Granger, and Simpson, 1928. U. Paleoc.; As.
?MAMMALIA of uncertain subclass or order:
†Fam. Microcleptidae Simpson, 1928a, p. 52 (= †Microlestidae Marsh, 1887, p. 344). U. Trias.; Eu.
†*Microcleptes* Simpson, 1928. U. Trias.; Eu.
†*Thomasia* Poche, 1908 (= †*Microlestes* Plieninger, 1847, *nec* Schmidt-Goebel, 1846). U. Trias.; Eu.
MAMMALIA of uncertain subclass:
†Order TRICONODONTA Osborn, 1888, p. 251.
†Fam. Triconodontidae Marsh, 1887, p. 341. ?U. Trias., M.–U. Juras.; Eu. U. Juras.; N.A.
†Subfam. Amphilestinae Osborn, 1888, p. 228. ?U. Trias., M. Juras.; Eu. U. Juras.; N.A.
†*Eozostrodon* Parrington, 1941. U. Trias.; Eu. (Affinities dubious.)
†*Amphilestes* Owen, 1859. M. Juras.; Eu.
†*Phascolotherium* Owen, 1838. M. Juras.; Eu.
†*Phascolodon* Simpson, 1925. U. Juras.; N.A.
†*Aploconodon* Simpson, 1925. U. Juras.; N.A.
†Subfam. Triconodontinae Hay, 1902, p. 566. U. Juras.; Eu., N.A.
†*Triconodon* Owen, 1859. U. Juras.; Eu.
†*Priacodon* Marsh, 1887. U. Juras.; N.A.
†*Trioracodon* Simpson, 1928. U. Juras.; Eu., N.A.
Subclass THERIA Parker and Haswell, 1897, p. 448 (= Eutheria Gill, 1872, but not Eutheria of Huxley and most other authors).
†Infraclass PANTOTHERIA Simpson, 1929a, p. 42.
†Order PANTOTHERIA Marsh, 1880, p. 239 (= †Trituberculata Zittel, *ex* Osborn, 1893, p. 96).
†Fam. Amphitheriidae Owen, 1846, p. 29. M. Juras.; Eu.
†*Amphitherium* De Blainville, 1838. M. Juras.; Eu.
†Fam. Paurodontidae Marsh, 1887, p. 341. U. Juras.; Eu., N.A., Af.
†*Paurodon* Marsh, 1887. U. Juras.; N.A.
†*Archaeotrigon* Simpson, 1927. U. Juras.; N.A.
†*Tathiodon* Simpson, 1927. U. Juras.; N.A.
†*Araeodon* Simpson, 1937. U. Juras.; N.A.
†*Peramus* Owen, 1871. U. Juras.; Eu.
†*Brancatherulum* Dietrich, 1927. U. Juras.; Af.
†Fam. Dryolestidae Marsh, 1879, p. 397 (= †Amblotheriidae Osborn, 1887, p. 7; †Kurtodontidae Osborn, 1888, p. 234; †Stylacodontidae Giebel, 1879, p. 629). U. Juras.; N.A., Eu.
†*Dryolestes* Marsh, 1878. U. Juras.; N.A.
†*Amblotherium* Owen, 1871. U. Juras.; Eu., N.A.
†*Laolestes* Simpson, 1927. U. Juras.; N.A.
†*Kepolestes* Simpson, 1927. U. Juras.; N.A.

†*Herpetairus* Simpson, 1927. U. Juras.; N.A.
†*Melanodon* Simpson, 1927. U. Juras.; N.A.
†*Euthlastus* Simpson, 1927. U. Juras.; N.A.
†*Miccylotyrans* Simpson, 1927. U. Juras.; N.A.
†*Malthacolestes* Simpson, 1927. U. Juras.; N.A.
†*Pelicopsis* Simpson, 1927. U. Juras.; N.A.
†*Kurtodon* Osborn, 1887. U. Juras.; Eu.
†*Peraspalax* Owen, 1871. U. Juras.; Eu.
†*Phascolestes* Owen, 1871. U. Juras.; Eu.

†Fam. Docodontidae Simpson, 1929a, p. 84 (=†Diplocynodontidae Marsh, 1887, p. 338; †Dicrocynodontidae Osborn, 1888, p. 263). U. Juras.; N.A., Eu.
†*Docodon* Marsh, 1881. [Including †*Dicrocynodon* Marsh, 1888 =†*Diplocynodon* Marsh, 1880, *nec* Pomel, 1846; †*Ennacodon* Marsh, 1890 =†*Enneodon* Marsh, 1887, *nec* Prangner, 1845.] U. Juras.; N.A.
†*Peraiocynodon* Simpson, 1928. U. Juras.; Eu.

†Order SYMMETRODONTA Simpson, 1925b, p. 560.
†Fam. Spalacotheriidae[1] Marsh, 1887, p. 343. U. Juras.; Eu., N.A.
†*Spalacotherium* Owen, 1854. U. Juras.; Eu.
†*Peralestes* Owen, 1871. U. Juras.; Eu.
†*Tinodon* Marsh, 1879. U. Juras.; N.A.
†*Eurylambda* Simpson, 1929. U. Juras.; N.A.
†Fam. Amphidontidae Simpson, 1925a, p. 460. U. Juras.; N.A.
†*Amphidon* Simpson, 1925. U. Juras.; N.A.

Infraclass METATHERIA Huxley, 1880, p. 654 (=Marsupialia *sensu lato*).
Order MARSUPIALIA Illiger, 1811, p. 75 (=Didelphia De Blainville, 1816, p. 109).
Superfam. Didelphoidea Osborn, 1910, p. 515.
Fam. Didelphidae Gray, 1821, p. 308. [Including †Microbiotheriidae Ameghino, 1887a, p. 6; Chironectidae (Anon.), 1897, *fide* Palmer, 1904, p. 734.] U. Cretac.–L. Mioc., Pleist.–R.; N.A. ?Paleoc.–Mioc.; Eu. Paleoc.–R.; S.A. Opossums.
†Subfam. Pediomyinae Simpson, 1927b, p. 122. U. Cretac.; N.A.
†*Pediomys* Marsh, 1889. U. Cretac.; N.A.
†*Eodelphis* Matthew, 1916. U. Cretac.; N.A.
†*Nyssodon* Simpson, 1927. U. Cretac.; N.A.
†*Euangelistes* Simpson, 1929. U. Cretac.; N.A.
†*Cimolestes* Marsh, 1889. U. Cretac.; N.A.
†*Diaphorodon* Simpson, 1927. U. Cretac.; N.A.
†*Delphodon* Simpson, 1927. U. Cretac.; N.A.
?Pediomyinae *incertae sedis:*
†*Coöna* Simpson, 1938. L. Eoc.; S.A.
†Subfam. Thlaeodontinae Hay, 1930, p. 390 (=†Thlaeodontidae Cope, 1892, p. 760; †Didelphodontinae Simpson, 1927b, p. 124, *nec* Matthew, 1918, p. 571). U. Cretac.; N.A.
†*Thlaeodon* Cope, 1892. U. Cretac.; N.A.
†*Didelphodon* Marsh, 1889. U. Cretac.; N.A.
†*Ectoconodon* Osborn, 1898. U. Cretac.; N.A.
†*Alphadon* Simpson, 1927. U. Cretac.; N.A.
†Subfam. Microbiotheriinae Simpson, 1929a, p. 116 (=†Microbiotheridae Ameghino, 1887a, p. 6). Eoc.–Mioc.; S.A.

[1] "Spalacotheridae" in Marsh.

†*Ideodelphys* Ameghino, 1902. Eoc.; S.A.

†*Microbiotherium* Ameghino, 1887. [Including †*Proteodidelphys* Ameghino, 1898; †*Pachybiotherium* Ameghino, 1902; etc.[1]] Olig.–Mioc.; S.A.

Subfam. Didelphinae Simpson, 1927a, p. 5. [Including †Herpetotherinae Trouessart, 1879, p. 225.] L. Paleoc.–L. Mioc., Pleist.–R.; N.A. ?Paleoc.; Eoc.–Mioc.; Eu. Plioc.–R.; S.A. Opossums.

†*Thylacodon* Matthew and Granger, 1921. L. Paleoc.; N.A.

†*Peradectes* Matthew and Granger, 1921. U. Paleoc.; N.A.

†*Peratherium* Aymard, 1850. [Including †*Herpetotherium* Cope, 1873; †*Oxygomphius* Meyer, 1846; †*Amphiperatherium* Filhol, 1879.] Eoc.–Mioc.; N.A., Eu.

†*Nanodelphys* McGrew, 1937. M. Olig.; N.A.

†*Paradidelphys* Ameghino, 1904. Plioc.; S.A.

†*Cladodidelphys* Ameghino, 1904. Plioc.; S.A.

Philander Brisson, 1762 (=*Caluromys* Allen, 1900). R.; S.A., Cent. A. Philander,[2] woolly opossum.

Monodelphis Burnett, 1830 (=*Peramys* Lesson, 1842). [Including *Minuania* Cabrera, 1919.] R.; S.A.

Dromiciops Thomas, 1894. R.; S.A.

Glironia Thomas, 1912. R.; S.A., Cent. A.

Notodelphis Thomas, 1921. R.; S.A. (Patagonia).

Marmosa Gray, 1821. [Including *Thylamys* Gray, 1843.] Pleist.–R.; S.A., Cent. A. Murine opossum.

Metachirops Matschie, 1916. (*Philander* Brisson may be the proper name for this genus.) R.; S.A., Cent. A. Pouched four-eyed opossum.

Metachirus Burmeister, 1854. [Including *Holothylax* Cabrera, 1919.] R.; S.A., Cent. A. Four-eyed opossum.

Lutreolina Thomas, 1910. Plioc.–R.; S.A.

Didelphis Linnaeus, 1758. Plioc.–R.; S.A. Pleist.–R.; N.A. Common opossum, Virginia opossum.

Chironectes Illiger, 1811. R.; S.A., Cent. A. Yapok, water opossum.

?Didelphidae *incertae sedis:*

†*Adapisoriculus* Lemoine, 1885. U. Paleoc.; Eu.

†*Perazoyphium* Cabrera, 1928. U. Plioc.; S.A.

†Fam. Caroloameghiniidae Ameghino, 1901, p. 353. L. Eoc.; S.A.

†*Caroloameghinia* Ameghino, 1901. L. Eoc.; S.A.

†Superfam. Borhyaenoidea Simpson, 1930, p. 9 (=†Sparassodonta Ameghino, 1894, p. 364).

†Fam. Borhyaenidae Ameghino, 1894, p. 371. [Including †Arminiheringiidae Ameghino, 1902a, p. 43; †Proborhyaenidae Ameghino, 1897a, p. 97; and several other supposed families.] Paleoc.–Plioc.; S.A. †Sparassodonts.

[1] There are six or seven other genera of Ameghino that may belong to this subfamily. Only two of these were figured (†*Notictis* and †*Prodidelphys*); these figures are barely recognizable, and the genera inadequately characterized. Until they are revised, their position in the system is so uncertain that it is hardly worth while to list these *nomina vana.*

[2] This pseudo-Greek name is of Malay origin and originally referred to *Tragulus*, the little ruminant, but is now entirely transferred to these opossums as a result of a history too complex to trace here. Tate, 1939, has shown that *Philander* should, following strict priority, be used for the four-eyed opossum usually called *Metachirops* Matschie, 1916. *Caluromys* would be valid for the woolly opossum.

†Subfam. Borhyaeninae Cabrera, 1927, p. 274. [Including †Proborhyaeninae Trouessart, 1898b, p. 1211; †Cladosictinae Cabrera, 1927, p. 273.] Paleoc.–Plioc.; S.A.
†*Patene* Simpson, 1935. U. Paleoc.–L. Eoc.; S.A.
†*Pharsophorus* Ameghino, 1897. [Including †*Plesiofelis* Roth, 1903.] U. Eoc.–L. Olig.; S.A.
†*Proborhyaena* Ameghino, 1904. L.–U. Olig.; S.A.
†*Stylocynus* Mercerat, 1917. Plioc.; S.A.
†*Procladosictis* Ameghino, 1902. U. Eoc.; S.A.
†*Notogale* Loomis, 1914. L. Olig.; S.A.
†*Cladosictis* Ameghino, 1887. U. Olig.–L. Mioc.; S.A.
†*Prothylacynus* Ameghino, 1891. L. Mioc.; S.A.
†*Agustylus* Ameghino, 1887. L. Mioc.; S.A.
†*Lycopsis* Cabrera, 1927. L. Mioc.; S.A.
†*Perathereutes* Ameghino, 1891. L. Mioc.; S.A.
†*Sipalocyon* Ameghino, 1887. L. Mioc.; S.A.
†*Thylacodictis* Mercerat, 1891 (=†*Amphiproviverra* Ameghino, 1891; †*Protoviverra* Ameghino, 1891, *nec* Lemoine, 1891). L. Mioc.; S.A.
†*Notocynus* Mercerat, 1891. Plioc.; S.A.
†*Sparassocynus* Mercerat, 1899. U. Plioc.; S.A.
†*Acrohyaenodon* Ameghino, 1904. Plioc.; S.A.
†*Arminiheringia* Ameghino, 1902. L. Eoc.; S.A.
†*Pseudoborhyaena* Ameghino, 1902. U. Olig.; S.A.
†*Borhyaena* Ameghino, 1887. U. Olig.–L. Mioc.; S.A.
†*Conodonictis* Ameghino, 1891. L. Mioc.; S.A.

†Subfam. Thylacosmilinae Riggs, 1933, p. 65. Plioc.; S.A.
†*Thylacosmilus* Riggs, 1933. Plioc.; S.A.

Superfam. Dasyuroidea Simpson, 1930, p. 9.

Fam. Dasyuridae Waterhouse, 1838, *fide* Waterhouse, 1841a, p. 60. [Including Myrmecobiidae Waterhouse, 1838, *fide* Waterhouse, 1841a, p. 60; Thylacinidae Bonaparte, 1838, p. 113.] Pleist.–R.; Aus.

Subfam. Phascogalinae Gill, 1872, p. 26 (=Phascogalina Bonaparte, 1850). Pleist.–R.; Aus. Pouched "mice," etc.
Phascogale Temminck, 1827 (=*Phascologale* Lenz, 1831). [Including *Antechinus* MacLeay, 1841; *Planigale* Troughton, 1928.] Pleist.–R.; Aus. R.; Tasmania, New Guinea. Broad-footed pouched "mice."
Dasyuroides Spencer, 1896. R.; Aus. Byrne's pouched "mouse."
Dasycercus Peters, 1875 (=*Chaetocercus* Krefft, 1866, *nec* Gray, 1855). R.; Aus. Crest-tailed pouched "mouse."
Sminthopsis Thomas, 1887. R.; Aus. Narrow-footed pouched "mice."
Antechinomys Krefft, 1866. R.; Aus. "Jerboa," pouched "mice."

Subfam. Dasyurinae Thomas, 1888, p. 253 (=Dasyurini Goldfuss, 1820, pp. xxxiii, 447). Pleist.–R.; Aus.
Dasyurus Geoffroy, 1796. [Including *Dasyurinus* Matschie, 1916; *Satanellus* Pocock, 1926; *Dasyurops* Matschie, 1916.] Pleist.–R.; Aus. R.; New Guinea. Native "cats," "tiger cats."

Sarcophilus Cuvier, 1837. Pleist.; Aus. R.; Tasmania. Tasmanian devil.

Subfam. Thylacininae Bensley, 1903, pp. 91, 107. Pleist.–R.; Aus.

Thylacinus Temminck, 1827 (=*Thylacynus* Temminck, 1827). Pleist.; Aus. R.; Tasmania. Tasmanian "wolf," "tiger," "hyena."

Subfam. Myrmecobiinae Gill, 1872, p. 26. R.; Aus.

Myrmecobius Waterhouse, 1836. R.; Aus. Banded "anteater," marsupial "anteater," white-banded "bandicoot."

Fam. Notoryctidae Ogilby, 1892, p. 5. R.; Aus.

Notoryctes Stirling, 1891. R.; Aus. Marsupial "mole," pouched "mole."

Superfam. Perameloidea Osborn, 1910, p. 516.

Fam. Peramelidae Waterhouse, 1838, *fide* Waterhouse, 1841a, p. 60 (=Peramelina Gray, 1825, p. 340). Pleist.–R.; Aus. Bandicoots.

Perameles Geoffroy, 1804. [Including *Peroryctes* Thomas, 1906.] Pleist.–R.; Aus. R.; New Guinea. Common bandicoots, long-nosed bandicoots.

Echymipera Lesson, 1842. [Including *Suillomeles* Allen and Barbour, 1909.] R.; New Guinea. New Guinea bandicoots.

Thylacomys Owen, 1840 (=*Thalacomys* Owen, 1840, misprint; *Macrotis* Reid, 1837, *nec* Dejean, 1833; *Paragalia* Gray, 1841). Pleist.–R.; Aus. Rabbit bandicoots, pinkies, bilbies.

Chaeropus Ogilby, 1838 (=*Choeropus* Gray, 1839). R.; Aus. Pig-footed bandicoots.

Thylacis Illiger, 1811 (=*Isoödon* Desmarest, 1817). Pleist.–R.; Aus. Short-nosed bandicoots.

Superfam. Caenolestoidea Osborn, 1910, p. 517.

Fam. Caenolestidae Trouessart, 1898b, p. 1205 (=†Epanorthidae Ameghino, 1889, pp. 268, 270). [Including †Abderitesidae Ameghino, 1889, pp. 268, 269; †Garzonidae Ameghino, 1891c, p. 307.] Eoc.–R.; S.A.

Subfam. Caenolestinae Sinclair, 1906, p. 416 (=Caenolestidae *sensu stricto*). [Including †Garzonidae Ameghino, 1891c, p. 307.] Eoc.–R.; S.A.

†*Progarzonia* Ameghino, 1904. L. Eoc.; S.A.

†*Pseudhalmarhiphus* Ameghino, 1903. Olig.; S.A.

†*Garzonia* Ameghino, 1891. [Including †*Phonocdromus* Ameghino, 1894.] U. Olig.–L. Mioc.; S.A.

†*Halmarhiphus* Ameghino, 1891. [Including †*Parhalmarhiphus* Ameghino, 1894.] L. Mioc.; S.A.

†*Stilotherium* Ameghino, 1887. L. Mioc.; S.A.

†*Zygolestes* Ameghino, 1898. Plioc.; S.A.

Caenolestes Thomas, 1895 (=*Hyracodon* Tomes, 1863, *nec* Leidy, 1856). R.; S.A. "Opossum-rat."

Orolestes Thomas, 1917. R.; S.A.

Rhyncholestes Osgood, 1924. R.; S.A.

†Subfam. Palaeothentinae Sinclair, 1906, p. 417 (=†Epanorthidae Ameghino, 1889, pp. 268, 270, *sensu stricto*). L. Olig.–L. Mioc.; S.A.

†*Palaeothentes* Ameghino, 1887 (=†*Epanorthus* Ameghino, 1889).[1] [Including †*Palaepanorthus* Ameghino, 1902; †*Prepanorthus* Ameghino, 1894; †*Metaepanorthus* Ameghino, 1894; †*Paraepanorthus* Ameghino, 1894.] L. Olig.–L. Mioc.; S.A.

†*Pilchenia* Ameghino, 1903. L. Olig.; S.A.

†*Acdestis* Ameghino, 1887. [Including †*Callomenus* Ameghino, 1891.] L. Olig.–L. Mioc.; S.A.

†*Dipilus* Ameghino, 1890. [Including †*Decastis* Ameghino, 1891; †*Metriodromus* Ameghino, 1894.] L. Mioc.; S.A.

†*Halmadromus* Ameghino, 1891.[2] L. Mioc.; S.A.

†Subfam. Abderitinae Sinclair, 1906, p. 417 (=†Abderitesidae Ameghino, 1889, pp. 268, 269). Olig.–L. Mioc.; S.A.

†*Parabderites* Ameghino, 1902. L. Olig.–L. Mioc.; S.A.

†*Micrabderites* Simpson, 1932. U. Olig.; S.A.

†*Abderites* Ameghino, 1887. U. Olig.–L. Mioc.; S.A.

†Fam. Polydolopidae Ameghino, 1897a, p. 92. Paleoc.–Eoc.; S.A.

†*Seumadia* Simpson, 1935. Paleoc.; S.A.

†*Polydolops* Ameghino, 1897. [Including †*Pseudolops* Ameghino, 1902; †*Pliodolops* Ameghino, 1902; †*Orthodolops* Ameghino, 1903; †*Anissodolops* Ameghino, 1903; †*Archaedolops* Ameghino, 1903.] ?Paleoc., Eoc.; S.A.

†*Amphidolops* Ameghino, 1902. [Including †*Anadolops* Ameghino, 1903.] Eoc.; S.A.

†*Eudolops* Ameghino, 1897. [Including †*Promysops* Ameghino, 1902; †*Propolymastodon* Ameghino, 1903.] Eoc.; S.A.

Superfam. Phalangeroidea Weber, 1928, p. xiii.

Fam. Phalangeridae Thomas, 1888, p. 126 (=Phalangistadae Gray, 1821, p. 308). [Including Phascolarctidae Owen, 1839, p. 19=Koalidae Burnett, 1830a, p. 351.] Plioc.–R.; Aus.

Subfam. Phalangerinae Thomas, 1888, p. 136. Plioc.–R.; Aus. Phalangers, Australian "opossums."

†*Wynyardia* Spencer, 1900. Plioc.; Tasmania.

Phalanger Storr, 1780. R.; Aus., New Guinea, Moluccas, Celebes. Cuscus.

Trichosurus Lesson, 1828. Pleist.–R.; Aus. Australian "opossums," common phalangers.

Acrobates Desmarest, 1817. R.; Aus. Pygmy flying "opossums," feather-tails, pygmy gliders.

Distoechurus Peters, 1874. R.; New Guinea. Pen-tailed phalanger.

Cercaërtus Burmeister, 1837 (=*Cercartetus* Gloger, 1841; *Dromicia* Gray, 1841). [Including *Eudromicia* Mjoberg,

[1] "*Palaeothentes*" was listed by Moreno in 1882 but was then a *nomen nudum* and was first defined by Ameghino in 1887. In 1889 Ameghino decided that this spelling is "impossible" and that the name should have been written "*Palaeoteuthis*" and hence was preoccupied by *Palaeoteuthis* D'Orbigny, 1847. On these grounds Ameghino substituted "*Epanorthus*." But the spelling "*Palaeothentes*" was original, intentional, and *ipso facto* is correct in nomenclature regardless of its etymology. Of course, it cannot be preoccupied by the quite different name "*Palaeoteuthis*."

[2] The status of this supposed genus is extremely dubious, and indeed this is true of most of the 14 supposed genera of †palaeothentines that have been described as contemporaneous in the Santa Cruz beds. Proper generic criteria for this group have not yet been worked out, and the published data are inadequate in several cases. Perhaps these still more dubious genera should also be mentioned: †*Essoprion* Ameghino, 1891; †*Halmaselus* Ameghino, 1891; †*Pichipilus* Ameghino, 1890. †*Tideus* Ameghino, 1890 (*nec Tydeus* Koch, 1842)=†*Mannodon* Ameghino, 1893. All L. Mioc.; S.A. These are all really *nomina vana* at present.

1916.] Pleist.–R.; Aus. R.; New Guinea. "Dormouse opossums."

Gymnobelideus McCoy, 1867. R.; Aus. Leadbeater's "opossum."

Petaurus Shaw, 1791. Pleist.–R.; Aus. R.; New Guinea. Flying "opossums," gliders.

†*Palaeopetaurus* Broom, 1895. Pleist.; Aus.

Dactylopsila Gray, 1858. [Including *Dactylonax* Thomas, 1910.] R.; New Guinea, Aus. Striped "opossums."

Wyulda Alexander, 1919. R.; Aus.

Spilocuscus Gray, 1862. R.; Aus.

Subfam. Tarsipedinae Thomas, 1888, p. 130. R.; Aus.

Tarsipes Gervais and Verreaux, 1842. R.; Aus. Long-snouted phalanger.

Subfam. Phascolarctinae Thomas, 1888, p. 209 (=Phascolarctidae Owen, 1839, p. 19; Koalidae Burnett, 1830a, p. 351). Pleist.–R.; Aus.

Phascolarctos De Blainville, 1816 (=*Koala* Burnett, 1830). Pleist.–R.; Aus. Koala, native "bear," native "sloth."

Pseudocheirus Ogilby, 1837. [Including *Pseudochirops* Matschie, 1915; *Hemibelideus* Collett, 1884; *Petropseudes* Thomas, 1923.] Pleist.–R.; Aus. R.; New Guinea. Ring-tailed "opossums."

Schoinobates Lesson, 1842 (=*Petaurista* Waterhouse, 1846, *nec* Link, 1795; *Petauroides* Thomas, 1888). R.; Aus. Gliders, flying phalangers, great flying phalangers.

†Subfam. Burramyinae Broom, 1898, p. 63. Pleist.; Aus.

†*Burramys* Broom, 1895. Pleist.; Aus.

†Fam. Thylacoleonidae Gill, 1872, p. 26 (=†Thylacoleontidae Cope, 1889c, p. 876). Pleist.; Aus.

†*Thylacoleo* Owen, 1859. Pleist.; Aus.

Fam. Phascolomidae Bonaparte, 1845, p. 6 (=Phascolomyda Goldfuss, 1820, pp. xxii, 444; Phascolomyidae Owen, 1839, p. 19). Pleist.–R.; Aus. Wombats.

†*Phascolonus* Owen, 1872. Pleist.; Aus.

Phascolomis Geoffroy, 1803 (=*Vombatus* Geoffroy, 1803). Pleist.–R.; Aus. Common wombat.

Lasiorhinus Gray, 1863. R.; Aus. Hairy-nosed wombat.

Wombatula Iredale and Troughton, 1934. R.; Aus. Queensland wombat.

Fam. Macropodidae Owen, 1839, p. 19 (=Macropidae Gray, 1821, p. 308; Halmaturidae Bonaparte, 1831, p. 8). [Including Potoridae Gray, 1821, p. 308; Hypsiprimnodontidae Collett, 1887, p. 906; and others.] Pleist.–R.; Aus.

Subfam. Macropodinae Thomas, 1888, p. 10. Pleist.–R.; Aus. Kangaroos and wallabies.

†*Procoptodon* Owen, 1873. Pleist.; Aus.

†*Sthenurus* Owen, 1873. Pleist.; Aus.

†*Palorchestes* Owen, 1873. Pleist.; Aus.

†*Brachalletes* De Vis, 1883. Pleist.; Aus.

†*Synaptodon* De Vis, 1889. Pleist.; Aus.

Lagorchestes Gould, 1841. [Including *Lagostrophus* Thomas, 1886.] R.; Aus. "Hare" wallabies.

Petrogale Gray, 1837. [Including *Peradorcus* Thomas, 1904.] Pleist.–R.; Aus. Rock wallabies.

Onychogalea Gray, 1841 (generally but incorrectly written *Onychogale*). R.; Aus. Silky wallabies, nail-tailed wallabies.

Thylogale Gray, 1837. Pleist.–R.; Aus. R.; New Guinea. Scrub wallabies, padamelons.

Protemnodon Owen, 1873 (=*Halmaturus*, auct.; *Wallabia*, auct.). Pleist.–R.; Aus. R.; S.E. New Guinea. Large wallabies.

Macropus Shaw, 1790 (=*Halmaturus* Illiger, 1811). [Including *Osphranter* Gould, 1842; *Megaleia* Gistel, 1848.[1]] Pleist.–R.; Aus. R.; New Guinea. Red and gray kangaroos, wallaroos, euros, wallabies, scrub wallabies, padamelons, etc.

Setonyx Lesson, 1842. R.; Aus. Short-tailed wallaby.

Dendrolagus Müller, 1839. R.; Aus., New Guinea. Tree kangaroo.

Dorcopsis Schlegel and Müller, 1842. R.; New Guinea.

Subfam. Potoroinae Trouessart, 1898b, p. 1195 (=Potoridae Gray, 1821, p. 308). [Including Bettongiinae Bensley, 1903, p. 143.] Pleist.–R.; Aus. "Rat" kangaroos, "jerboa" kangaroos.

Bettongia Gray, 1837. Pleist.–R.; Aus. Bettongs, tungoos, squeakers, "jerboa" kangaroos, brush-tailed "rat" kangaroos, etc.

Aepyprymnus Garrod, 1875. Pleist.-R.; Aus. Large "rat" kangaroo, rufous "rat" kangaroo.

Caloprymnus Thomas, 1888. R.; Aus. Plain "rat" kangaroo.

Potorous Desmarest, 1804. Pleist.–R.; Aus. Potoroos, common "rat" kangaroos.

†*Propleopus* Longman, 1924 (=*Triclis* De Vis, 1889, *nec* Loew, 1851). Pleist.; Aus.

Hypsiprymnodon Ramsay, 1876. R.; Aus. Musk kangaroo, Australian "muskrat."

†Fam. Diprotodontidae Gill, 1872, p. 26. [Including †Nototheriidae Lydekker, 1887, p. 161.] Pleist.; Aus.

†*Diprotodon* Owen, 1838. Pleist.; Aus.

†*Euryzygoma* Longman, 1921. Pleist.; Aus.

†*Nototherium* Owen, 1845. Pleist.; Aus.

†*Euowenia* De Vis, 1891 (=†*Owenia* De Vis, 1888, *nec* Presch, 1847). Pleist.; Aus.

†*Sthenomerus* De Vis, 1883. Pleist.; Aus.

†*Zygomaturus* Owen, 1858 (or Macleay, 1857).[2] Pleist.; Aus.

?MARSUPIALIA *incertae sedis:*

†*Argyrolagus* Ameghino, 1904. Plioc.; S.A.

Infraclass EUTHERIA Gill, 1872, p. 1[3] (=Monodelphia De Blainville, 1816, p. 109; Placentaria Fleming, 1822, p. 169; Placentalia Owen, 1837, p. 903).

[1] *Macropus* (*Osphranter*) includes the wallaroos, *Macropus* (*Megaleia*) the red kangaroos, and *Macropus* (*Macropus*) the gray kangaroos.

[2] Macleay is said to have published the name in a newspaper, and it is not known whether he really established a genus or not. Owen characterized it properly.

[3] Huxley, 1880, p. 657, more nearly in the sense here adopted; see p. 164, this paper.

Cohort UNGUICULATA Linnaeus, 1766, p. 21.
Order INSECTIVORA Bowdich, 1821, pp. 24, 31.
†Superfam. Deltatheridioidea Simpson, 1931a, p. 268.
†Fam. Deltatheridiidae Gregory and Simpson, 1926, p. 6. U. Cretac.; As. L. Paleoc.–M. Eoc.; N.A.
†Subfam. Deltatheridiinae, new. U. Cretac.; As.
†*Deltatheridium* Gregory and Simpson, 1926. U. Cretac.; As.
†*Deltatheroides* Gregory and Simpson, 1926. U. Cretac.; As.
†*Hyotheridium* Gregory and Simpson, 1926. U. Cretac.; As.
†Subfam. Didelphodontinae Matthew, 1918, p. 571. L. Paleoc.–Eoc.; N.A.
†*Puercolestes* Reynolds, 1936. L. Paleoc.; N.A.
†*Gelastops* Simpson, 1935. M. Paleoc.; N.A.
†*Didelphodus* Cope, 1882. L. Eoc.; N.A.
†*Phenacops* Matthew, 1909. M. Eoc.; N.A.
Superfam. Tenrecoidea Simpson, 1931a, p. 268 (=Centetoidea Gill, 1872, p. 19; with Chrysochloroidea=Zalambdodonta Gill, 1884, p. 120).
†Fam. Palaeoryctidae Simpson, 1931a, p. 268. M. Paleoc.; N.A.
†*Palaeoryctes* Matthew, 1913. M. Paleoc.; N.A.
Fam. Solenodontidae Dobson, 1882, p. 87. L.–M. Olig.; N.A. R.; W. Indies.
†Subfam. Apternodontinae Matthew, 1910a, p. 35. Olig.; N.A.
†*Apternodus* Matthew, 1903. L.–M. Olig.; N.A.
Subfam. Solenodontinae Gill, 1872, p. 19. L. Olig.; N.A. R.; W. Indies.
†*Micropternodus* Matthew, 1903. L. Olig.; N.A.
†*Clinopternodus* Clark, 1937 (=†*Clinodon* Clark, 1936, *nec* Regan, 1920). L. Olig.; N.A.
Solenodon Brandt, 1833. [Including *Atopogale* Cabrera, 1925.] R.; W. Indies (Cuba, Haiti). Alamiqui.
Fam. Tenrecidae Gray, 1821, p. 301 (=Centetidae Murray, 1866, pp. xiv, 232; Centetina Bonaparte, 1838, p. 111). [Including Oryzoryctidae Gill, 1882, p. 120.] Pleist.–R.; Madagascar.
Subfam. Tenrecinae Cabrera, 1925, pp. 183, 191 (=Centetinae Murray, 1866, p. 319[1]; and most other authors). Pleist.–R.; Madagascar.
Tenrec Lacépède, 1799 (=*Centetes* Illiger, 1811). R.; Madagascar. Tenrec.
Setifer Froriep, 1806 (=*Ericulus* Geoffroy, 1837). R.; Madagascar. "Hedgehog" tenrec.
Hemicentetes Mivart, 1871. R.; Madagascar. Streaked tenrec.
Dasogale Grandidier, 1928. R.; Madagascar.
Echinops Martin, 1838. R.; Madagascar.
Subfam. Oryzorictinae Dobson, 1882, p. 71. [Including Geogalinae Trouessart, 1879, p. 275.] Pleist.–R.; Madagascar.
Oryzorictes Grandidier, 1870. [Including *Nesoryctes* Thomas, 1918.] R.; Madagascar. Rice tenrec.
Microgale Thomas, 1882. [Including *Nesogale* Thomas, 1918; *Leptogale* Thomas, 1918; *Paramicrogale* Grandidier and Petit, 1931.] R.; Madagascar. Long-tailed tenrec.
Cryptogale Grandidier, 1928. R.; Madagascar.

[1] Credited to Pomel, 1848, but this spelling was not used by Pomel.

Limnogale Major, 1896. R.; Madagascar.
Geogale Milne Edwards and Grandidier, 1872. R.; Madagascar.
Fam. Potamogalidae Allman, 1865, p. 467. R.; Af.
Potamogale Du Chaillu, 1860. R.; W. Af. Jes.
Superfam. Chrysochloroidea Gregory, 1910, p. 267 (=Chrysochloridoidea Gill, 1872, p. 19).
Fam. Chrysochloridae Mivart, 1868, p. 150 (=Chrysochlorina Gray, 1825, p. 335). R.; Af.
Chrysochloris Lacépède, 1799. [Including *Eremitalpa* Roberts, 1924; *Chrysotricha* Broom, 1907; *Huetia* Forcart, 1942.] R.; S. Af. Cape golden "mole."
†*Proamblysomus* Broom, 1941. Pleist.; S. Af.
Amblysomus Pomel, 1848. R.; S. Af.
Chlorotalpa Roberts, 1924. Pleist.–R.; S. Af.
Chrysospalax Gill, 1883 (=*Bematiscus* Cope, 1892). R.; S. Af.
Superfam. Erinaceoidea Gill, 1872, p. 18.
†Fam. Zalambdalestidae Gregory and Simpson, 1926, p. 14. U. Cretac.; As.
†*Zalambdalestes* Gregory and Simpson, 1926. U. Cretac.; As.
†Fam. Leptictidae Gill, 1872, p. 19 (=†Ictopsidae Schlosser, 1887, p. 140).[1] [Including †Adapisoricidae Schlosser, 1887, p. 138.] U. Cretac.–Olig.; N.A. U. Paleoc.–Eoc.; Eu.
†*Gypsonictops* Simpson, 1927. U. Cretac.; N.A.
†*Prodiacodon* Matthew, 1929 (=†*Palaeolestes* Matthew, 1918, *nec* De Vis, 1911). M. Paleoc.; N.A.
†*Acmeodon* Matthew and Granger, 1921. M. Paleoc.; N.A.
†*Emperodon* Simpson, 1935. M. Paleoc.; N.A.
†*Myrmecoboides* Gidley, 1915. M. Paleoc.; N.A.
†*Adapisorex* Lemoine, 1883. U. Paleoc.–L. Eoc.; Eu.
†*Diacodon* Cope, 1875. U. Paleoc.–L. Eoc.; N.A.
†*Parictops* Granger, 1910. L. Eoc.; N.A.
†*Protictops* Peterson, 1934. U. Eoc. (or L. Olig.); N.A.
†*Ictops* Leidy, 1868. [Including †*Mesodectes* Cope, 1875.] L.–M. Olig.; N.A.
†*Leptictis* Leidy, 1868. M. Olig.; N.A.
?†Leptictidae *incertae sedis:*
†*Xenacodon* Matthew and Granger, 1921. U. Paleoc.; N.A.
†*Sespedectes* Stock, 1935. U. Eoc.; N.A.
Fam. Erinaceidae Bonaparte, 1838, p. 111 (=Erinacidae Gray, 1821, p. 300; Erinacini Fischer, 1817, p. 372). U. Eoc.–R.; Eu. Olig.–R.; As. L. Eoc.–L. Plioc.; N.A. R.; Af. Hedgehogs.
Subfam. Echinosoricinae Cabrera, 1925, pp. 57, 58 (=Gymnurinae Gill, 1872, p. 19). U. Eoc.–U. Mioc.; Eu. L. Eoc.–L. Plioc.; N.A. R.; As. Hairy hedgehogs.
†*Entomolestes* Matthew, 1909. L. Eoc.; N.A.
†*Proterixoides* Stock, 1935. U. Eoc.; N.A.
†*Metacodon* Clark, 1936. L.–M. Olig.; N.A.
†*Ankylodon* Patterson and McGrew, 1937. M. Olig.; N.A.
†*Proterix* Matthew, 1903. M. Olig.; N.A.
†*Brachyerix* Matthew, 1933. U. Mioc.; N.A.
†*Metechinus* Matthew, 1929. L. Mioc.–L. Plioc.; N.A.

[1] Schlosser's type is greatly preferable, but the name "Leptictidae" is older and is in customary use.

†*Meterix* Hall, 1929. L. Plioc.; N.A.
†*Neurogymnurus* Filhol, 1877 (=†*Necrogymnurus* Lydekker, 1891; and most authors). U. Eoc.; Eu.
†*Lantanotherium* Filhol, 1888 (=†*Lanthanotherium* of most later authors). M. Mioc.; Eu.
†*Galerix* Pomel, 1848. [Including †*Parasorex* Meyer, 1865.] U. Mioc.; Eu.
†*Pseudogalerix* Gaillard, 1929. U. Mioc.; Eu.
Echinosorex De Blainville, 1838 (=*Gymnura* Lesson, 1827, *nec* Kuhl, 1824). R.; S. As. Bulau.
Hylomys Müller, 1839. R.; S.As.
Podogymnura Mearns, 1905. R.; Philippines.
Neotetracus Trouessart, 1909. R.; E.As.

Subfam. Erinaceinae Gill, 1872, p. 18. Olig.–R.; Eu., As. U. Mioc.; ?N.A. R.; Af. (True or spiny) hedgehogs.
†*Tetracus* Aymard, 1850. Olig.; Eu.
†*Palaeoerinaceus* Filhol, 1879. U. Olig.–L. Mioc.; Eu.
†*Tupaiodon* Matthew and Granger, 1924. Olig.; As.
†*Palaeoscaptor* Matthew and Granger, 1924. Olig.; As.
†*Parvericius*[1] Koerner, 1940. U. Mioc.; N.A.
Aethechinus Thomas, 1918. R.; Af. Fikifa.
Erinaceus Linnaeus, 1758. Mioc.–R.; Eu. Pleist.-R.; As. Hedgehog.
Atelerix Pomel, 1840. R.; Af. African hedgehog.
Hemiechinus Fitzinger, 1866 (=*Ericius* Sundevall, 1841, *nec* Tilesius, 1813). R.; As., N. Af.
Paraechinus Trouessart, 1879. [Including *Macroechinus* Satunin, 1907.] R.; S. As., N. Af.

†Fam. Dimylidae Schlosser, 1887, p. 103. U. Olig.–U. Mioc.; Eu.
†*Dimylus* Meyer, 1846. U. Olig.–Mioc.; Eu.
†*Cordylodon* Meyer, 1859. U. Olig.–L. Mioc.; Eu.
†*Plesiodimylus* Gaillard, 1897. Mioc.; Eu.
†*Metacordylodon* Schlosser, 1911. U. Mioc.; Eu.

Superfam. Macroscelidoidea Gill, 1872, p. 19.

Fam. Macroscelididae Mivart, 1868, p. 143 (=Macroscelidina Bonaparte, 1838, p. 113). [Including Rhynchocyonidae Gill, 1882, p. 119=Rhynchocyoninae Gill, 1872, p. 19.] R.; Af. "Elephant shrews."
Macroscelides Smith, 1829. R.; Af. Common "elephant shrew."
Nasilio Thomas and Schwann, 1906. R.; S. Af., Cent. Af. Sakutopi, dengoli.
Elephantulus Thomas and Schwann, 1906. R.; Af.
Petrodromus Peters, 1846. R.; Cent. Af.
Rhynchocyon Peters, 1847. [Including *Rhinonax* Thomas, 1918.] R.; E. Af.

Superfam. Soricoidea Gill, 1872, p. 18.

†Fam. Nyctitheriidae Simpson, 1928b, p. 2. M. Paleoc.–M. Eoc.; N.A. L. Eoc.; Eu.[2]
†*Stilpnodon* Simpson, 1935. M. Paleoc.; N.A.

[1] The author is uncertain that this genus belongs in the Erinaceinae.
[2] The probable European member of this family has been called †*Adapisoriculus* Lemoine, 1885, but it is doubtful whether it really belongs to that poorly known and ill-defined genus, which is of most uncertain affinities.

†*Protentomodon* Simpson, 1928. U. Paleoc.; N.A.
†*Nyctitherium* Marsh, 1872. L.–M. Eoc.; N.A.
†*Centetodon* Marsh, 1872. M. Eoc.; N.A.
†*Myolestes* Matthew, 1909. M. Eoc.; N.A.

Fam. Soricidae Gray, 1821, p. 300 (=Soricini Fischer, 1817, p. 372). L. Olig.–R.; Eu. M. Olig.–R.; N.A. L. Plioc.–R.; As. R.; Af. Shrews.

Subfam. Soricinae Murray, 1866, p. 231[1] (=Sorexineae Lesson, 1842, p. 87). U. Eoc.–R.; Eu. L. Olig.–R.; N. A. L. Plioc.–R.; As. Red-toothed shrews.

†*Saturninia* Stehlin, 1940. U. Eoc.; Eu.
†*Necrosorex* Filhol, 1889. L. Olig.; Eu.
†*Domnina* Cope, 1873 (=†*Protosorex* Scott, 1895). L.–M. Olig.; N.A.
†*Heterosorex* Gaillard, 1915. M. Mioc.; Eu.
†*Mystipterus* Hall, 1930. L. Plioc.; N.A.[2]
Sorex Linnaeus, 1758. [Including *Neosorex* Baird, 1857; *Atophyrax* Merriam, 1884.] ?L. Olig., L. Mioc.–R.; Eu. U. Plioc.–R.; N.A. R.; As. Common shrew.
Microsorex Baird, 1877. Pleist.–R.; N.A. Pygmy shrew.
Soriculus Blyth, 1855. [Including *Chodsigoa* Kashtchenko, 1906.] R.; As. Oriental shrew.
Neomys Kaup, 1829. R.; Eu., As. (Old World) water shrew.
Blarina Gray, 1838. U. Plioc.–R.; N.A. Short-tailed shrew.
Blarinella Thomas, 1911. L. Plioc., R.; E. As.
Cryptotis Pomel, 1848. R.; N.A., northern S.A.[3] Little shrew.
Notiosorex Baird, 1877. Pleist.–R.; N.A. Crawford shrew.

Subfam. Crocidurinae Milne Edwards, 1868–1874, p. 256. U. Mioc.; N.A. U. Mioc.–R.; Eu. L. Plioc.–R.; As. R.; Af. White-toothed shrews.

†*Limnoecus* Stirton, 1930. U. Mioc.; N.A.
Crocidura Wagler, 1832. [Including *Heliosorex* Heller, 1910; etc.] U. Mioc.–R.; Eu. L. Plioc.–R.; As. R.; Af. House shrew, musk shrew.
Praesorex Thomas, 1913. R.; W. Af.
Suncus Ehrenberg, 1832 (=*Pachyura* Sélys-Longchamps, 1839). R.; Eu., Af., As.[4] Thick-tailed shrew.
Feroculus Kelaart, 1852. R.; Ceylon.
Solisorex Thomas, 1924. R.; Ceylon.
Sylvisorex Thomas, 1904. R.; Af. Forest shrew.
Myosorex Gray, 1838. R.; S. Af. "Mouse" shrew.
Surdisorex Thomas, 1906. R.; E. Af.
Diplomesodon Brandt, 1853. R.; As.
Anourosorex Milne Edwards, 1870.[5] L. Plioc., R.; As. Short-tailed shrew, "mole" shrew.
Chimarrogale Anderson, 1877. [Including *Crossogale* Thomas, 1921.] R.; As. Asiatic water shrew.

[1] Credited to Pomel, 1848, by Murray, p. 319, but this spelling is not used by Pomel.
[2] Described as a bat, but a soricid according to a note by Patterson and McGrew, 1937.
[3] The only insectivore of South America and an obviously recently immigrant North American marginal form, not a true Neotropical animal.
[4] The smallest living mammal belongs to this genus.
[5] Not "*Anurosorex*" as usually spelled.

Nectogale Milne Edwards, 1870. R.; As. Tibetan water shrew, web-footed shrew.

Subfam. Scutisoricinae Allen, 1917, p. 781. R.; Af. Armored shrew.

Scutisorex Thomas, 1913. R.; Af. Armored shrew.

Fam. Talpidae Gray, 1825, p. 335 (=Talpini Fischer, 1817, p. 372). [Including Scalopidae Cope, 1889c, p. 876; Myogalidae Milne Edwards, 1868–1874, pp. 267, 272=Myaladae Gray, 1821, p. 300.] U. Eoc.–R.; Eu. U. Olig.–R.; N.A. R.; As. Moles.

Subfam. Uropsilinae Thomas, 1912, p. 397. R.; As. "Shrew" moles.

Uropsilus Milne Edwards, 1871. [Including *Rhynchonax* Thomas, 1911.] R.; As. "Shrew" mole.

Nasillus Thomas, 1911. R.; E. As.

Subfam. Desmaninae Thomas, 1912, p. 397 (=Myogalina Bonaparte, 1845, p. 5; Myaladae Gray, 1821, p. 300, *sensu stricto*). U. Mioc.–R.; Eu. R.; As. Desmans, etc.

†*Mygalea* Schreuder, 1940. U. Mioc.; Eu.

†*Mygalinia* Schreuder, 1940. L. Plioc.; Eu.

Desmana Guldenstadt, 1777 (=*Mygale* Cuvier, 1800; *Myogale* Brandt, 1836). L. Plioc.–R.; Eu. R.; As. Desman, water mole.

Galemys Kaup, 1829. R.; Eu. Almizilero.

Subfam. Talpinae Murray, 1866, p. 319.[1] U. Eoc.–R.; Eu. R.; As. ?M.–U. Mioc.; ?N.A. Old World moles.

†*Amphidozotherium* Filhol, 1876. U. Eoc.; Eu.

†*Geotrypus* Pomel, 1848. M. Olig.; Eu.

†*Proscapanus* Gaillard, 1899. Mioc.; Eu.

Talpa Linnaeus, 1758. Mioc.–R.; Eu. ?M.–U. Mioc.; ?N.A. R.; As. Common (Old World) mole.

Mogera Pomel, 1848. R.; E. As.

Parascaptor Gill, 1875. R.; S. As.

Scaptochirus Milne Edwards, 1867. R.; As.

Subfam. Scalopinae Thomas, 1912, p. 397 (=Scalopidae Cope, 1889c, p. 876). U. Olig.–R.; N.A. R.; E. As. ?M. Mioc.; ?Eu. American moles, etc.

†*Proscalops* Matthew, 1901. U. Olig.–L. Mioc.; N.A.

Scaptonyx Milne Edwards, 1871. ?M. Mioc.; ?Eu. R.; E. As.

Dymecodon True, 1886. R.; Japan.

Neurotrichus Günther, 1880. R.; N.A. (American) "shrew" mole.

Urotrichus Temminck, 1838–1839. R.; Japan.

Scapanulus Thomas, 1912. R.; E. As.

Parascalops True, 1894. Pleist.–R.; N.A. Hairy-tailed mole.

†*Hesperoscalops* Hibbard, 1941. U. Plioc.; N.A.

Scapanus Pomel, 1848. Pleist.–R.; N.A. Western (American) mole.

Scalopus Geoffroy, 1803 (=*Scalops* Illiger, 1811). Plioc.–R.; N.A. Eastern (American) mole.

Subfam. Condylurinae Thomas, 1912, p. 397. R.; N.A.

Condylura Illiger, 1811. R.; N.A. Star-nosed mole.

[1] Credited to Pomel, 1848, by Murray, but this spelling is not used by Pomel.

?Talpidae *incertae sedis:*
†*Scaptogale* Trouessart, 1897 (=†*Echinogale* Pomel, 1848, *nec* Wagner, 1841). L. Mioc.; Eu.
†Fam. Nesophontidae Anthony, 1916, p. 728. Pleist. or R.; W. Indies.
†*Nesophontes* Anthony, 1916. Pleist. or R.; W. Indies (Puerto Rico, Cuba).
†Superfam. Pantolestoidea Cope, 1887b, p. 378.
†Fam. Pantolestidae Cope, 1884d, p. 719. M. Paleoc.–M. Eoc.; N.A. L. Eoc.; Eu.
†Subfam. Pantolestinae Simpson, 1937a, p. 121. M. Paleoc.–M. Eoc.; N.A. L. Eoc.; Eu.
†*Bessoecetor* Simpson, 1936. M.–U. Paleoc.; N.A.
†*Propalaeosinopa* Simpson, 1927. U. Paleoc.; N.A.
†*Palaeosinopa* Matthew, 1901. L. Eoc.; N.A., Eu.
†*Pantolestes* Cope, 1872. M. Eoc.; N.A.
†Subfam. Pentacodontinae Simpson, 1937a, p. 123. L.–?U. Paleoc.; N.A.
†*Pentacodon* Scott, 1892. M. Paleoc.; N.A.
†*Aphronorus* Simpson, 1935. M. Paleoc.; N.A.
†Superfam. Mixodectoidea, new name (=†Mixodectoidae Hay, 1930, p. 445). M. Paleoc.–U. Eoc.; N.A.
†Fam. Mixodectidae Cope, 1883a, p. 80. [Including †Microsyopsidae Osborn, 1892, p. 101.] M. Paleoc.–U. Eoc.; N.A.
†*Mixodectes* Cope, 1883. M. Paleoc.; N.A.
†*Indrodon* Cope, 1884. M. Paleoc.; N.A.
†*Eudaemonema* Simpson, 1935. M. Paleoc.; N.A.
†*Dracontolestes* Gazin, 1941. M. Paleoc.; N.A.
†*Elpidophorus* Simpson, 1927. M.–U. Paleoc.; N.A.
†*Cynodontomys* Cope, 1882. L. Eoc.; N.A.
†*Microsyops* Leidy, 1872. M. Eoc.; N.A.
†*Craseops* Stock, 1934. U. Eoc.; N.A.
?INSECTIVORA, *familiae incertae sedis:*
†Fam. Picrodontidae Simpson, 1937a, p. 134. M.–U. Paleoc.; N.A.
†*Picrodus* Douglass, 1908 (=†*Megopterna* Douglass, 1908). M. Paleoc.; N.A.
†*Zanycteris* Matthew, 1917. U. Paleoc.; N.A.
†Fam. Apheliscidae Matthew, 1918, p. 592. U. Paleoc.–L. Eoc.; N.A.
†*Apheliscus* Cope, 1875. U. Paleoc.–L. Eoc.; N.A.
†Fam. Necrolestidae Ameghino, 1894, p. 259. L. Mioc.; S.A.
†*Necrolestes* Ameghino, 1891. L. Mioc.; S.A.
?INSECTIVORA, *genera incertae sedis:*
†*Adapisoriculus* Lemoine, 1885. U. Paleoc.; Eu.
†*Praolestes* Matthew, Granger, and Simpson, 1929. U. Paleoc.; As.
†*Pseudictops* Matthew, Granger, and Simpson, 1929. U. Paleoc.; As.
†*Unuchinia* Simpson, 1937 (=†*Apator* Simpson, 1936, *nec* Semenow, 1898). U. Paleoc.; N.A.
†*Arctoryctes* Matthew, 1907. L. Mioc.; N.A.
†*Geolabis* Cope, 1884. M. Olig.; N.A.
Order DERMOPTERA Illiger, 1811, p. 116.
†Fam. Plagiomenidae Matthew, 1918, p. 598. U. Paleoc.-L. Eoc.; N.A.

†*Planetetherium* Simpson, 1928. U. Paleoc.; N.A.
†*Plagiomene* Matthew, 1918. L. Eoc.; N.A.
Fam. Cynocephalidae, new name (=Galeopithecidae Gray, 1821, p. 300, *nec* Cynocephalidae Ameghino, 1889, p. 893).[1] R.; As.
Cynocephalus Boddaërt, 1768 (=*Galeopithecus* Pallas, 1780; *nec Cynocephalus* Cuvier and Geoffroy, 1795). [Including *Galeopterus* Thomas, 1908.] R.; As. Colugo, caguan, kubuk, "flying lemur."
Order CHIROPTERA Blumenbach, 1779, pp. 58, 74. Bats.
Suborder MEGACHIROPTERA Dobson, 1875, p. 346 (=Frugivora Gill, 1872, p. 18; Fructivorae Gray, 1821, p. 299). Olig.; Eu. R.; As., Aus., Pacific, Af. Fruit-eating bats.
Fam. Pteropidae Gray, 1821, p. 299 (or Pteropodidae Bonaparte, 1838, p. 111). [Including Cephalotidae Gray, 1821, p. 299.] Olig.; Eu. R.; As., Aus., Pacific, Af.
†Subfam. Archaeopteropodinae, new. Olig.; Eu.
†*Archaeopteropus* Meschinelli, 1902. M. Olig.; Italy.
Subfam. Pteropinae Trouessart, 1897, p. 77 (or Pteropodinae Flower and Lydekker, 1891, p. 650). R.; As., Aus., Pacific, Af.
Cynopterus Cuvier, 1825. [Including *Niadius* Miller, 1906; *Thoopterus* Matschie, 1899; *Chironax* Andersen, 1912; *Dyacopterus* Andersen, 1912; *Penthetor* Andersen, 1912.] R.; S. As., E. Indies. Short-nosed fruit bats.
Sphaerias Miller, 1906. R.; Burma.
Ptenochirus Peters, 1861. [Including *Megaerops* Peters, 1865 =*Megaera* Temminck, 1841, *nec* Wagler, 1830.] R.; E. Indies.
Balionycteris Matschie, 1899. R.; Borneo.
Rousettus Gray, 1821 (=*Cynonycteris* Peters, 1852). [Including *Pterocyon* Peters, 1861; *Myonycteris* Matschie, 1899.] R.; Af., S. As., W. Pacific. Dog bats, rousette bats.
Pteropus Brisson, 1762. [Including *Acerodon* Jourdan, 1837; *Desmalopex* Miller, 1907; *Pteralopex* Thomas, 1888; *Sericonycteris* Matschie, 1899; *Eunycteris* Matschie, 1899; *Spectrum* Matschie, 1899.] R.; Madagascar, S. As., Aus., S. and W. Pacific. Flying "foxes."
Boneia Jentink, 1879. R.; Celebes.
Styloctenium Matschie, 1899. R.; Celebes.
Dobsonia Palmer, 1898 (=*Hypoderma* Geoffroy, 1828, *nec* Latreille, 1825). R.; S.W. Pacific. Bare-backed fruit bat.
Epomophorus Bennett, 1836. [Including *Epomops* Gray, 1860; *Hypsignathus* Allen, 1861; *Scotonycteris* Matschie, 1894; *Micropteropus* Matschie, 1899; *Nanonycteris* Matschie, 1899; *Plerotes* Andersen, 1912.] R.; Af. Epauleted fruit bats.
Casinycteris Thomas, 1910. R.; Af.
Eidolon Rafinesque, 1815. R.; Af., As. Yellow-haired fruit bats.
Subfam. Macroglossinae Trouessart, 1897, p. 89 (=Kiodontinae Palmer, 1898, p. 111; Carponycterinae Flower and Lydekker, 1891, p. 659; Macroglossi Dobson, 1875, p. 346). R.; As., Af., Aus., Pacific.

[1] Ameghino's family was based on *Cynocephalus* Cuvier and Geoffroy, 1795, a genus of baboons, not on *Cynocephalus* Boddaërt, 1768.

Eonycteris Dobson, 1873. R.; S. As., E. Indies.
Callinycteris Jentink, 1889. R.; Celebes.
Macroglossus Schinz, 1824, *nec Macroglossum* Scopoli, 1777[1] (=*Kiodotus* Blyth, 1840; *Carponycteris* Lydekker, 1891). [Including *Odontonycteris* Jentink, 1902; *Syconycteris* Matschie, 1899.] R.; S. As., Aus., W. Pacific. Long-tongued fruit bats.
Megaloglossus Pagenstecher, 1885, *nec Megaglossa* Rondani, 1865 (=*Trygenycteris* Lydekker, 1891). R.; W. Af.
Melonycteris Dobson, 1877. R.; W. Pacific.
Nesonycteris Thomas, 1887. R.; Solomons.
Notopteris Gray, 1859. R.; W. Pacific.

Subfam. Nyctimeninae Miller, 1907, p. 75[2] (=Cephalotidae Gray, 1821, p. 299). R.; Aus., E. Indies.
Nyctimene Borkhausen, 1797 (=*Nyctymene* Bechstein, 1800; *Cephalotes* Geoffroy, 1810; *Harpyia* Illiger, 1811). R.; E. Indies, Aus. Tube-nosed fruit bats.

Subfam. Harpyionycterinae Miller, 1907, p. 77. R.; Philippines.
Harpyionycteris Thomas, 1896. R.; Philippines. Harpy bat.

Suborder MICROCHIROPTERA Dobson, 1875, p. 346 (=Animalivora Gill, 1872, p. 16; Chiroptera Insectivorae Gray, 1821, p. 299).

Superfam. Emballonuroidea Weber, 1928, pp. xiv, 154.

Fam. Rhinopomatidae Dobson, 1872, p. 221 (=Rhinopomina Bonaparte, 1838, p. 112). R.; N. Af., S. As.
Rhinopoma Geoffroy, 1813. R.; N. Af., S. As. Mouse-tailed bats.

Fam. Emballonuridae Dobson, 1875, p. 349 (=Emballonurina Gervais, 1855, p. 62, note). Eoc. or Olig.; Eu. R.; tropics except Aus. and New Zealand.

Subfam. Emballonurinae Flower and Lydekker, 1891, p. 666 (=Emballonurina Gray, 1866b, p. 92). Eoc. or Olig.; Eu. R.; tropics.
†*Vespertiliavus* Schlosser, 1887. U. Eoc. or L. Olig.; Eu.
Emballonura Temminck, 1838. R.; Madagascar, S. As., S. Pacific. Sheath-tailed bats.
Coleura Peters, 1867. R.; E. Af.
Rhynchonycteris Peters, 1867, *nec Rhinchonycteris* Tschudi, 1844–1846 (=*Proboscidea* Spix, 1823, *nec* Brugière, 1791; *Rhynchiscus* Miller, 1907). R.; tropical A. Proboscis bats.
Saccopteryx Illiger, 1811. [Including *Comura* Peters, 1867; *Peropteryx* Peters, 1867; *Peronymus* Peters, 1868; *Centronycteris* Gray, 1838; *Balantiopteryx* Peters, 1867.[3]] R.; tropical A. Sac-winged or pouch-winged bats.

[1] This has been generally recognized as constituting preoccupation, and *Kiodotus* is usually used, but the Rules (Article 36) are specific on the point involved and make *Macroglossus* surely valid. The same rule makes *Megaloglossus* valid in place of the more usual *Trygenycteris*.

[2] Spelled "Nyctymeninae" by Miller.

[3] As in many other cases, but to an exaggerated degree, I here unite a number of units almost universally called genera by modern mammalogists. They are, however, manifestly and closely allied, cover less morphologic range than do many genera, and include so few species that generic separation has no practical value. This seems an obvious case, one of many, in which subgeneric rank has everything to be said for it, both as better representing the real situation and as practically more convenient to everyone but the *Saccopteryx* specialist.

Drepanycteris Thomas, 1920. R.; S.A.
Myropteryx Miller, 1906. R.; S.A.
Taphozous Geoffroy, 1813. [Including *Saccolaimus* Lesson, 1842 = *Taphonycteris* Dobson, 1875; *Liponycteris* Thomas, 1922.] R.; Af., S. As., Aus. Tomb bats.

Subfam. Diclidurinae Miller, 1907, p. 94 (= Diclidurina Gray, 1866b, p. 92). R.; tropical A.
Diclidurus Maximilian, 1820. R.; tropical A. White bat, ghost bat.

Fam. Noctilionidae Gray, 1821, p. 299. R.; tropical A.
Noctilio Linnaeus, 1776. [Including *Dirias* Miller, 1904.] R.; tropical A. Hare-lipped bat, mastiff bat.

Superfam. Rhinolophoidea Weber, 1928, p. 152.

Fam. Nycteridae Dobson, 1875, p. 347 (= Nycterina van der Hoeven, 1855, p. 1028, *fide* Palmer, 1904, p. 757). R.; Af., Malaya.
Nycteris Geoffroy and Cuvier, 1795 (= *Petalia* Gray, 1838).[1] R.; Af., Malaya. Hispid bats, hollow-faced bats.

Fam. Megadermatidae Allen, 1864, p. 1 (= Megadermidae Gill, 1872, p. 17). Eoc. or Olig.–Mioc.; Eu. R.; tropical Af., As., Aus.
†*Necromantis* Weithofer, 1887, *nec Necromantes* Gistel, 1848 (= †*Necronycteris* Palmer, 1903). U. Eoc. or L. Olig.; Eu.
†*Miomegaderma* Gaillard, 1929. M. Mioc.; Eu.
Megaderma Geoffroy, 1810. [Including *Lyroderma* Peters, 1872 = *Eucheira* Hodgson, 1847, *nec* Westwood, 1836; *Cardioderma* Peters, 1873.] R.; S. As. False vampires.
Macroderma Miller, 1906. R.; Aus.
Lavia Gray, 1838. R.; tropical Af. Yellow-winged bat.

Fam. Rhinolophidae Bell, 1836, p. 599 (= Rhinolophina Gray, 1825, p. 338). U. Eoc.–R.; Eu. R.; As., Aus.
†*Palaeonycteris* Pomel, 1854. U. Olig.; Eu.
Rhinolophus Lacépède, 1799. U. Eoc.–R.; Eu. R.; As., Aus. Horseshoe bats.

Fam. Hipposideridae Miller, 1907, p. 109. Eoc.–Olig., ?Mioc.; Eu. R.; tropical Old World.

†Subfam. Palaeophyllophorinae Revilliod, 1917a–1922, p. 41. Eoc.–?Mioc.; Eu.
†*Palaeophyllophora* Revilliod, 1917. U. Eoc.–L. Olig.; Eu.
†*Paraphyllophora* Revilliod, 1922. U. Eoc. or L. Olig.; ?Mioc.; Eu.

Subfam. Hipposiderinae Flower and Lydekker, 1891, p. 657. Eoc.–Olig., ?Mioc.; Eu. R.; tropical Old World.
†*Pseudorhinolophus* Schlosser, 1887. M. Eoc.–L. Olig., ?Mioc.; Eu.
Hipposideros Gray, 1831 (= *Phyllorhina* Bonaparte, 1837). [Including *Anthops* Thomas, 1888.] R.; tropical Old World. (Old World) leaf-nosed bats, cyclops bats, horseshoe bats.

[1] *Nycteris* Geoffroy and Cuvier, 1795, was a *nomen nudum*. According to the Rules, then, the correct name of this genus would be *Petalia* Gray, 1838. *Nycteris* would then date from Borkhausen, 1797, and would not be this genus but the same as *Lasiurus* Gray, 1831. Miller (subsequent to 1907) and some others followed this revised nomenclature, but the Commission eventually suspended the Rules (Opinion 111) and made *Nycteris* and *Lasiurus* valid names as used by Miller in 1907 and as given here.

Asellia Gray, 1838. R.; N.E. Af., S.E. As. Trident bats.
Coelops Blyth, 1848 (= *Chilophylla* Miller, 1910). R.; S. As.
Cloeotis Thomas, 1901. R.; E. Af.
Rhinonicteris Gray, 1847. R.; Aus.
Triaenops Dobson, 1871. R.; E. Af., Madagascar, Persia.

Superfam. Phyllostomatoidea Weber, 1928, pp. xiv, 153.

✓Fam. Phyllostomatidae Coues and Yarrow, 1875, p. 80 (= Phyllostomidae Waterhouse, 1839c, p. 1; Phyllostomina Gray, 1825, p. 338). R.; N.A., S.A.

Subfam. Chilonycteriinae Flower and Lydekker, 1891, p. 672 (= Mormopida Koch, 1862–1863, p. 358; Lobostominae Dobson, 1875, p. 350). R.; tropical A.

Chilonycteris Gray, 1839 (= *Lobostoma* Gundlach, 1840). R.; tropical A. Leaf-lipped bat.
Pteronotus Gray, 1838. R.; tropical A. Naked-backed bat.
Mormoops Leach, 1821. R.; tropical A. (to Texas). Cinnamon bat.

Subfam. Phyllostomatinae Flower and Lydekker, 1891, p. 673 (= phyllostomines Gill, 1884, p. 173; Phyllostominae "Gill" Miller, 1907, p. 122; Phyllostomineae Lesson, 1842, p. 30). R.; tropical A.

Micronycteris Gray, 1866 (= *Schizostoma* Gervais, 1856, *nec* Brown, 1835). [Including *Xenoctenes* Miller, 1907; *Glyphonycteris* Thomas, 1896.] R.; tropical A.
Macrotus Gray, 1843, *nec Macrotis* Reid, 1837 (= *Otopterus* Lydekker, 1891). R.; southern N.A., W. Indies. American leaf-nosed bats.
Lonchorhina Tomes, 1863. R.; northern S.A., W. Indies. Long-eared bat.
Macrophyllum Gray, 1838, *nec Macrophylla* Hope, 1837 (= *Dolichophyllum* Lydekker, 1891). R.; Brazil.
Tonatia Gray, 1827 (= *Lophostoma* D'Orbigny, 1836). R.; tropical A.
Mimon Gray, 1847. [Including *Anthorhina* Lydekker, 1891.] R.; tropical A.
Phyllostomus Lacépède, 1799. R.; tropical A. Javelin bat, spear-nosed bat.
Phylloderma Peters, 1865, R.; Guiana.
Trachops Gray, 1847. R.; tropical A.
Chrotopterus Peters, 1865. R.; tropical A.
Vampyrum Rafinesque, 1815 (= *Vampyrus* Leach, 1821). R.; tropical A. Spear-nosed bat, "vampire."[1]

Subfam. Glossophaginae Gill, 1872, p. 17 (= Glossophagina Bonaparte, 1845, p. 5). R.; tropical A.

Glossophaga Geoffroy, 1818. R.; tropical A. Long-tongued "vampire."
Lonchophylla Thomas, 1903. R.; tropical S.A.
Monophyllus Leach, 1821. R.; W. Indies.
Lonchoglossa Peters, 1818. [Including *Anoura* Gray, 1838.] R.; tropical A.

[1] Not the blood-lapping vampire of fact. Several bats of this family are called "vampires" and often believed to be such, but only *Desmodus* and *Diphylla* are true vampires in the sense of living exclusively on blood.

Choeronycteris Tschudi, 1844. [Including *Hylonycteris* Thomas, 1903.] R.; tropical A. (to Arizona).

Leptonycteris Lydekker, 1891 (=*Ischnoglossa* De Saussure, 1860, *nec* Kraatz, 1856). R.; Cent. A. (and Curaçao).

Lichonycteris Thomas, 1895. R.; Cent. A., Guiana.

Subfam. Carolliinae Miller, 1924, p. 53 (=Hemiderminae Miller, 1907, p. 144). R.; tropical A.

Carollia Gray, 1838, *nec Carolia* Cantraine, 1837 (=*Hemiderma* Gervais, 1855). R.; tropical A. Short-tailed bat.

Rhinophylla Peters, 1865. R.; tropical S.A.

Subfam. Sturnirinae Miller, 1907, p. 38. R.; tropical A.

Sturnira Gray, 1842. R.; tropical A.

Subfam. Stenoderminae Gill, 1872, p. 17 (=Stenodermina Gervais, 1855, p. 33; Centurioninae Rehn, 1901, p. 296). R.; tropical A.

Brachyphylla Gray, 1834. R.; Antilles. Cavern leaf-nosed bat.

Uroderma Peters, 1865. R.; tropical A. Yellow-eared bat.

Vampyrops Peters, 1865 (=*Platyrhinus* De Saussure, 1860, *nec* Clairville, 1798). [Including *Vampyrodes* Thomas, 1900; *Vampyressa* Thomas, 1900; *Vampyriscus* Thomas, 1900.] R.; tropical A. White-striped bats.

Chiroderma Peters, 1860. R.; tropical A.

Ectophylla Allen, 1892. [Including *Mesophylla* Thomas, 1901.] R.; Cent. A., Guiana.

Artibeus Leach, 1821. [Including *Enchisthenes* Andersen, 1906.] R.; tropical A. American fruit bat, short-nosed "vampire."

Stenoderma Geoffroy, 1813. [Including *Ariteus* Gray, 1837; *Phyllops* Peters, 1865; *Ardops* Miller, 1906.] R.; tropical A.

Pygoderma Peters, 1863. R.; tropical A.

Centurio Gray, 1842. [Including *Ametrida* Gray, 1847; *Sphaeronycteris* Peters, 1882.] R.; Cent. A., tropical S.A. Centurion bats.

Subfam. Phyllonycterinae Miller, 1907, p. 171. R.; W. Indies.

Phyllonycteris Gundlach, 1865. [Including *Reithronycteris* Miller, 1898.] R.; W. Indies.

Erophylla Miller, 1906. R.; W. Indies.

Fam. Desmodontidae Gill, 1884, p. 175 (=Desmodidae I. Geoffroy, *fide* Palmer, 1904, p. 737; Desmodina Bonaparte, 1845, p. 5). R.; tropical A. Vampires, true vampires.

Desmodus Maximilian, 1824. [Including *Diaemus* Miller, 1906.] R.; tropical S.A.

Diphylla Spix, 1823. R.; tropical A.

Superfam. Vespertilionoidea Weber, 1928, p. 155.

Fam. Natalidae Miller, 1899, p. 245 (=Natalinia Gray, 1866b, p. 90). R.; tropical A.

Natalus Gray, 1838 (=*Spectrellum* Gervais, 1855). [Including *Phodotes* Miller, 1906; *Chilonatalus* Miller, 1898.] R.; tropical A. Tall-crowned bats, long-legged bats.

Nyctiellus Gervais, 1855. R.; Cuba. Graceful bat.

Fam. Furipteridae Miller, 1907, pp. 84, 186 (=Furipterina Gray, 1866b, p. 91). R.; S.A.

Furipterus Bonaparte, 1837 (=*Furia* Cuvier, 1828, *nec* Linnaeus, 1758). [Including *Amorphochilus* Peters, 1877.] R.; tropical S.A. Furies, smoky bats.

Fam. Thyropteridae Miller, 1907, pp. 84, 186. R.; tropical A.

Thyroptera Spix, 1823. R.; tropical A. Disk-winged bats, tricolor bats.

Fam. Myzopodidae Thomas, 1904, p. 5. R.; Madagascar.

Myzopoda Milne Edwards and Grandidier, 1878. R.; Madagascar. Golden bat, sucker-footed bat.

Fam. Vespertilionidae Gray, 1821, p. 299. L. Olig.–R.; Eu. L. Plioc.–R.; N.A. Pleist.–R.; S.A., As. R.; worldwide.

Subfam. Vespertilioninae Miller, 1897, pp. 41, 54 (=Vespertiliones Dobson, 1878, p. 168). L. Olig.–R.; Eu. L. Plioc.–R.; N.A. Pleist.–R.; S.A., As. R.; world wide.

†*Stehlinia* Revilliod, 1919. U. Eoc. or L. Olig.; Eu.

†*Revilliodia*, new name (=†*Nycterobius* Revilliod, 1922, *nec* MacLeay, 1832). U. Eoc. or L. Olig.; Eu.

Myotis Kaup, 1829. [Including *Pizonyx* Miller, 1906.] M. Olig.–R.; Eu. Pleist.–R.; N.A. R.; virtually world wide. Common bats, brown bats, pale bats; innumerable local names.

†*Samonycteris* Revilliod, 1922. L. Plioc.; Samos.

†*Simonycteris* Stirton, 1931. L. Plioc.; N.A.

Lasionycteris Peters, 1865. R.; N.A. Silver-haired bat.

Pipistrellus Kaup, 1829 (=*Vesperugo* Keyserling and Blasius, 1839). [Including *Glischropus* Dobson, 1875; *Scotozous* Dobson, 1875; *Nyctalus* Bowdich, 1825; *Pterygistes* Kaup, 1829; *Ia* Thomas, 1902; *Eptesicops* Roberts, 1926.] Pleist.–R.; N.A. R.; most of Eastern Hemisphere. Pipistrelles, noctules, etc.; many local names.

Discopus Osgood, 1932. R.; Philippines.

Eptesicus Rafinesque, 1820 (with many synonyms and including, or very closely allied to: *Rhinopterus* Miller, 1906; *Hesperoptenus* Peters, 1868; *Tylonycteris* Peters, 1872; *Mimetillus* Thomas, 1905; *Philetor* Thomas, 1902; *Histiotus* Gervais, 1855; *Laephotis* Thomas, 1901). Pleist.–R.; N.A., As. R.; S.A., Af., Aus. Brown bats, common bats, serotine bats, etc.

Vespertilio Linnaeus, 1758. R.; Eu., As. Common European bats.

Otonycteris Peters, 1859. R.; N. Af., As.

Nycticeius Rafinesque, 1819. [Including *Scotoecus* Thomas, 1901; *Scoteinus* Dobson, 1875; *Scotomanes* Dobson, 1875.] R.; N.A., As., Aus., Af. Evening bats, white-winged bats, harlequin bats, etc.

Rhogeëssa Allen, 1866. [Including *Baeodon* Miller, 1906.] R.; tropical A.

Scotophilus Leach, 1821, *nec Scotophila* Hübner, 1816 (=*Pachyotus* Gray, 1831). R.; Af., As. House bats, brown bats.

Chalinolobus Peters, 1866. [Including *Glauconycteris* Dobson, 1875.] R.; Af., Aus., New Zealand. Groove-lipped bats, butterfly bat.

Cistugo Thomas, 1912. R.; Af.

Lasiurus Gray, 1831 (=*Nycteris* Borkhausen, 1797, *nec* Geoffroy and Cuvier, 1795; *Atalapha* Peters, 1870). [Including *Dasypterus* Peters, 1871.] R.; N.A., S.A., W. Indies, Hawaii. Hoary bat, red bat, etc.

Barbastella Gray, 1821. R.; N. Af., Eu., W. As. Barbastelles.

Plecotus Geoffroy, 1813. [Including *Corynorhinus* Allen, 1865;

Synotus Allen, 1864, *nec* Keyserling and Blasius, 1839.] R.; Eu., As., N. Af., N.A. Long-eared bats, lump-nosed bats.

Idionycteris Anthony, 1923. R.; N.A.

Euderma Allen, 1892. R.; N.A. Spotted bat.

Subfam. Miniopterinae Miller, 1907, p. 227 (=Miniopteri Dobson, 1875, p. 349). R.; Af., Eu., As.

Miniopterus Bonaparte, 1837. R.; N. Af., S. Eu., S. As. Long-winged bats, long-fingered bats.

Subfam. Murininae Miller, 1907, p. 229. R.; As.

Murina Gray, 1842. R.; S. As., Malaya, Japan.

Harpiocephalus Gray, 1842. R.; S. As. Tube-nosed bat.

Subfam. Kerivoulinae Miller, 1907, p. 232. R.; Af., As.

Kerivoula Gray, 1842. [Including *Phoniscus* Miller, 1905; *Chrysopteron* Jentink, 1910.] R.; Af., S. As. (to New Guinea). Painted bats.

Anamygdon Troughton, 1929. R.; Solomons.

Subfam. Nyctophilinae Miller, 1907, p. 234 (=Nyctophili Peters, 1865, p. 524). Pleist.–R.; N.A. R.; E. Indies, Aus.

Antrozous Allen, 1862. Pleist.–R.; N.A. Pale bat, big-eared bat, desert bat, cave bat.

Nyctophilus Leach, 1822. R.; E. Indies, Aus. Big-eared bats.

Subfam. Tomopeatinae Miller, 1907, p. 237. R.; S.A.

Tomopeas Miller, 1900. R.; S.A. (Peru).

Fam. Mystacinidae, new name? (=Mystacinae Dobson, 1875, p. 349; Mystacopidae Miller, 1907, p. 239). R.; New Zealand.

Mystacina Gray, 1843, *nec Mystacinus* Boie, 1822 (=*Mystacops* Lydekker, 1891). R.; New Zealand. New Zealand short-tailed bats.

Fam. Molossidae Gill, 1872, p. 17 (=Molossina Gervais, 1855, p. 53, note 1). L. Olig.–R.; Eu. Pleist.; N.A. R.; world wide in warmer regions.

Eomops Thomas, 1905.[1] R.; Af.

Molossops Peters, 1865. R.; S.A.

Cheiromeles Horsfield, 1824. R.; S. As., E. Indies.

Xiphonycteris Dollmann, 1911. R.; Af.

Tadarida Rafinesque, 1814 (=*Nyctinomus* Geoffroy, 1818). [Including *Mops* Lesson, 1842; *Mormopterus* Peters, 1865; *Chaerophon* Dobson, 1874; *Platymops* Thomas, 1906; *Otomops* Thomas, 1913.] U. Olig.–R.; Eu. R.; world wide in warmer regions. Free-tailed bats.

†*Molossides* Allen, 1932. Pleist.; N.A.

Molossus Geoffroy, 1805. [Including *Promops* Gervais, 1855; *Eumops* Miller, 1906; *Cynomops* Thomas, 1920.] R.; tropical A. (to California and Texas). Bonneted bats, mastiff bats.

Superfam. uncertain:

†Fam. Archaeonycteridae Revilliod, 1917b, p. 190. Eoc.; Eu.

†*Archaeonycteris* Revilliod, 1917. M. Eoc.; Eu.

†Fam. Palaeochiropterygidae Revilliod, 1917b, p. 190. Eoc.; Eu.

†*Palaeochiropteryx* Revilliod, 1917. M. Eoc.; Eu.

[1] Possibly the same as *Myopterus* Geoffroy, 1813, but the latter is a *nomen vanum*.

?Palaeochiropterygidae *incertae sedis:*
†*Cecilionycteris* Heller, 1935. M. Eoc.; Eu.
CHIROPTERA *incertae sedis:*
†*Paleunycteris* Revilliod, 1926. M. Eoc.–L. Olig.; Eu.
†*Paradoxonycteris* Revilliod, 1926. U. Eoc.; Eu.
Order PRIMATES Linnaeus, 1758, p. 20.
Suborder PROSIMII Illiger, 1811, p. 72 (=Lemuroidea Mivart, 1864, p. 637; Prosimiae Haeckel, 1866, p. cxlviii).
Infraorder LEMURIFORMES Gregory, 1915, p. 432.
Superfam. Tupaioidea Dobson, 1882, p. 4.
†Fam. Anagalidae Simpson, 1931a, p. 269. Olig.; As.
†*Anagale* Simpson, 1931. L. Olig.; Mongolia.
Fam. Tupaiidae Mivart, 1868, p. 145 (=Tupaina Gray, 1825, p. 339; Tupaiadae Bell, 1839, p. 994). R.; As. Tree "shrews."
Subfam. Tupaiinae Lyon, 1913, p. 4. R.; As.
Tupaia Raffles, 1822. R.; India, China, E. Indies, Philippines. Common tree "shrew."
Anathana Lyon, 1913. R.; India.
Dendrogale Gray, 1848. R.; Indo-China, Borneo.
Tana Lyon, 1913. R.; Borneo, Sumatra.
Urogale Mearns, 1905. R.; Philippines.
Subfam. Ptilocercinae Lyon, 1913, p. 4. R.; S.E. As.
Ptilocercus Gray, 1848. R.; E. Indies, Borneo, Malaya. Pen-tailed tree "shrew."
Superfam. Lemuroidea Mivart, 1864, p. 637 (as suborder; Gill, 1872, p. 2, as superfamily).
†Fam. Plesiadapidae Trouessart, 1897, p. 75. Paleoc.–Eoc.; N.A., Eu.
†*Pronothodectes* Gidley, 1923. M. Paleoc.; U.S.A.
†*Plesiadapis* Gervais, 1877. [Including †*Nothodectes* Matthew, 1915.] U. Paleoc.; U.S.A., France. ?L. Eoc.; U.S.A.
†*Chiromyoides* Stehlin, 1916. U. Paleoc.; France.
†*Platychoerops* Charlesworth, 1854. L. Eoc.; England, France, Belgium.
†*Megachiromyoides* Weigelt, 1933. M. Eoc.; Germany.
†Fam. Adapidae Trouessart, 1879, p. 225. [Including †Notharctidae Trouessart, 1879, p. 230.] Eoc.; Eu., N.A.
†Subfam. Adapinae Trouessart, 1879, p. 226 (=†Adapidae Trouessart, 1879, p. 225). Eoc.; Eu.
†*Adapis* Cuvier, 1821. M.–U. Eoc.; Eu.
†*Pronycticebus* Grandidier, 1904. U. Eoc.; France.
†*Anchomomys* Stehlin, 1916. M.–U. Eoc.; France, Switzerland.
†Subfam. Notharctinae Trouessart, 1879, p. 230 (=†Notharctidae Trouessart, 1879, p. 230). Eoc.; N.A., Eu.
†*Pelycodus* Cope, 1875. L. Eoc.; U.S.A.
†*Notharctus* Leidy, 1870. L.–M. Eoc.; U.S.A.
†*Protoadapis* Lemoine, 1878. L. Eoc.; France.
†Adapidae *incertae sedis:*
†*Aphanolemur* Granger and Gregory, 1917. M. Eoc.; U.S.A.
†*Caenopithecus* Rütimeyer, 1862. M. Eoc.; Switzerland.
†*Amphilemur* Heller, 1935. M. Eoc.; Germany.
Fam. Lemuridae Gray, 1821, p. 298. [Including †Megaladapidae Forsyth Major, 1893a, p. 178; †Nesopithecidae Forsyth Major, 1896, p. 436.] Pleist.–R.; Madagascar.

Subfam. Lemurinae Mivart, 1864, p. 638 (=Lepilemurina Gray, 1870, p. 132). Pleist.–R.; Madagascar.

Hapalemur Geoffroy, 1851. R.; Madagascar.

Lemur Linnaeus, 1758. Pleist.–R.; Madagascar. Common lemurs.

Lepilemur Geoffroy, 1851 (=*Lepidolemur* Peters, 1874; *Galeocebus* Wagner, 1855). [Including *Mixocebus* Peters, 1874.] Pleist.–R.; Madagascar. Sportive lemurs, weasel lemurs, nattocks.

Subfam. Cheirogaleinae Gregory, 1915, p. 434 (=Cheirogaleina Gray, 1872b, p. 858; Hapalemurina Gray, 1870, p. 131; Microcebina Gray, 1870, p. 131). R.; Madagascar.

Cheirogaleus Geoffroy, 1812 (=*Chirogale* Gloger, 1841, and most later authors). [Including *Atililemur* Elliot, 1913=*Opolemur* auct., but not *Opolemur* Gray, 1872; *Mioxicebus* Lesser, 1840=*Myoxicebus* Agassiz, 1846=*Hapalemur* Geoffroy, 1851.] R.; Madagascar. Mouse lemurs, gentle lemurs, etc.

Microcebus Geoffroy, 1828. R.; Madagascar. Dwarf lemurs.

Phaner Gray, 1870. R.; Madagascar.

†Subfam. Megaladapinae Flower and Lydekker, 1891, p. 6 (=†Megaladapidae Forsyth Major, 1893a, p. 178). Pleist.; Madagascar.

†*Megaladapis* Forsyth Major, 1893. Pleist.; Madagascar.

†*Megalindris* Standing, 1908. Pleist.; Madagascar.

†Subfam. Archaeolemurinae Standing, 1908, p. 72 (=†Nesopithecidae Forsyth Major, 1896, p. 436). Pleist.; Madagascar.

†*Archaeolemur* Filhol, 1895 (=†*Nesopithecus* Forsyth Major 1896). [Including †*Bradylemur* Grandidier, 1899.] Pleist.; Madagascar.

†Subfam. Hadropithecinae Abel, 1931a, p. 222. Pleist.; Madagascar.

†*Hadropithecus* Lorenz, 1900. Pleist.; Madagascar.

Fam. Indridae Burnett, 1828, p. 306 (=Indrisina Geoffroy, 1851, p. 67; Indrisidae Alston, 1878, p. 10). Pleist.–R.; Madagascar.

Lichanotus Illiger, 1811 (=*Avahi* Jourdan, 1834). Pleist.–R.; Madagascar. Avahis, woolly "lemurs."

†*Palaeopropithecus* Grandidier, 1899. Pleist.; Madagascar.

†*Mesopropithecus* Standing, 1908. Pleist.; Madagascar.

†*Neopropithecus* Lambert, 1939. Pleist.; Madagascar.

Propithecus Bennett, 1832. Pleist.–R.; Madagascar. Sifakas.

Indri Geoffroy, 1796 (=*Indris* Cuvier, 1800, and most later authors). Pleist.–R.; Madagascar. Indris, babakatos.

Superfam. Daubentonioidea Gill, 1872, p. 3.

Fam. Daubentoniidae Gray, 1870, pp. 2, 96 (=Daubentoniadae Gray, 1863a, p. 151; Cheiromydae Gray, 1821, p. 309). R.; Madagascar.

Daubentonia Geoffroy, 1795 (=*Cheiromys* Cuvier, 1800). R.; Madagascar. Aye-aye.

Infraorder LORISIFORMES Gregory, 1915, p. 435.

Fam. Lorisidae Gregory, 1915, p. 436 (=Loridae[1] Gray, 1821, p. 298;

[1] Many authors use "Loridae" for the family and "Lorisinae" for the subfamily, which is inconsistent. Because the root (not Latin) is *Loris-*, forms retaining the *-is-* are here preferred.

Nycticebidae Nicholson, 1870, p. 553; Nycticebinae Mivart, 1864, p. 637). Plioc., R.; As. R.; Af.

Subfam. Lorisinae Flower and Lydekker, 1891, p. 691. Plioc., R.; As. R.; Af.

†*Indraloris* Lewis, 1933. Plioc.; India.

Loris Geoffroy, 1796. R.; India, Ceylon. Slender loris.

Nycticebus Geoffroy, 1812. R.; S. As., E. Indies, to Philippines. Slow loris, gray loris.

Arctocebus Gray, 1863. R.; Af. Angwantibo, Calabar potto.

Perodicticus Bennett, 1831. R.; equatorial Af. Pottos.

Subfam. Galaginae Mivart, 1864, p. 637 (=Galagonina Gray, 1825, p. 338; Galaginidae Alston, 1878, p. 10). R.; Af.

Galago Geoffroy, 1796. [Including *Galagoides* Smith, 1833 =*Hemigalago* Dahlbom, 1857.] R.; S. and equatorial Af. Bush babies, galagos, ojams.

Euoticus Gray, 1863. R.; equatorial Af.

Infraorder TARSIIFORMES Gregory, 1915, p. 437.

†Fam. Anaptomorphidae Cope, 1883a, p. 80 (=Tetoniidae Abel, 1931a, pl., p. 199). M. Paleoc.–M. Eoc.; N.A. Eoc.; Eu. Olig.; ?As.

†Subfam. Paromomyinae Simpson, 1940a, p. 198. M.–U. Paleoc.; N.A.

†*Palenochtha* Simpson, 1935. M. Paleoc.; U.S.A.

†*Palaechthon* Gidley, 1923. M. Paleoc.; U.S.A.

†*Plesiolestes* Jepsen, 1930. M. Paleoc.; U.S.A.

†*Paromomys* Gidley, 1923. M. Paleoc., ?U. Paleoc.; U.S.A.

†Subfam. Omomyinae Wortman, 1904, p. 29 (=Omomynae Trouessart, 1879, p. 225). U. Paleoc.–M. Eoc.; N.A. L. Eoc.; Eu.

†*Navajovius* Matthew and Granger, 1921. U. Paleoc.; U.S.A.

†*Teilhardina* Simpson, 1940. L. Eoc.; Belgium.

†*Loveina* Simpson, 1940. L. Eoc.; U.S.A.

†*Shoshonius* Granger, 1910. L. Eoc.; U.S.A.

†*Omomys* Leidy, 1869. ?L. Eoc., M. Eoc.; U S.A.

†*Hemiacodon* Marsh, 1872. M. Eoc.; U.S.A.

†*Washakius* Leidy, 1873. M. Eoc.; U.S.A.

†*Chumashius* Stock, 1933. U. Eoc.; U.S.A.

†*Dyseolemur* Stock, 1934. U. Eoc.; U.S.A.

†*Macrotarsius* Clark, 1941. L. Olig.; U.S.A.

†Subfam. Anaptomorphinae Simpson, 1940a, p. 198 (approximately =Tetoniidae Abel, 1931a, p. 199). L.–M. Eoc.; N.A.

†*Absarokius* Matthew, 1915. L. Eoc.; U.S.A.

†*Tetonius* Matthew, 1915. L. Eoc.; U.S.A.

†*Paratetonius* Seton, 1940. L. Eoc.; U.S.A.

†*Anaptomorphus* Cope, 1872 (probably =†*Euryacodon* Marsh, 1872, which appears to have priority). ?L. Eoc., M. Eoc.; U.S.A.

†*Euryacodon* Marsh, 1872. M. Eoc.; U.S.A.

†*Uintanius* Matthew, 1915. M. Eoc.; U.S.A.

†Subfam. Necrolemurinae Simpson, 1940a, p. 198 (=Microchoeridae Lydekker, 1887, p. 303; Necrolemuridae auct.). M.–U. Eoc.; Eu.

†*Necrolemur* Filhol, 1873. M.–U. Eoc.; France, Germany.

†*Microchoerus* Wood, 1846. U. Eoc.; England, France, Switzerland.

†Subfam. Pseudolorisinae Simpson, 1940a, p. 198. U. Eoc.; Eu.
†*Pseudoloris* Stehlin, 1916. U. Eoc.; France.
†Anaptomorphidae *incertae sedis:*
†*Nannopithex* Stehlin, 1916. M. Eoc.; Switzerland.
†*Periconodon* Stehlin, 1916. M. Eoc.; Eu.
†*Yumanius* Stock, 1938. U. Eoc.; N.A.
Fam. Tarsiidae Gill, 1872, p. 3 (=Tarsidae Burnett, 1828, p. 306; Tarsina Gray, 1825, p. 338).
Tarsius Starr, 1780. R.; E. Indies to Philippines. Tarsier, spectral tarsier.
PROSIMII, infraorder uncertain:
†Fam. Apatemyidae Matthew, 1909a, p. 543. M. Paleoc.–U. Eoc.; N.A. Eoc.; Eu.
†*Jepsenella* Simpson, 1940. M. Paleoc.; U.S.A.
†*Labidolemur* Matthew and Granger, 1921. U. Paleoc.; U.S.A.
†*Teilhardella* Jepsen, 1930. L. Eoc.; U.S.A.
†*Apatemys* Marsh, 1872. M. Eoc.; U.S.A.
†*Stehlinella* Matthew, 1929 (=*Stehlinius* Matthew, 1921, preoccupied). U. Eoc.; U.S.A.
†*Sinclairella* Jepsen, 1934. L. Olig.; U.S.A.
†*Eochiromys* Teilhard de Chardin, 1927. L. Eoc.; Belgium.
†*Heterohyus* Gervais, 1848–1852 (=or including †*Necrosorex* Filhol, 1890; †*Heterochiromys* Stehlin, 1916; †*Amphichiromys* Stehlin, 1916). M.–U. Eoc.; France, Germany, Switzerland, ?Belgium.
†Fam. Carpolestidae Simpson, 1935e, p. 9. M.–U. Paleoc.; N.A.
†*Elphidotarsius* Gidley, 1923. M. Paleoc.; U.S.A.
†*Carpodaptes* Matthew and Granger, 1921. U. Paleoc.; U.S.A.
†*Carpolestes* Simpson, 1928. U. Paleoc.; U.S.A.
?PROSIMII of uncertain infraorder or family:
†*Phenacolemur* Matthew, 1915. [Including †*Ignacius* Matthew and Granger, 1921.] U. Paleoc.–L. Eoc.; U.S.A.
†*Trogolemur* Matthew, 1909. M. Eoc.; U.S.A.
†*Uintasorex* Matthew, 1909. M. Eoc.; U.S.A.
†*Ceciliolemur* Weigelt, 1933. M. Eoc.; Germany.
†*Europolemur* Weigelt, 1933. M. Eoc.; Germany.
†*Megatarsius* Weigelt, 1933. M. Eoc.; Germany.
†*Microtarsioides* Weigelt, 1933. M. Eoc.; Germany.
†*Hoanghonius* Zdansky, 1930. U. Eoc. or L. Olig.; China.
†*Adapidium* Young, 1937. U. Eoc. or L. Olig.; China.
Suborder ANTHROPOIDEA Mivart, 1864, p. 635.
Superfam. Ceboidea Simpson, 1931a, p. 271 (=Platyrrhina Hemprich, 1820, p. 19).
Fam. Cebidae Swainson, 1835, pp. 76, 81, 350 (=Cebina Bonaparte, 1831, pp. 6, 14). [Including †Homunculidae Ameghino, 1894, p. 265, and many other supposed families.]
Subfam. Aotinae Elliot, 1913, vol. 1, pp. xxiv, xliii, liii (=Nyctipithecinae Mivart, 1865, p. 547). [Including †Homunculidae Ameghino, 1894, p. 265.] Mioc., Pleist.–R.; S.A.
†*Homunculus* Ameghino, 1891. Mioc.; Argentina.
Aotes Humboldt, 1811 (=*Aotus* Humboldt, 1811; *Nyctipithecus* Spix, 1823). R.; tropical S.A. Douroucoulis.

Callicebus Thomas, 1903 (=*Callithrix* auct.; ***non*** ***Callithrix*** Erxleben, 1777). Pleist., R.; tropical S.A. Pleist.; Brazil. Titis.

Subfam. Pitheciinae Mivart, 1865, p. 547 (=Pithecina Gray, 1870, pp. 37, 58). R.; S.A.

Cacajao Lesson, 1840 (=*Brachyurus* Spix, 1823, preoccupied; *Ouakaria* Gray, 1849, antedated). R.; Amazon Basin. Uakaris.

Pithecia Desmarest, 1804. R.; Guianas and Amazon Basin. Sakis.

Chiropotes Lesson, 1840. R.; Guianas and Amazon Basin. Sakis.

Subfam. Alouattinae Elliot, 1904, p. 725 (=Alouatinae Trouessart, 1897, p. 32; Mycetina Gray, 1825, p. 338). Pleist.–R.; S.A.

Alouatta Lacépède, 1799 (=*Mycetes* Illiger, 1811, p. 70). Pleist.–R.; tropical A. to Mexico. Howling monkeys, howlers, aluatas, carayas.

Subfam. Cebinae Mivart, 1865, p. 547 (=Cebina Bonaparte, 1831, pp. 6, 14). Pleist.–R.; tropical A.

Cebus Erxleben, 1777. Pleist.–R.; tropical A., Nicaragua to S. Brazil. Capuchins, sapajous, caiarara, cay, etc.

Saimiri Voigt, 1831 (=*Saimiris* Geoffroy, 1843, and most later authors; *Chrysothrix* Kaup, 1835, antedated). R.; tropical Cent. and S.A. "Squirrel" monkeys, "titis" (better confined to *Callicebus*), saimiris.

Subfam. Atelinae Miller, 1924, p. 170 (=Atelina Gray, 1825, p. 338). R.; tropical A.

Ateles Geoffroy, 1806 (=*Ateleus* Fischer, 1813, invalid emendation). R.; tropical A., Mexico to Amazon Basin. "Spider" monkeys, coaitas.

Brachyteles Spix, 1823 (=*Brachyteleus* Elliot, 1913, invalid emendation). R.; S.E. Brazil. Woolly spider monkeys, mirikis.

Lagothrix Geoffroy, 1812. R.; tropical S.A., chiefly Amazon Basin. Woolly monkeys, belly monkeys, maricamicos.

Subfam. Callimiconinae Thomas, 1913, p. 132.

Callimico Ribeiro, 1911. R.; Amazon. Goeldi's "marmoset," callimico.

Fam. Callithricidae Thomas, 1903, p. 457 (=Callithricina Gray, 1825, p. 338; Callitricidae Gray, 1821, p. 298; Hapalidae Wagner, 1840, p. 238; Harpaladae Gray, 1821, p. 298). R.; tropical A.

Callithrix Erxleben, 1777 (=*Hapale* Illiger, 1811). R.; Brazil, Bolivia, Colombia. Marmosets.

Leontocebus Wagner, 1839 (=or including *Cercopithecus* Gronow, 1763, ***non*** Brünnich, 1772, eliminated by suspension of Rules; *Midas* Geoffroy, 1812, preoccupied; and the following, all antedated: *Oedipomidas* Reichenbach, 1862, *Marikina* Reichenbach, 1862, *Mystax* Gray, 1870, *Seniocebus* Gray, 1870, *Tamarin* Gray, 1870). R.; tropical A., Costa Rica to S. Brazil. Tamarins.

Superfam. Cercopithecoidea Simpson, 1931a, p. 271 (=Cynomorpha Huxley, 1872, p. 397; with Hominoidea=Catarrhina Hemprich, 1820, p. 17).

Fam. Cercopithecidae Gray, 1821, p. 297 (=Cynocephalidae Ameghino, 1889, p. 893; Cynocephalina Gray, 1825, p. 338; Macacidae Owen, 1843a, p. 55; Papionidae Burnett, 1828, p. 306; etc.). Olig., Plioc.–R.; Af. Plioc.–R.; As., Eu. Old World monkeys.

Subfam. Cercopithecinae Blanford, 1888, p. 10. Plioc.–R.; Af., As. R.; Gibraltar.

Macaca Lacépède, 1799 (=*Macacus* Desmarest, 1820; =or including *Silenus* Goldfuss, 1820; *Gymnopyga* Gray, 1866; *Rhesus* Lesson, 1840; *Magus* Lesson, 1827; and many others). M. Plioc.; India. R.; Gibraltar, N. Af., S. As. (with Tibet, China), E. Indies, Philippines, Japan. Macaques, Barbary ape, rhesus monkey, kra, wanderoo, toque.

†*Lybipithecus* Stromer, 1913. M. Plioc.; Egypt.

†*Simopithecus* Andrews, 1916. U. Plioc. or L. Pleist.; E. Af.

Cynopithecus Geoffroy, 1835. R.; Celebes. Black ape.

Cercocebus Geoffroy, 1812. R.; equatorial Af. Mangabeys.

†*Parapapio* Jones, 1937. Pleist.; S. Af.

†*Dinopithecus* Broom, 1936. Pleist.; S. Af.

Papio Erxleben, 1777 (=*Cynocephalus* Cuvier and Geoffroy, 1795; *Papiones* [not a binomial name] Linnaeus, 1758). L. Pleist.; India. R.; Af. Baboons, chacma.

Comopithecus Allen, 1925. R.; E. Af., S.W. As. Hamadryas baboon.

Mandrillus Ritgen, 1824. R.; Senegambia to Congo, Cameroon. Mandrill, drill.

Theropithecus Geoffroy, 1843 (=*Gelada* Gray, 1843, probably antedated). R.; Abyssinia. Gelada.

Cercopithecus Brünnich, 1772 (=or including *Lasiopyga* Illiger, 1811; *Miopithecus* Geoffroy, 1842; *Rhinostigma* Elliot, 1913). M. Plioc.; India. R.; Af. (except N.W.). Guenons, common African monkeys, cercopitheques, avem, osok, grivet, talapoin, etc.

Allenopithecus Lang, 1923. R.; Af.

Erythrocebus Trouessart, 1897. R.; equatorial Af. Patas guenon and Nisnas guenon, red monkeys.

Subfam. Colobinae Elliot, 1913, pp. xxv, xliii (=Colobidae Blyth, 1875, p. 9; Cynopithecidae Gill, 1872, p. 2; Cynopithecina Geoffroy, 1843, p. 495; Presbytina Gray, 1825, p. 338). Plioc.; Eu. Plioc.–R.; As. R.; Af.

†*Mesopithecus* Wagner, 1839. L. Plioc.; Greece, Czechoslovakia, S. Russia, Persia.

†*Dolichopithecus* Depéret, 1889. Plioc.; France.

Presbytis Eschscholtz, 1821 (=*Semnopithecus* Cuvier, 1825). L. Pleist.; India. R.; S. As., E. Indies. Langurs, hanuman, common oriental monkeys.

Pygathrix Geoffroy, 1812. R.; French Indo-China, Hainan. Douc langur.

Rhinopithecus Milne Edwards, 1872. R.; China, Tongking, Tibet. Retrousée-nosed langurs, snub-nosed langurs.
Simias Miller, 1903. R.; Sumatra. Pagi Island langur.
Nasalis Geoffroy, 1812. R.; Borneo. Proboscis monkey.
Colobus Illiger, 1811. R.; equatorial Af. Guerezas, colobs.
Subfam. uncertain:
†*Moeripithecus* Schlosser, 1911. L. Olig.; Egypt.
†*Apidium* Osborn, 1918. L. Olig.; Egypt.
†*Oreopithecus* Gervais, 1872. L. Plioc.; Italy, Bessarabia.
Superfam. Hominoidea Simpson, 1931a, p. 272.
†Fam. Parapithecidae Schlosser, 1911a, p. 58. Olig.; Af.
†*Parapithecus* Schlosser, 1911. L. Olig.; Egypt.
Fam. Pongidae Elliot, 1913, errata page, vol. 1 (=Simiidae Bonaparte, 1850; Simiadae Fleming, 1822, p. 172). Mioc., Pleist.–R.; Af. Mioc.–Plioc.; Eu. Plioc.–R.; As. Apes.
Subfam. Hylobatinae Gill, 1872, pp. 2, 52 (=Hylobatina Gray, 1870, pp. 4, 9; Hylobatidae Blyth, 1875, p. 1). Olig.–Mioc.; Af. Mioc.–Plioc.; Eu. Pleist.–R.; As. Gibbons.
†*Propliopithecus* Schlosser, 1911. L. Olig.; Egypt.
†*Limnopithecus* Hopwood, 1933. L. Mioc.; Kenya.
†*Pliopithecus* Gervais, 1849. [Including †*Prohylobates* Fourteau, 1920.] L. Mioc.; Egypt. M. Mioc.–L. Plioc.; Eu.: Germany, Austria, Czechoslovakia, Switzerland, France. ?Pleist.; ?Mongolia.
†*Paidopithex* Pohlig, 1895. L. Plioc.; Germany.
Hylobates Illiger, 1811. R.; S.E. As. from Bhutan, E. Indies. Gibbons, hoolock, wau-wau.
Symphalangus Gloger, 1841. R.; Sumatra, Malay Peninsula. Siamang, siamang gibbon.
†Subfam. Dryopithecinae Gregory and Hellman, 1939b, p. 370. L. Mioc.; Af. M. Mioc.–Plioc.; Eu. Plioc.; As.
†*Proconsul* Hopwood, 1933. L. Mioc.; Kenya.
†*Dryopithecus* Lartet, 1856. [Including †*Anthropodus* Schlosser, 1901, preoccupied = †*Neopithecus* Abel, 1903; †*Griphopithecus* Abel, 1902; †*Austriacopithecus* Ehrenberg, 1937.[1]] M. Mioc.–Plioc.; Eu., Cent. Eu., France, Spain. Doubtful in Mioc. of N. Af. and Plioc. of India.
†*Sivapithecus* Pilgrim, 1927 (= †*Palaeopithecus* Lydekker, 1879, *nec* Voigt, 1835).[2] L. Plioc.; India.
†*Hylopithecus* Pilgrim, 1927. L. Plioc.; India.
†*Palaeosimia* Pilgrim, 1915. L. Plioc.; India.
†*Sugrivapithecus* Lewis, 1934. L. Plioc.; India.
†*Bramapithecus* Lewis, 1934. L. Plioc.; India.
†*Ramapithecus* Lewis, 1934. U. Plioc.; India.
Subfam. Ponginae Allen, 1925, p. 477 (=Pongidae or Simiidae, *sensu stricto*, of authors). Pleist.–R.; Af., As.
†*Gigantopithecus* von Koenigswald, 1939. Pleist.; China.

[1] Undoubtedly a heterogeneous group and probably of more than one genus, but it does not now seem possible to establish good generic separations on any objective basis.

[2] Voigt's "genus" was based on a fanciful concept of Triassic tracks and should not, in my opinion, be permitted to invalidate a name applied to a real, known animal and properly established. Recent students have, however, accepted †*Sivapithecus*, and I reluctantly follow them.

Pongo Lacépède, 1799 (=*Simia* of authors). L. Pleist.; India. R.; Borneo, Sumatra. Orang-utan, ourang, orang.

Pan Oken, 1816 (=*Anthropopithecus* De Blainville, 1839; *Troglodytes* Geoffroy, 1812, *nec* Viellot, 1806). R.; equatorial Af. Chimpanzee.

Gorilla Geoffroy, 1852. R.; equatorial Af. Gorilla.

†Subfam. Australopithecinae Gregory and Hellman, 1939b, p. 370. Pleist.; S. Af.

†*Australopithecus* Dart, 1925. [Including †*Plesianthropus* Broom, 1938; †*Paranthropus* Broom, 1938.] Pleist.; S. Af.

Possible pongids of uncertain affinities:

†*Pondaungia* Pilgrim, 1927. U. Eoc.; Burma.

†*Amphipithecus* Colbert, 1937. U. Eoc.; Burma.

†*Xenopithecus* Hopwood, 1933. L. Mioc.; Kenya.

Fam. Hominidae Gray, 1825, p. 338. Pleist.–R.; world wide. Men.

†*Pithecanthropus* Dubois, 1894. [Including †*Sinanthropus* Black, 1927.] Pleist.; Java, China. Java man, Java ape-man, Peking man.

†*Eoanthropus* Smith Woodward, 1913. Pleist.; England. Piltdown man.

Homo Linnaeus, 1758. [Including †*Protanthropus* Haeckel, 1895; †*Cyphanthropus* Pycraft, 1928; and other proposed genera.] Pleist.–R.; world wide. Men (including all living races and also Heidelberg man, Neanderthal man, Rhodesian man, and other prehistoric races).

†Order TILLODONTIA Marsh, 1875, p. 221.

†Fam. Tillotheriidae [Tillotheridae] Marsh, 1875, p. 221 (=†Anchippodontidae Gill, 1872, p. 11, validity doubtful). [Including †Esthonychidae Cope, 1883a, p. 80.] U. Paleoc.–M. Eoc.; N.A. L. Eoc.; Eu.

†*Esthonyx* Cope, 1874. [Including †*Plesiesthonyx* Lemoine, 1891.] U. Paleoc.–L. Eoc.; N.A. L. Eoc.; Eu.

†*Anchippodus* Leidy, 1868. ?M. Eoc.; N.A.

†*Trogosus* Leidy, 1871. M. Eoc.; N.A.

†*Tillotherium* Marsh, 1873. M. Eoc.; N.A.

†Order TAENIODONTA Cope, 1876, p. 39 (=†Ganodonta Wortman, 1896, p. 259; †Stylinodontia Marsh, 1897, p. 144).

†Fam. Stylinodontidae Marsh, 1875, p. 221 (=or including †Calamodontidae Cope, 1876, p. 39; †Ectoganidae Cope, 1876, p. 39; †Conoryctidae Wortman, 1896, p. 260). L. Paleoc.–U. Eoc.; N.A.

†Subfam. Conoryctinae Schlosser, 1911b, p. 414 (=†Conoryctidae Wortman, 1896, p. 260). [Including †Onychodectini Winge, 1923, p. 136.] L.–M. Paleoc.; N.A.

†*Onychodectes* Cope, 1888. L. Paleoc.; N.A.

†*Conoryctella* Gazin, 1939. M. Paleoc.; N.A.

†*Conoryctes* Cope, 1881. M. Paleoc.; N.A.

†Subfam. Stylinodontinae Schlosser, 1911b, p. 414 (=†Stylinodontini Winge, 1923, p. 136; essentially=†Stylinodontidae in original sense). [Including †Psittacotheriinae Matthew, 1937, p. 255.] L. Paleoc.–U. Eoc.; N.A.

†*Wortmania* Hay, 1899 (=†*Hemiganus* Wortman, 1897, invalid). L. Paleoc.; N.A.
†*Psittacotherium* Cope, 1882 (=†*Hemiganus* Cope, 1882, *nec* Wortman, 1897). M.–?U. Paleoc.; N.A.
†*Ectoganus* Cope, 1874 (=†*Calamodon* Cope, 1874).[1] L. Eoc.; N.A.
†*Stylinodon* Marsh, 1874. L.–U. Eoc.; N.A.

Order EDENTATA Cuvier, 1798, p. 142 (=Edentati Vicq d'Azyr, 1792, p. ciii; Bruta Linnaeus, 1758, p. 33, in part).
†Suborder PALAEANODONTA Matthew, 1918, p. 620.
†Fam. Metacheiromyidae Wortman, 1903, p. 347. U. Paleoc.–M. Eoc.; N.A.
†*Palaeanodon* Matthew, 1918. U. Paleoc.–L. Eoc.; N.A.
†*Metacheiromys* Wortman, 1903. M. Eoc.; N.A.
†Fam. Epoicotheriidae Simpson, 1927c, p. 285. L. Olig.; N.A.
†*Epoicotherium* Simpson, 1927 (=†*Xenotherium* Douglass, 1906, *nec* Ameghino, 1904). L. Olig.; N.A.
†*Xenocranium* Colbert, 1942. L. Olig.; N.A.
Suborder XENARTHRA Cope, 1889b, p. 657.
Infraorder PILOSA Flower, 1883, p. 184 (=Anicanodonta Ameghino, 1889, pp. 653, 657). U. Eoc.–R.; S.A. M. Plioc.–Pleist.; N.A. Pleist.; W. Indies. R.; Cent. A.
†Superfam. Megalonychoidea Simpson, 1931a, p. 272 (=†Megatherioidae Hay, 1930, p. 403; †Gravigrada Owen, 1842, p. 168). U. Eoc.–Pleist.; S.A. M. Plioc.–Pleist.; N.A. Pleist.; W. Indies. †Ground sloths, †gravigrades.
†Fam. Megalonychidae Zittel, 1892, p. 133 (=†Megalonycidae Ameghino, 1889, pp. 690, 695). ?U. Eoc., Olig.–Pleist.; S.A. M. Plioc.–Pleist.; N.A. Pleist.; W. Indies.
†Subfam. Nothrotheriinae[2] Kraglievich, 1923, p. 55. ?U. Eoc., Olig.–Pleist.; S.A. Pleist.; N.A.
†*Orophodon* Ameghino, 1895.[3] L. or M. Olig.; S.A.
†*Proschismotherium* Ameghino, 1902. U. Olig.; S.A.
†*Eucholoeops* Ameghino, 1887. L. Mioc.; S.A.
†*Hapaloides* Ameghino, 1902. U. Olig.; S.A.
†*Hapalops* Ameghino, 1887. [Including †*Xyophorus* Ameghino, 1887; †*Parhapalops* Ameghino, 1891; etc.] L.–M. Mioc.; S.A.
†*Hyperleptus* Ameghino, 1891. L. Mioc.; S.A.
†*Megalonychotherium* Scott, 1904. L. Mioc.; S.A.
†*Schismotherium* Ameghino, 1887. L. Mioc.; S.A.
†*Pelecyodon* Ameghino, 1891. L. Mioc.; S.A.
†*Analcimorphus* Ameghino, 1891. L. Mioc.; S.A.

[1] †*Ectoganus* and †*Calamodon* were published simultaneously, and Gazin, 1936, has demonstrated that they are synonyms. Unfortunately he followed "page priority" and selected the less familiar of the two names as valid. "Page priority" is not priority in fact and has no bearing under the International Rules or the rules of common sense, but the first selection of a name by a reviser is binding and must be followed.

[2] The subfamily names accredited to Kraglievich in 1923 are spelled with a single "i," e.g., Nothrotherinae. Since, otherwise, the usage agrees with the author's conception, it has been decided to retain Kraglievich as author of the subfamilies but to amend the spelling.

[3] Affinities highly dubious and place here quite uncertain. There are possible members of this group in the Musters (Late Eocene ?), but they have not been truly defined.

†*Neohapalops* Kraglievich, 1923. U. Mioc.; S.A.
†*Pronothrotherium* Ameghino, 1907. [Including †*Senetia* Kraglievich, 1925.] U. Mioc.–Plioc.; S.A.
†*Diheterocnus* Kraglievich, 1928 (= †*Heterocnus* Kraglievich, 1925, *nec* Sharpe, 1895). U. Plioc.; S.A.
†*Synhapalops* Kraglievich, 1930. U. Plioc. or L. Pleist.; S.A.
†*Nothropus* Burmeister, 1882. Pleist.; S.A.
†*Nothrotherium* Lydekker, 1889 (= †*Coelodon* Lund, 1838, *nec* Serville, 1832). Pleist.; S.A., N.A.

†Subfam. Ortotheriinae[1] Kraglievich, 1923, p. 55 (= †Ortotheridae Ameghino, 1889, p. 665). U. Mioc.; S.A. Pleist.; W. Indies.
†*Ortotherium* Ameghino, 1885. U. Mioc.; S.A.
†*Pliomorphus* Ameghino, 1885. U. Mioc.; S.A.
†*Acratocnus* Anthony, 1918. Pleist.; W. Indies.
†*Mesocnus* Matthew, 1931. Pleist.; W. Indies.

†Subfam. Megalocninae Kraglievich, 1923, p. 54. U. Mioc.; ?S.A. Pleist.; W. Indies.
†*Amphiocnus* Kraglievich, 1922.[2] U. Mioc.; S.A.
†*Microcnus* Matthew, 1931. Pleist.; W. Indies.
†*Megalocnus* Leidy, 1868. Pleist.; W. Indies.

†Subfam. Megalonychinae Trouessart, 1904, p. 793. U. Mioc., ?Pleist.; S.A. M. Plioc.[3]–Pleist.; N.A.
†*Protomegalonyx* Kraglievich, 1925. U. Mioc.; S.A.
†*Megalonychops* Kraglievich, 1926. U. Mioc., ?Pleist.; S.A.
†*Megalonyx* Harlan, 1825.[4] Pleist.; N.A.

†Fam. Megatheriidae Owen, 1843b, p. 359 (= †Megatheriadae Gray, 1821, p. 305). L. Mioc.–Pleist.; S.A. Pleist.; N.A.

†Subfam. Planopsinae, new form? (= †Planopsidae Scott, 1904a, p. 320 = †Prepotheridae Ameghino, 1894, p. 161). L. Mioc.; S.A.
†*Planops* Ameghino, 1887. L. Mioc.; S.A.
†*Prepotherium* Ameghino, 1891. L. Mioc.; N.A.

†Subfam. Megatheriinae Gill, 1872, p. 24. L. Mioc.–Pleist.; S.A. Pleist.; N.A.
†*Megathericulus* Ameghino, 1904. L.–M. Mioc.; S.A.
†*Promegatherium* Ameghino, 1883. [Including †*Eomegatherium* Kraglievich, 1926.] M.–U. Mioc.; S.A.
†*Plesiomegatherium* Roth, 1911. U. Mioc.; S.A.
†*Megatheridium* Cabrera, 1928. [Including †*Pliomegatherium* Kraglievich, 1930.] U. Mioc.–L. Plioc.; S.A.
†*Pyramiodontherium* Rovereto, 1914. [Including †*Megatheriops* C. Ameghino, 1921.] ?U. Mioc., L.–?U. Plioc.; S.A.
√ †*Megatherium* Cuvier, 1796. [Including †*Paramegatherium* Kraglievich, 1925.] U. Plioc.–Pleist.; S.A. M. Plioc.–Pleist.; N.A.

[1] "Ortotherinae" in the original reference.
[2] Based on very fragmentary material; pertinence to subfamily doubtful.
[3] The North American Pliocene forms have not been diagnosed as to genus.
[4] The supposed genus "†*Megalonyx* Jefferson, 1799," long sentimentally cherished by American palaeontologists, is non-existent. Jefferson definitely did not establish such a genus in zoological nomenclature, but it can be ascribed to Harlan.

†Fam. Mylodontidae Ameghino, 1889, pp. 665, 895. ?Olig., L. Mioc.–Pleist.; S.A. Pleist.; N.A.

†Subfam. Mylodontinae Gill, 1872, p. 24. ?Olig., L. Mioc.–Pleist.; S.A. Pleist.; N.A.

†*Octodontotherium* Ameghino, 1895.[1] Olig.; S.A.

†*Nematherium* Ameghino, 1887. [Including †*Lymodon* Ameghino, 1891.] L. Mioc.; S.A.

†*Analcitherium* Ameghino, 1891. L. Mioc.; S.A.

†*Neonematherium* Ameghino, 1904. M. Mioc.; S.A.

†*Promylodon* Ameghino, 1883. U. Mioc.; S.A.

†*Sphenotherus* Ameghino, 1891. U. Mioc.; S.A.

†*Ranculcus* Ameghino, 1891. U. Mioc.; S.A.

†*Pleurolestodon* Rovereto, 1914. L. Plioc.; S.A.

†*Glossotherium* Owen, 1840 (= †*Eumylodon* Ameghino, 1904; †*Mylodon* of most authors, but not of Owen as fixed by type). [Including †*Pseudolestodon* Gervais and Ameghino, 1880.] U. Plioc.–Pleist.; S.A.

†*Paramylodon* Brown, 1903 (= †*Orycterotherium* Harlan, 1841, *nec* Bronn, 1838; †*Mylodon sensu lato* of most authors, but not of Owen as fixed by type).[2] Pleist.; N.A.

†*Mylodon* Owen, 1840 (= †*Neomylodon* Ameghino, 1898; †*Grypotherium* Reinhardt, 1879; †*Glossotherium* of most authors, but not of Owen as fixed by type). Pleist.; S.A.

†*Lestodon* Gervais, 1865. Pleist.; S.A.

†Subfam. Scelidotheriinae Ameghino, 1904, p. 182 (= †Scelidotheridae Ameghino, 1889, pp. 665, 895). U. Mioc.–Pleist.; S.A.

†*Scelidotherium* Owen, 1840. [Including †*Scelidodon* Ameghino, 1881.] U. Mioc.–Pleist.; S.A.

Superfam. Myrmecophagoidea Simpson, 1931a, p. 273 (= Vermilingua Illiger, 1811, p. 112, as emended). L. Plioc.–R.; S.A. R.; Cent. A.

Fam. Myrmecophagidae Bonaparte, 1838, p. 111 (= Myrmecophagina Gray, 1825, p. 343). L. Plioc.–R.; S.A. R.; Cent. A. (True, or South American) anteaters.

†*Promyrmephagus* Ameghino, 1904.[3] L. Mioc.; S.A.

†*Protamandua* Ameghino, 1904.[3] L. Mioc.; S.A.

†*Neotamandua* Rovereto, 1914. L. Plioc.; S.A.

†*Palaeomyrmedon* Rovereto, 1914. L. Plioc.; S.A.

†*Nuñezia* Kraglievich, 1934. M. Plioc.; S.A.

✓*Myrmecophaga* Linnaeus, 1758. Pleist.–R.; S.A. R.; Cent. A. Jurumi, giant anteater, "ant bear."

✓*Tamandua* Frisch, 1775. Pleist.–R.; S.A. R.; Cent. A. Tamandua, collared anteater.

✓*Cyclopes* Gray, 1821 (= *Cyclothurus* Lesson, 1842, *ex* Gray, 1825). R.; S.A., Cent. A. Little anteater, two-toed anteater.

Superfam. Bradypodoidea Simpson, 1931a, p. 273 (= Tardigrada Forster, *fide* Blumenbach, 1779, p. 71). R.; S.A., Cent. A.

[1] Systematic position very doubtful.

[2] If the North American forms are not separated generically from the South American, they belong in †*Glossotherium*, not in †*Mylodon* where they are usually placed.

[3] It is certain that there are myrmecophagids in the Santa Cruz formation, but it is not certain whether these names apply to them, or which name applies.

Fam. Bradypodidae Bonaparte, 1831, p. 22 (=Bradypidae Gray, 1821, p. 304). R.; S.A., Cent. A. Tree sloths, sloths.

Bradypus Linnaeus, 1758. R.; S.A., Cent. A. Ai, three-toed (tree) sloth.

Choloepus Illiger, 1811. R.; S.A., Cent. A. Unau, two-toed (tree) sloth.

Infraorder CINGULATA Illiger, 1811, p. 110 (=Loricati Vicq d'Azyr, 1792, p. ciii; Loricata Owen, 1842, p. 167, *nec* Merrem, 1820, pp. 7, 34; Hicanodonta Ameghino, 1889, p. 758). Paleoc.–R.; S.A. U. Plioc.–R.; N.A.

Superfam. Dasypodoidea Simpson, 1931a, p. 273 (=Dasypodoidae Hay, 1930, p. 415; Dasypoda Hoernes, 1886, p. 662). Paleoc.–R.; S.A. Pleist.–R.; N A

Fam. Dasypodidae Bonaparte, 1838, p. 111 (=Dasipidae Gray, 1821, p. 305). [Including Chlamydophoridae Gray, 1869a, pp. 362, 387; †Chlamydotheridae Ameghino, 1889, p. 853; †Stegotheridae Ameghino, 1889, pp. 878, 895; and many other proposed families.] Paleoc.–R.; S.A. Pleist.–R.; N.A. Armadillos.

Subfam. Dasypodinae Gill, 1872, p. 24. [Including proposed subfamilies corresponding with the tribes listed below, except †Utaetini.] Paleoc.–R.; S.A. Pleist.–R.; N.A.

†Tribe Utaetini, new. Paleoc.–Eoc.; S.A.

†*Utaetus* Ameghino, 1902. [Including †*Anteutatus* Ameghino, 1902; †*Orthutaetus* Ameghino, 1902; etc.] Paleoc.–Eoc.; S.A.

Tribe Euphractini, new rank (=Euphractinae Weber, 1928, p. 217, or Yepes, 1928, p. 30; Euphracti Weber, 1928, p. 220). Olig.–R.; S.A.

†*Prozaedius* Ameghino, 1891. Olig.–M. Mioc.; S.A.

†*Stenotatus* Ameghino, 1891. [Including †*Prodasypus* Ameghino, 1894.] Olig.–M. Mioc.; S.A.

†*Proeuphractus* Ameghino, 1886. U. Mioc.–U. Plioc.; S.A.

†*Macroeuphractus* Ameghino, 1887. L.–U. Plioc.; S.A.

†*Paleuphractus* Kraglievich, 1934. L. Plioc.; S.A.

Chaetophractus Fitzinger, 1871.[1] ?Plioc., Pleist.–R.; S.A. Peludo, quirquincho.

Euphractus Wagler, 1830.[1] [Including *Scleropleura* Milne Edwards, 1871.[2]] Pleist.–R.; S.A. Peludo, tatú-poyú, six-banded armadillo.

Zaedyus Ameghino, 1889. Pleist.–R.; S.A. Pichi (pichy, or piche).

†Tribe Eutatini, new rank (=†Eutatinae Bordas, 1933, p. 598). ?Eoc., Olig.–Pleist.; S.A.

†*Meteutatus* Ameghino, 1902.[3] Eoc.–Olig.; S.A.

†*Proeutatus* Ameghino, 1891. Olig.–M. Mioc.; S.A.

†*Doellotatus* Bordas, 1932 (=†*Eutatopsis* Kraglievich, 1934).[4]

[1] In much of the literature *Chaetophractus* and *Euphractus* (together, or either one of them) are called *Dasypus*, and the genus to which the latter name is now confined is then usually called *Tatu* or *Tatusia*.

[2] Although it is still frequently listed as a distinct genus, there is little doubt that *Scleropleura* was founded on an injured or teratological *Euphractus*.

[3] Reference to this tribe very uncertain.

[4] Castellanos has recently adopted †*Eutatopsis* in preference to †*Doellotatus* because it was named first in museum labels. †*Doellotatus* was, however, published first and is necessarily valid.

?L., M.–U. Plioc.; S.A.
†*Eutatus* Gervais, 1867. Pleist.; S.A.
Tribe Priodontini Weber, 1928, p. 220 (=Prionodontina Gray, 1873a, p. 20, *nec* 1864). Pleist.–R.; S.A.
Priodontes Cuvier, 1827 (=*Priodon* McMurtrie, 1842). R.; S.A. Tatuasu, giant armadillo.
Cabassous McMurtrie, 1831 (=*Xenurus* Wagler, 1830, *nec* Boie, 1826). Pleist.–R.; S.A. Cabassu, eleven-banded armadillo.
Tribe Tolypeutini Weber, 1928, p. 220 (=Tolypeutina Gray, 1865b, p. 365). Pleist.–R.; S.A.
Tolypeutes Illiger, 1811. Pleist.–R.; S.A. Apara, mataco.
Tribe Dasypodini, new rank (=Dasypodinae *sensu stricto* of most authors). ?U. Mioc., Pleist.–R.; S.A. Pleist.–R.; N.A.
†*Propraopus* Ameghino, 1881. Pleist.; S.A.
✓*Dasypus* Linnaeus, 1758 (=*Tatu* Frisch, 1775; *Tatusia* Lesson, 1827). [Including *Praopus* Burmeister, 1854; *Muletia* Gray, 1874.] Pleist.–R.; S.A., N.A. Peba, tatu, (common, American, or Texas) armadillo, nine-banded armadillo, cachicamo, mulita, etc.
†Subfam. Stegotheriinae[1] Trouessart, 1898, p. 1123 (=†Stegotheridae Ameghino, 1889, pp. 878, 895). ?Eoc., Olig.–L. Mioc.; S.A.
†*Astegotherium* Ameghino, 1902.[2] Eoc.; S.A.
†*Pseudostegotherium* Ameghino, 1902. ?Eoc., Olig.; S.A.
†*Stegotheriopsis* Bordas, 1939. U. Olig.; S.A.
†*Stegotherium* Ameghino, 1887. L. Mioc.; S.A.
†Subfam. Chlamytheriinae Hay, 1930, p. 417 (=†Chlamydotheridae Ameghino, 1889, p. 853). ?Eoc., Plioc.–Pleist.; S.A. Pleist.; N.A.
†*Machlydotherium* Ameghino, 1902.[3] Eoc.; S.A.
†*Vassallia* Castellanos, 1927. L. Plioc.; S.A.
†*Kraglievichia* Castellanos, 1927. U. Mioc.; S.A.
†*Plaina* Castellanos, 1937. M.–U. Plioc.; S.A.
†*Chlamytherium* Lund, 1838 (=†*Chlamydotherium* Lund, 1839, *nec* Bronn, 1838). Pleist.; S.A.
†*Holmesina* Simpson, 1930. Pleist.; N.A.
Subfam. Chlamyphorinae Yepes, 1928, p. 11 (=Chlamydophorina Bonaparte, 1850). Pleist.–R.; S.A.
✓*Chlamyphorus* Harlan, 1825 (=*Chlamydophorus* Wagler, 1830). Pleist.–R.; S.A. Pichiciego, lesser pichiciego.
Burmeisteria Gray, 1865. R.; S.A. Pichiciego, greater pichiciego.
†Fam. Peltephilidae Ameghino, 1894, p. 433. Olig.–?L. Plioc.; S.A.
†*Peltephilus* Ameghino, 1887. Olig.–L. Mioc.; S.A.
†*Parapeltocoelus* Bordas, 1938. U. Olig.; S.A.
†*Peltocoelus* Ameghino, 1902. U. Olig.–L. Mioc.; S.A.
†*Anantiosodon* Ameghino, 1891. L. Mioc.; S.A.
†*Epipeltephilus* Ameghino, 1904. ?M. Mioc.–?L. Plioc.; S.A.
†Superfam. Glyptodontoidea Simpson, 1931a, p. 273 (=†Glyptodontoidae Hay, 1930, p. 418; †Glyptodontia Ameghino, 1902b, p. 133). U. Eoc.–Pleist.; S.A. U. Plioc.–Pleist.; N.A.

[1] Spelled "Stegotherinae" in Trouessart.
[2] The pertinence of this and several other proposed early genera to the subfamily is highly uncertain.
[3] Pertinence to this subfamily very uncertain.

†Fam. Glyptodontidae Burmeister, 1879, p. 421 (=†Hoplophoridae Huxley, 1864, p. 108). [Including proposed families corresponding with the subfamilies given below.] U. Eoc.–Pleist.; S.A. U. Plioc.–Pleist.; N.A. †Glyptodonts.

†Subfam. Propalaeohoplophorinae Castellanos, 1932, p. 92 (=†Propalaeohoplophoridae Ameghino, 1891b, p. 251). [Including, somewhat doubtfully, †Glyptatelinae Castellanos, 1932, p. 93.] U. Eoc.–M. Mioc.; S.A.

†*Glyptatelus* Ameghino, 1897. U. Eoc.–Olig.; S.A.

†*Propalaeohoplophorus* Ameghino, 1887. U. Olig.–M. Mioc.; S.A.

†*Cochlops* Ameghino, 1889. L. Mioc.; S.A.

†*Eucinepeltus* Ameghino, 1891. L. Mioc.; S.A.

†*Asterostemma* Ameghino, 1889. L. Mioc.; S.A.

†*Metopotoxus* Ameghino, 1898. L. Mioc.; S.A.

†Subfam. Hoplophorinae Weber, 1928, p. 224 (=†Sclerocalyptinae Trouessart, 1898, p. 1128). U. Mioc.–Pleist.; S.A. Pleist.; N.A.

†*Palaehoplophorus* Ameghino, 1883 (=†*Palaeohoplophorus* Roger, 1896, and most later authors). M.–U. Mioc.; S.A.

†*Protoglyptodon* Ameghino, 1885. U. Mioc.; S.A.

†*Trachycalyptus* Ameghino, 1908. U. Mioc., U. Plioc.; S.A.

†*Plohophorus* Ameghino, 1887. U. Mioc., M. Plioc.; S.A.

†*Parahoplophorus* Castellanos, 1931. U. Mioc.; S.A.

†*Lomaphorops* Castellanos, 1931. L. Plioc.; S.A.

†*Stromaphorus* Castellanos, 1926. L. Plioc.; S.A.

†*Stromaphoropsis* Kraglievich, 1932. Plioc., ?Pleist.; S.A.

†*Eosclerocalyptus* C. Ameghino, 1916. L. Plioc.; S.A.

†*Plohophoroides* Castellanos, 1928. U. Plioc.; S.A.

†*Lomaphorus* Ameghino, 1889. Pleist.; S.A.

†*Hoplophorus* Lund, 1838, *nec Hoplophora* Perty, 1830, *nec Oplophorus* Milne Edwards, 1837 (=†*Sclerocalyptus* Ameghino, 1891).[1] Pleist.; S.A.

†*Brachyostracon* Brown, 1912. Pleist.; N.A. (Mexico).

†*Pseudoeuryurus* Ameghino, 1889. U. Mioc.; S.A.

†*Urotherium* Castellanos, 1926. U. Mioc.–U. Plioc.; S.A.

†*Neuryurus* Ameghino, 1889 (=†*Euryurus* Gervais and Ameghino, 1880, *nec* Koch, 1847). Pleist.; S.A.

†Subfam. Doedicurinae Trouessart, 1898, p. 1134 (=†Doedicuridae Ameghino, 1889, pp. 774, 840). U. Mioc.–Pleist.; S.A.

†Tribe Panochthini, new rank (=†Panochthinae Castellanos, 1927, p. 266). Plioc.–Pleist.; S.A.

†*Nopachtus* (*nec* †*Nopachthus*) Ameghino, 1888. Plioc.; S.A.

†*Propanochthus* Castellanos, 1925. Plioc.; S.A.

†*Panochthus* Burmeister, 1866. Pleist.; S.A.

†Tribe Doedicurini, new rank (=†Doedicurinae *sensu stricto* of authors). U. Mioc.–Pleist.; S.A.

†*Comaphorus* Ameghino, 1886. U. Mioc.; S.A.

†*Eleutherocercus* Koken, 1888. U. Mioc.–M. Plioc.; S.A.

†*Prodaedicurus* Castellanos, 1927. [Including †*Palaeodoedicurus*

[1] Authors since 1891 have used †*Sclerocalyptus* almost without exception, but †*Hoplophorus* Lund, 1838, is not legally preoccupied and is unquestionably the correct name of this genus.

Castellanos, 1927.] M.–U. Plioc.; S.A.
†*Xiphuroides* Castellanos, 1927. U. Plioc. or L. Pleist.; S.A.
†*Plaxhaplous* (*nec* †*Plaxhaplus*, *nec* †*Plaxaplus*) Ameghino, 1884. Pleist.; S.A.
†*Doedicurus* Burmeister, 1874. Pleist.; S.A.
†Subfam. Glyptodontinae Trouessart, 1898, p. 1125, or Cope, 1898, p. 134 (=†Glyptodontidae *sensu stricto* of some authors). U. Plioc.–Pleist.; S.A., N.A.
†*Paraglyptodon* Castellanos, 1932. U. Plioc.; S.A.
†*Glyptotherium* Osborn, 1903. U. Plioc.; N.A.
†*Neothoracophorus* Ameghino, 1889 (=†*Thoracophorus* Gervais and Ameghino, 1880, *nec* Hope, 1840).[1] Pleist.; S.A.
†*Glyptodon* Owen, 1838. Pleist.; S.A., ?N.A.
†*Boreostracon* Simpson, 1929. Pleist.; N.A.
†Glyptodontoidea *incertae sedis* (†Palaeopeltidae Ameghino, 1895, p. 659):
†*Palaeopeltis* Ameghino, 1895. U. Eoc.–Olig.; S.A.
Order PHOLIDOTA Weber, 1904, p. 412, *nec* Merrem, 1820, p. 5 (=Squamata Huxley, 1872, p. 287, *nec* Oppel, 1811, p. 14; Nomarthra Gill, 1910, p. 56, *nec* Gill, 1884, p. 66).
Fam. Manidae Gray, 1821, p. 305 (=Manididae Gray, 1865b, p. 362). Pleist.–R.; As. R.; Af. Olig.–Mioc., Pleist.; ?Eu.
Manis Linnaeus, 1758 (=*Pholidotus* Brisson, 1762; *Pangolinus* Rafinesque, 1821). [Including *Phataginus* Rafinesque, 1821; *Phatages* Sundevall, 1843; *Smutsia* Gray, 1865; *Paramanis* Pocock, 1924; *Uromanis* Pocock, 1924.] Pleist.; ?Eu. Pleist.–R.; As. R.; Af. Pangolins, scaly anteaters.
?PHOLIDOTA *incertae sedis:*
†*Necromanis* Filhol, 1893. Olig.; Eu.
†*Teutomanis* Ameghino, 1905. Mioc.; Eu.
†*Galliaetatus* Ameghino, 1905. Mioc.; Eu.
Cohort GLIRES Linnaeus, 1758, p. 56.
Order LAGOMORPHA Brandt, 1855, p. 295 (=Duplicidentata Illiger, 1811, p. 91).
†Fam. Eurymylidae Matthew, Granger, and Simpson, 1929. pp. 1, 5. U. Paleoc.; As.
†*Eurymylus* Matthew and Granger, 1925. U. Paleoc.; As.
Fam. Ochotonidae Thomas, 1897, p. 1026 (=Lagomyidae Lilljeborg, 1866, pp. 9, 58; Lagomina Gray, 1825, p. 341). U. Olig.–R.; Eu., As. M. Mioc., Pleist.–R.; N.A. Mioc.; Af. Pikas.
†*Sinolagomys* Bohlin, 1937. U. Olig.; As.
†*Titanomys* Meyer, 1843. U. Olig.–M. Mioc.; Eu.
†*Prolagus* Pomel, 1853. M. Mioc.–Pleist.; Eu.
†*Lagopsis* Schlosser, 1884.[2] Mioc.; Eu.
†*Austrolagomys* Stromer, 1926. L. Mioc.; Af.
†*Proöchotona* Khomenko, 1916. Plioc.; As.
†*Ochotonoides* Teilhard de Chardin and Young, 1931. Pleist.; As.
Ochotona Link, 1795 (=*Lagomys* Cuvier, 1800). Plioc.–R.; As.,

[1] It has been suggested that this genus (the validity of which is not beyond question) should be called †*Myloglyptodon* Ameghino, 1884. There is room for dispute, but it is my opinion that "*Myloglyptodon*" was mentioned only as a morphological, theoretical term and was not technically introduced into zoological nomenclature. Ameghino himself evidently assumed and definitely implied this to be the case, for he never after used it as if it were a real zoological name.

[2] *Lagopsis* Rafinesque, 1815, is a *nomen nudum* and does not preoccupy †*Lagopsis* Schlosser.

Eu. Pleist.–R.; N.A. Pika, cony, "mouse hare," rock "rabbit."

Fam. Leporidae Gray, 1821, p. 304 (=Leporinorum Fischer, 1817, p. 409). U. Eoc.–R.; N.A. Olig., Plioc.–R.; As. U. Olig.–R.; Eu. Pleist.–R.; Af., S.A. Hares and rabbits.

Subfam. Palaeolaginae Dice, 1929, p. 340 (in part=Palaeolagida Haeckel, 1895, p. 503). [Including †Archaeolaginae Dice, 1929, p. 343; †Protolaginae Walker, 1931, p. 122; †Megalaginae Walker, 1931, p. 123; †Mytonolaginae Burke, 1941, p. 1; †Desmatolaginae Burke, 1941, p. 13.] U. Eoc.–R.; N.A. ?Olig., ?Mioc., U. Plioc.–Pleist.; Eu. ?Olig., R.; As. Pleist.–R.; Af.

†*Mytonolagus* Burke, 1934. U. Eoc.; N.A.

†*Shamolagus* Burke, 1941. U. Eoc.; As.

†*Gobiolagus* Burke, 1941. U. Eoc.–L. Olig., ?U. Olig.; As.

†*Palaeolagus* Leidy, 1856. [Including †*Protolagus* Walker, 1931.] L.–U. Olig.; N.A.

†*Megalagus* Walker, 1931. L.–U. Olig.; N.A.

†*Archaeolagus* Dice, 1917. L. Mioc.; N.A.

†*Hypolagus* Dice, 1917. M. Mioc.–Pleist.; N.A. U. Plioc.–Pleist.; Eu., As.

†*Notolagus* Wilson, 1938. [Including †*Dicea* Hibbard, 1939.] Plioc.; N.A.

†*Alilepus* Dice, 1931. (=†*Allolagus* Dice, 1929, *nec* Ognev, 1929). Plioc.; As., ?N.A. Mioc.; ?Eu.

†*Pratilepus* Hibbard, 1939. U. Plioc.; N.A.

Pentalagus Lyon, 1903. R.; As.

Pronolagus Lyon, 1903. Pleist.–R.; Af. Rock "hares."

Romerolagus Merriam, 1896. R.; N.A.

?Palaeolaginae, *incertae sedis:*

†*Desmatolagus* Matthew and Granger, 1923. Olig.; As., N.A.

†*Oreolagus* Dice, 1917. L.–U. Mioc.; N.A.

†*Amphilagus* Pomel, 1854. U. Olig.–Mioc.; Eu.

†*Piezodus* Viret, 1929. U. Olig.; Eu.

Palaeolaginae or Leporinae:

†*Nekrolagus* Hibbard, 1939. U. Plioc.; N.A.

Subfam. Leporinae Trouessart, 1880, p. 200. ?Plioc., Pleist.–R.; N.A. Plioc.–R.; Eu., As. Pleist.–R.; S.A., Af.

Caprolagus Blyth, 1845. Plioc.–R.; As. Plioc.; Eu. Bristly rabbit.

Lepus Linnaeus, 1785. [Including *Bunolagus* Thomas, 1929; *Poelagus* St. Leger, 1932; and other subgenera.] Pleist.–R.; Eu., As., Af., N.A. (True) hares, including snowshoe "rabbit," jack "rabbit," etc.

Sylvilagus Gray, 1867. ?Plioc., Pleist.–R.; N.A. Pleist.–R.; S.A. Cottontail, tapetis, marsh "rabbit," etc.

Oryctolagus Lilljeborg, 1874. Pleist.–R.; Eu. R.; N.Af. (True or European) rabbits.

Brachylagus Miller, 1900. R.; N.A. Pygmy "rabbits."

Nesolagus Major, 1899. R.; As. (Sumatra). Short-eared "rabbit."

Order RODENTIA Bowdich, 1821, pp. 7, 51 (=Rodentes Vicq d'Azyr, 1792, p. xcvii). Rodents.

Suborder SCIUROMORPHA Brandt, 1855, p. 144.
Superfam. Aplodontoidea Matthew, 1910b, p. 69 (=Haploodontoidea Gill, 1872, p. 22).
†Fam. Ischyromyidae Alston, 1876, pl. 4, pp. 67, 78. U. Paleoc.–L. Mioc.; N.A. L.–U. Eoc.; Eu. Olig.; As.
†Subfam. Paramyinae, new rank? (=†Paramyidae Miller and Gidley, 1918, p. 439; †Paramyida Haeckel, 1895, p. 502). U. Paleoc.–M. Olig.; N.A. L.–U. Eoc.; Eu.
†*Paramys* Leidy, 1871 (certainly including several distinct genera, not yet clearly defined). U. Paleoc.–U. Eoc.; N.A.
†*Decticadapis* Lemoine, 1883. L. Eoc.; Eu.
†*Reithroparamys* Matthew, 1920. M. Eoc.; N.A.
†*Pseudotomus* Cope, 1872. M. Eoc.; N.A.
†*Ischyrotomus* Matthew, 1910. U. Eoc.; N.A.
†*Manitsha* Simpson, 1941. M. Olig.; N.A.
†*Leptotomus* Matthew, 1910. U. Eoc.; N.A.
†*Rapamys* Wilson, 1940. U. Eoc.; N.A.
?†Paramyinae *incertae sedis:*
†*Plesiarctomys* Bravard, 1848–1852. U. Eoc.; Eu.
†Subfam. Sciuravinae, new rank? (=†Sciuravidae Miller and Gidley, 1918, p. 442). M. Eoc.–U. Olig.; N.A. Olig.; As.
†*Sciuravus* Marsh, 1871. M.–U. Eoc.; N.A.
†*Tillomys* Marsh, 1872. M. Eoc.; N.A.
†*Taxymys* Marsh, 1872. M. Eoc.; N.A.
†*Prosciurus* Matthew, 1903. L.–U. Olig.; N.A., As.
†Subfam. Ischyromyinae Schlosser, 1911b, p. 425 (=†Ischyromynae Trouessart, 1880, p. 98). Olig.; N.A.
†*Ischyromys* Leidy, 1856. L.–U. Olig.; N.A.
†*Titanotheriomys* Matthew, 1910. L. Olig.; N.A.
†Subfam. Cylindrodontinae, new rank (=†Tsaganomyinae Matthew and Granger, 1923a, p. 4; †Cylindrodontidae Miller and Gidley, 1918, p. 440). L. Eoc.–L. Olig.; N.A. Olig.; As.
†*Mysops* Leidy, 1871. L.–M. Eoc.; N.A.
†*Pareumys* Peterson, 1919. U. Eoc.; N.A.
†*Cylindrodon* Douglass, 1902. L. Olig.; N.A.
†*Pseudocylindrodon* Burke, 1935. L. Olig.; N.A.
†*Ardynomys* Matthew and Granger, 1925. L. Olig.; N.A., As.
†*Cyclomylus* Matthew and Granger, 1923. Olig.; As.
†*Tsaganomys* Matthew and Granger, 1923. Olig.; As.
?†Cylindrodontinae *incertae sedis:*
†*Sespemys* Wilson, 1934. U. Olig.; N.A.
Fam. Aplodontidae Trouessart, 1897, p. 450 (=Haploodontini Brandt, 1855, pp. 145, 151; Haplodontidae Alston, 1876, p. 78). [Including †Allomyidae Marsh, 1877a, p. 253.] U. Eoc.–R.; N.A. L. Plioc.; As.
†*Eohaplomys* Stock, 1925. U. Eoc.; N.A.
†*Haplomys* Miller and Gidley, 1918. L. Mioc.; N.A.
†*Allomys* Marsh, 1877. L. Mioc.; N.A.
†*Meniscomys* Cope, 1879. L. Mioc.; N.A.
†*Liodontia* Miller and Gidley, 1918. M. Mioc.; N.A.
†*Pseudaplodon* Miller, 1927. L. Plioc.; As.
Aplodontia Richardson, 1829. Pleist.–R.; N.A. Sewellel, mountain "beaver."

†Fam. Mylagaulidae Cope, 1881d, p. 362. L. Mioc.–M. Plioc.; N.A.
†*Promylagaulus* McGrew, 1941. L. Mioc.; N.A.
†*Mylagaulodon* Sinclair, 1903. L. Mioc.; N.A.
†*Mesogaulus* Riggs, 1899. M.–U. Mioc.; N.A.
†*Ceratogaulus* Matthew, 1902. U. Mioc.; N.A.
†*Mylagaulus* Cope, 1878. U. Mioc.–L. Plioc.; N.A.
†*Epigaulus* Gidley, 1907. L. Plioc.; N.A.
†Fam. Protoptychidae Wood, 1937, p. 261 (=†Protoptychinae Schlosser, 1911b, p. 427). U. Eoc.; N.A.
†*Protoptychus* Scott, 1895. U. Eoc.; N.A.
†Fam. Eomyidae Depéret and Douxami, 1902, p. 71. [Including †Adjidaumidae Miller and Gidley, 1918, p. 434.] U. Eoc.–L. Mioc.; Eu. U. Eoc.–M. Olig.; N.A.
†*Eomys* Schlosser, 1884. U. Eoc.; Eu.
†*Omegodus* Pomel, 1854. L. Mioc.; Eu.
†*Rhodanomys* Depéret, 1902. U. Olig.; Eu.
†*Protadjidaumo* Burke, 1934. U. Eoc.; N.A.
†*Adjidaumo* Hay, 1899 (†*Gymnoptychus* of most authors).[1] L.–M. Olig.; N.A.
†*Paradjidaumo* Burke, 1934. L.–M. Olig.; N.A.
?Aplodontoidea *incertae sedis:*
†*Kansasimys* Wood, 1936. M. Plioc.; N.A.
Superfam. Sciuroidea Gill, 1872, p. 21.
Fam. Sciuridae Gray, 1821, p. 304. Mioc.–R.; Eu., N.A. Pleist.–R.; As. R.; S.A., Af. Squirrels.
Subfam. Sciurinae Baird, 1857a, p. 240. Mioc.–R.; Eu., N.A. R.; S.A., As., Af. Ground and tree squirrels.
Tribe Sciurini Burmeister, 1854, p. 145 (=Sciurinae *sensu stricto* of authors). Mioc.– R.; N.A., Eu. R.; S.A. European and American tree squirrels.
Sciurus Linnaeus, 1758. [Including (mostly as subgenera, all but *Tenes* in the Western Hemisphere) *Neosciurus* Trouessart, 1880; *Otosciurus* Nelson, 1899; *Hesperosciurus* Nelson, 1899; *Echinosciurus* Trouessart, 1880; *Baiosciurus* Nelson, 1899; *Parasciurus* Trouessart, 1880; *Leptosciurus* Allen, 1915; *Notosciurus* Allen, 1914; *Mesosciurus* Allen, 1915; *Guerlinguetus* Gray, 1821; *Macroxus* Cuvier, 1823; *Hadrosciurus* Allen, 1915; *Urosciurus* Allen, 1915; *Simosciurus* Allen, 1915; *Tenes* Thomas, 1909.] Pleist.–R.; Eu., As., N.A. *Sensu lato* also from the Miocene in Eu. and N.A. R.; S.A. Tree squirrels.
Syntheosciurus Bangs, 1902. R.; Cent. A.
Microsciurus Allen, 1895. R.; S.A., Cent. A.
Sciurillus Thomas, 1914. R.; S.A.
?Sciurini *incertae sedis:*
Rheithrosciurus Gray, 1867. R.; Borneo.
Tribe Tamiasciurini, new form (=Tamiasciurinae Pocock, 1923b, p. 237). Pleist.–R.; N.A.
Tamiasciurus Trouessart, 1880. Pleist.–R.; N.A. Red squirrel, chickaree.

[1] It appears that †*Gymnoptychus* Cope, 1873, as fixed by type, is synonymous with †*Ischyromys* Leidy, 1856, while †*Gymnoptychus* as used by Cope in 1874 and most later authors is, for the most part, the genus now properly called †*Adjidaumo*.

Tribe Funambulini, new form (=Funambulinae Pocock, 1923b, p. 237). R.; As., Af. African tree squirrels (and allied Asiatic genera).

Funambulus Lesson, 1832. [Including *Tamiodes* Pocock, 1923.] R.; As. Palm squirrel.

Ratufa Gray, 1867. R.; As. (Oriental) giant squirrels.

Protoxerus Major, 1893. [Including *Myrsilus* Thomas, 1909.] R.; Af. Oil-palm squirrels, African giant squirrels.

Epixerus Thomas, 1909. R.; Af.

Funisciurus Trouessart, 1880. R.; Af. Common African tree squirrel, isindi, (also other genera).

Paraxerus Major, 1893. [Including *Tamiscus* Thomas, 1918.] R.; Af. African bush squirrels, striped squirrels.

Heliosciurus Trouessart, 1880. [Including *Aethosciurus* Thomas, 1916.] R.; Af. Isindi.

Myosciurus Thomas, 1909. R.; Af. African pygmy (or dwarf) squirrel.

Tribe Callosciurini, new form (=Callosciurinae Pocock, 1923b, p. 239).[1] Pleist.–R.; As. Oriental tree squirrels.

Callosciurus Gray, 1867. [Including *Tomeutes* Thomas, 1915; *Tamiops* Allen, 1906.] R.; As.

Menetes Thomas, 1908. R.; As.

Rhinosciurus Gray, 1843. R.; As.

Lariscus Thomas and Wroughton, 1909 (=*Laria* Gray, 1867, *nec* Scopoli, 1763). R.; As.

Dremomys Heude, 1898. [Including *Zetis* Thomas, 1908.] R.; As.

Sciurotamias Miller, 1901. [Including *Rupestes* Thomas, 1922.] Pleist.–R.; As.

Glyphotes Thomas, 1898. R.; As. (Borneo).

Nannosciurus Trouessart, 1880. R.; S.E. As. Oriental pygmy (or dwarf) squirrel.

Tribe Xerini, new form (=Xerinae Osborn, 1910, p. 535). R.; Af. African ground squirrels.

Atlantoxerus Major, 1893. R.; N. Af.

Xerus Hemprich and Ehrenberg, 1832. [Including *Euxerus* Thomas, 1909; *Geosciurus* Smith, 1834.] R.; Af. African ground squirrels.

?Xerini, *incertae sedis:*

Spermophilopsis Blasius, 1884. R.; Cent. As.

Tribe Marmotini, new form (=Marmotinae Pocock, 1923b, p. 240; Arctomydae Gray, 1821, p. 303). M. Mioc.–R.; N.A. Pleist.–R.; Eu. R.; As. Northern ground squirrels.

Marmota Frisch, 1775 (=*Arctomys* Schreber, 1780). [Including *Marmotops* Pocock, 1922.] M. Plioc.–R.; N.A. Pleist.–R.; Eu., As. Marmot, woodchuck.

Cynomys Rafinesque, 1817. ?Plioc., Pleist.–R.; N.A. R.; As. Prairie "dog."

Citellus Oken, 1816 (=*Spermophilus* Cuvier, 1825). [Including *Otospermophilus* Brandt, 1844; *Ammospermophilus* Mer-

[1] Nannosciurinae Major, 1893b, pp. 187–189, is a prior name, the type genus of which is now placed in the Callosciurini, but its retention is inadvisable because the concept that it is still used to designate is radically different and because *Nannosciurus* is in no way a type of the tribe as here considered, but on the contrary is considered of somewhat doubtful pertinence to it.

riam, 1892; *Callospermophilus* Merriam, 1897; and other subgenera.] ?M. Mioc., Plioc.–R.; N.A. Pleist.–R.; Eu., As. Ground squirrel, spermophile, gopher, suslik, ziesel, etc.

Tamias Illiger, 1811. Pleist.–R.; N.A. Chipmunk, eastern chipmunk, hackee.

Eutamias Trouessart, 1880. Plioc.–R.; As. Pleist.–R.; N.A. R.; E. Eu. Chipmunk, western chipmunk, borunduk.

Subfam. Petauristinae, new rank? (= Petauristidae Miller, 1912, p. 940; Pteromidae Anderson, 1879, p. 278; Pteromyini Brandt, 1855, p. 157). Pleist.–R.; N.A. R.; Eu., As. Flying squirrels.

Petaurista Link, 1795 (= *Pteromys*[1] Cuvier, 1800). [Including *Aeromys* Robinson and Kloss, 1915.] Pleist.–R.; As. Taguan.

Eupetaurus Thomas, 1888. R.; As. (Kashmir). Woolly flying squirrel.

Sciuropterus[1] Cuvier, 1825. R.; Eu., As. (Old World) flying squirrel.

Glaucomys Thomas, 1908. Pleist.–R.; N.A. (American) flying squirrel.

Eoglaucomys Howell, 1915. R.; As. Himalayan flying squirrel.

Hylopetes Thomas, 1908. [Including *Petinomys* Thomas, 1908.] R.; S. As.

Aeretes Allen, 1940. R.; As. (China).

Trogopterus Heude, 1898. R.; As.

Belomys Thomas, 1908. R.; As.

Pteromyscus Thomas, 1908. R.; As.

Petaurillus Thomas, 1908. R.; S.E. As.

Iomys Thomas, 1908. R.; S.E. As.

Superfam. Geomyoidea Weber, 1904, p. 490 (=Saccomyoidea Gill, 1872, p. 21).

Fam. Geomyidae Gill, 1872, p. 21 (=Geomyina Bonaparte, 1850). M. Olig.–R.; N.A.

†Subfam. Entoptychinae Miller and Gidley, 1918, p. 434. L. Mioc.; N.A.

†*Entoptychus* Cope, 1878. L. Mioc.; N.A.

†*Pleurolicus* Cope, 1878. L. Mioc.; N.A.

†*Gregorymys* Wood, 1936. L. Mioc.; N.A.

†*Grangerimus* Wood, 1936. L. Mioc.; N.A.

Subfam. Geomyinae Baird, 1857, p. 366. L. Mioc.–R.; N.A. Pocket gophers.

†*Dikkomys* Wood, 1936. L. Mioc.; N.A.

†*Pliosaccomys* Wilson, 1936. M. Plioc.; N.A.

†*Plesiothomomys* Gidley and Gazin, 1933. Pleist.; N.A.

Geomys Rafinesque, 1817. Plioc.–R.; N.A. Eastern pocket gophers.

Thomomys Maximilian, 1839. U. Mioc.–R.; N.A. Western

[1] Some recent authors, including Ellerman, 1940, regretfully adopt *Pteromys* as the name for the genus here called *Sciuropterus*. The question is debatable, but it seems possible, if not necessary, to conclude that the type of *Pteromys* was fixed as a species of *Petaurista* in 1826 if not earlier, making *Pteromys* = *Petaurista* and leaving *Sciuropterus* as valid.

pocket gophers.
Pappogeomys Merriam, 1895. R.; N.A. (Mexico).
Cratogeomys Merriam, 1895. U. Plioc.–R.; N.A.
Platygeomys Merriam, 1895. R.; N.A. (Mexico).
Orthogeomys Merriam, 1895. R.; N.A. (Mexico, Cent. A.).
Heterogeomys Merriam, 1895. R.; N.A. (Mexico).
Macrogeomys Merriam, 1895. R.; Cent. A.
Zygogeomys Merriam, 1895. R.; N.A. (Mexico).
?Geomyidae *incertae sedis:*
†*Diplolophus* Troxell, 1923 (=†*Gidleumys* Wood, 1936). M. Olig.; N.A.
†*Griphomys* Wilson, 1940. U. Eoc.; N.A.
Fam. Heteromyidae Allen and Chapman, 1893, p. 233 (=Heteromyina Gray, 1868b, p. 200; Saccomyidae Baird, 1857, pp. 236, 365; Saccomyna Gray, 1843, pp. xxiv, 120). M. Olig.–R.; N.A. R.; northern S.A.
Subfam. Perognathinae Wood, 1935, p. 88 (=Perognathidinae Coues, 1875a, p. 277). ?M. Olig., L. Mioc.–R.; N.A.
†*Heliscomys* Cope, 1873.[1] L. Olig.–L. Mioc.; N.A.
†*Mookomys* Wood, 1931. L.–M. Mioc.; N.A.
†*Perognathoides* Wood, 1935. U. Mioc.–L. Plioc.; N.A.
Perognathus Maximilian, 1839. Mioc.–R.; N.A. Pocket "mice" (or "rats").
Microdipodops Merriam, 1891. R.; N.A. Dwarf pocket "rats."
Subfam. Dipodomyinae Coues, 1875a, p. 277. L. Plioc.–R.; N.A.
†*Cupidinomys* Wood, 1935. L.–U. Plioc.; N.A.
†*Prodipodomys* Hibbard, 1939. M. Plioc.; N.A.
Dipodomys Gray, 1841. U. Plioc.–R.; N.A. "Kangaroo rats."
Subfam. Heteromyinae Alston, 1876, p. 88. L. Mioc.–R.; N.A. R.; northern S.A.
†*Proheteromys* Wood, 1932. L.–M. Mioc.; N.A.
†*Peridiomys* Matthew, 1924. M.–U. Mioc.; N.A.
†*Diprionomys* Kellogg, 1910. L.–M. Plioc.; N.A.
Liomys Merriam, 1902. U. Plioc.–R.; N.A.
Heteromys Desmarest, 1817 (=*Saccomys* Cuvier, 1823). R.; Cent. A., northern S.A. Spiny (pocket) "mice."
†Subfam. Florentiamyinae Wood, 1936a, p. 41. L. Mioc.; N.A.
†*Florentiamys* Wood, 1936. L. Mioc.; N.A.
Superfam. Castoroidea Gill, 1872, p. 21.
Fam. Castoridae Gray, 1821, p. 302 (=Castorina Hemprich, 1820, p. 33). [Including †Castoroididae Allen, 1877, p. 419; †Chalicomyidae Miller and Gidley, 1918, p. 435.] L. Olig.–R.; N.A. U. Olig.–R.; Eu. U. Mioc.–R.; As.
Subfam. Castorinae Gray, 1825, p. 341 (=Castoridae *sensu stricto* of most recent authors). L. Olig.–R.; N.A. U. Mioc.–R.; Eu. L. Plioc.–R.; As.
†*Agnotocastor* Stirton, 1935. L.–U. Olig.; N.A.
†*Palaeocastor* Leidy, 1869 (included in †*Steneofiber* by most authors). L. Mioc.; N.A.

[1] According to Wood, 1935, the subfamily position of this genus is uncertain, but it is perhaps nearest to the Perognathinae. (In a later paper, Wood, 1939, placed different species of this one genus in all three subfamilies, an arrangement less fantastic than it appears at first sight, but still quite unacceptable.)

†*Euhapsis* Peterson, 1905. L. Mioc.; N.A.
†*Palaeomys* Kaup, 1832. [Including †*Chalicomys* Kaup, 1832.] U. Mioc.–L. Plioc.; Eu.
†*Sinocastor* Young, 1934. Plioc.; As.
Castor Linnaeus, 1758. Plioc.–R.; N.A., Eu., As. Beaver.
†Subfam. Castoroidinae Trouessart, 1880, p. 189 (=†Castoroididae Allen, 1877, p. 419). U. Olig.–Pleist.; Eu. Mioc.–Pleist.; N.A., As.
†*Steneofiber* Geoffroy, 1833. U. Olig.–M. Mioc.; Eu.
†*Monosaulax* Stirton, 1935 (included in †*Steneofiber* by most authors). L. Mioc.–L. Plioc.; N.A., Eu.
†*Eucastor* Leidy, 1858. [Including †*Sigmogomphius* Merriam, 1896.] L.–M. Plioc.; N.A.
†*Dipoides* Schlosser, 1902, *ex* Jager, 1835. Plioc.; Eu., N.A., As.
†*Amblycastor* Matthew, 1918. M.–U. Mioc.; N.A., As.
†*Procastoroides* Barbour and Schultz, 1937. U. Plioc.; N.A.
†*Castoroides* Foster, 1838. Pleist.; N.A.
†*Trogontherium* Fischer, 1809. [Including †*Conodontes* Laugel, 1862.] U. Plioc.–Pleist.; Eu. Pleist.; As.
†Fam. Eutypomyidae Miller and Gidley, 1918, p. 435. L.–M. Olig.; N.A.
†*Eutypomys* Matthew, 1905. L.–M. Olig.; N.A.

?SCIUROMORPHA *incertae sedis:*
Superfam. Anomaluroidea Gill, 1872, p. 21.
Fam. Anomaluridae Gill, 1872, p. 21 (=Anomalurina Gervais, 1849, p. 203). R.; Af.
Subfam. Anomalurinae Alston, 1875, p. 95. R.; Af.
Anomalurus Waterhouse, 1843. [Including *Anomalurella* Matschie, 1914; *Anomalurops* Matschie, 1914; *Anomalurodon* Matschie, 1914.] R.; Af. Scaly-tailed "squirrels."
Subfam. Zenkerellinae Matschie, 1898, p. 26 (=Idiuridae Miller and Gidley, 1918, p. 442. [Including Idiurinae Miller and Gidley, 1918, p. 442.] R.; Af.
Idiurus Matschie, 1894. R.; Af.
Zenkerella Matschie, 1898 (=*Aëthurus* De Winton, 1898). R.; Af.
?Anomaluroidea *incertae sedis:*
†Fam. Pseudosciuridae Zittel, 1893, p. 523 (=†Pseudosciurini Winge, 1887, pp. 108, 118). U. Eoc.–M. Olig.; Eu.
†*Suevosciurus* Dehm, 1937. U. Eoc.–M. Olig.; Eu.
†*Pseudosciurus* Hensel, 1856. U. Eoc.–L. Olig.; Eu.
†*Sciuroides* Major, 1873. U. Eoc.–L. Olig.; Eu.
†Fam. Theridomyidae Alston, 1876, pl. 4, pp. 75, 78. [Including †Archaeomyidae Schlosser, 1884, p. 327; †Nesokerodontidae Schlosser, 1884, p. 327; †Trechomyini Winge, 1887, pp. 108, 118; etc.] U. Eoc.–M. Olig.; Eu.
†*Trechomys* Lartet, 1869. U. Eoc.; Eu.
†*Theridomys* Jourdan, 1837. L.–M. Olig.; Eu.
†*Protechimys* Schlosser, 1884. ?L.–M. Olig.; Eu.
†*Archaeomys* Laizer and Parieu, 1839. M. Olig.; Eu.
†*Issiodoromys* Croizet, 1845. M. Olig.; Eu.
†*Nesokerodon* Schlosser, 1884. M. Olig.; Eu.
Cf. ?†Theridomyidae *incertae sedis:*
†*Phiomys* Osborn, 1908. Olig.; Af. (Egypt).

†*Metaphiomys* Osborn, 1908. Olig.; Af. (Egypt).
†*Paraphiomys* Andrews, 1914. L. Mioc.; Af.
†*Diamantomys* Stromer, 1922. L. Mioc.; Af.
†*Pomonomys* Stromer, 1922. L. Mioc.; Af.
†*Apodecter* Hopwood, 1929. L. Mioc.; Af.
†*Phthinylla* Hopwood, 1929. L. Mioc.; Af.
†*Tataromys* Matthew and Granger, 1923. U. Olig.; As.
†*Karakoromys* Matthew and Granger, 1923. U. Olig.; As.

Fam. Pedetidae Owen, 1847a, p. 242 (=Pedestina Gray, 1825, p. 342; Halamydae Gray, 1821, p. 303). L. Mioc., R.; Af.
†*Parapedetes* Stromer, 1926. L. Mioc.; Af.
Pedetes Illiger, 1811 (=*Helamys* Cuvier, 1817). Pleist.–R.; Af. Spring haas.

Suborder MYOMORPHA Brandt, 1855, p. 292.

Superfam. Muroidea[1] Miller and Gidley, 1918, p. 435 (=Myoidea Gill, 1872, p. 20).

Fam. Cricetidae Rochebrune, 1883, pp. 66, 153 (=Cricetinorum Fischer, 1817, p. 410). [Including Hesperomyidae Ameghino, 1889, p. 109 =Hesperomyinae Murray, 1866, p. 358; Nesomyidae Weber, 1904, p. 502=Nesomyinae Major, 1897, p. 718; Microtidae Cope, 1891a, p. 90=Arvicolidae Gray, 1821, p. 303; Gerbillidae De Kay, 1842, pp. xv, 70=Gerbillina Gray, 1825, p. 342; Merionidae Burmeister, 1850, p. 16 =Merionina Brandt, 1844, p. 231; Lophiomyidae Gill, 1872, p. 20; †Cricetodontidae Schaub, 1925, p. 5; †Anomalomyidae Schaub, 1925, p. 97; †Melissiodontidae Schaub, 1925, p. 97, etc.] Olig.–R.; N.A., Eu., As. Plioc.–R.; S.A. R.; Af. Pleist.–R.; Madagascar.

Subfam. Cricetinae Murray, 1866, p. 358 (=Cricetinorum Fischer, 1817, p. 410). [Including Hesperomyinae Murray, 1866, p. 358; †Cricetodontidae Schaub, 1925, p. 5; †Anomalomyidae Schaub, 1925, p. 97; †Melissiodontidae Schaub, 1925, p. 97; Sigmodontinae Thomas, 1897, p. 1019; Neotominae Merriam, 1894, p. 228; †Cricetopidae Matthew and Granger, 1923a, p. 1.] M. Olig.–R.; N.A. U. Plioc.–R.; S.A. L. Olig.–R.; Eu. U. Olig., L. Plioc.–R.; As. R.; Af.

†Tribe Eumyini, new name. M. Olig.–L. Mioc., ?U. Mioc., ?L. Plioc.; N.A. U. Olig.; As.
†*Eumys* Leidy, 1856. M.–U. Olig.; N.A. U. Olig.; As.
†*Leidymys* Wood, 1936. M. Olig.–L. Mioc.; N.A.
†*Scottimus* Wood, 1937. U. Olig.; N.A.

†Eumyini or Hesperomyini *incertae sedis:*
†*Paciculus* Cope, 1879. L. Mioc.; N.A.
†*Schaubeumys* Wood, 1935. L. Mioc.; N.A.
†*Horatiomys* Wood, 1935. U. Mioc.; N.A.
†*Copemys* Wood, 1936. L. Plioc.; N.A.

Tribe Hesperomyini, new form (=Hesperomyinae Murray, 1866, p. 358). L. Plioc.–R.; N.A. U. Plioc.–R.; S.A. New World mice.

[1] Almost all authors use "Myoidea," constructed on the Greek root, but all other family and superfamily names use Latin or neo-Latin roots, and the Rules explicitly demand this. The Latin root of *Mus* is *mur-*, not *my-*. It was spelled "Muroidae" by Miller and Gidley.

†*Macrognathomys* Hall, 1930. L. Plioc.; N.A.
Oryzomys Baird, 1857. [Including *Nesoryzomys* Heller, 1904; *Oligoryzomys* Bangs, 1900; *Thallomyscus* Thomas, 1926; *Oecomys* Thomas, 1906; and other subgenera and synonyms.] Pleist.-R.; N.A., S.A., Galápagos. Rice rat.
†*Megalomys* Trouessart, 1881. Sub-R.; W. Indies.
Melanomys Thomas, 1902. R.; S.A.
Neacomys Thomas, 1900. R.; S.A., Cent. A.
Scolomys Anthony, 1924. R.; S.A.
Nectomys Peters, 1861. R.; S.A., Cent. A.
Rhipidomys Tschudi, 1844. R.; S.A., Cent. A.
Thomasomys Coues, 1884. [Including *Inomys* Thomas, 1917; *Delomys* Thomas, 1917; *Aepeomys* Thomas, 1898.] R.; S.A.
Phaenomys Thomas, 1917. R.; S.A.
Chilomys Thomas, 1897. R.; S.A.
Tylomys Peters, 1866. R.; S.A.
Ototylomys Merriam, 1901. R.; Cent. A.
Nyctomys De Saussure, 1860. R.; Cent. A.
Otonyctomys Anthony, 1929. R.; Mexico.
Rhagomys Thomas, 1917. R.; S.A.
Reithrodontomys Giglioli, 1873. Pleist.-R.; N.A. R.; northern S.A. Harvest mouse.
Peromyscus Gloger, 1841. L. Plioc.[1]-R.; N.A. White-footed mouse, deer mouse, etc.
Baiomys True, 1894. U. Plioc.-R.; N.A.
Onychomys Baird, 1857. U. Plioc.-R.; N.A. Grasshopper mouse.
†*Symmetrodontomys* Hibbard, 1941. U. Plioc.; N.A.
Akodon Meyen, 1833. [Including *Chalcomys* Thomas, 1916; *Thalpomys* Thomas, 1916; *Deltamys* Thomas, 1917; *Hypsimys* Thomas, 1918; *Thaptomys* Thomas, 1918; *Bolomys* Thomas, 1916; *Abrothrix* Waterhouse, 1837; *Chraeomys* Thomas, 1916.] R.; S.A.
Zygodontomys Allen, 1897. R.; S.A., Cent. A.
Microxus Thomas, 1909. R.; S.A.
Podoxymys Anthony, 1929. R.; S.A.
Lenoxus Thomas, 1909. R.; S.A.
Oxymycterus Waterhouse, 1873. Pleist.-R.; S.A.
Blarinomys Thomas, 1896. Pleist.-R.; S.A.[2]
Notiomys Thomas, 1890. [Including *Geoxus* Thomas, 1919; *Chelemys* Thomas, 1903.] R.; S.A.
Scapteromys Waterhouse, 1837. R.; S.A.
Scotinomys Thomas, 1913. R.; Cent. A.
Hesperomys Waterhouse, 1839. [Including *Paralomys* Thomas, 1926.] R.; S.A.
Eligmodontia Cuvier, 1837. U. Plioc.-Pleist.; N.A. R.; S.A.
Graomys Thomas, 1916. R.; S.A.
Phyllotis Waterhouse, 1873. [Including *Auliscomys* Osgood, 1915; *Galenomys* Thomas, 1916.] Pleist.-R.; S.A.

[1] As is also true of some other apparently long-lived rodent genera, the older records are probably not this genus, *sensu stricto*, but are doubtless allied to it and have not been separated.
[2] Discovered as a fossil and later found living.

†*Necromys* Ameghino, 1889. Pleist.; S.A.
†*Ptyssophorus* Ameghino, 1889. Pleist.; S.A.
†*Tretomys* Ameghino, 1889. Pleist.; S.A.
†*Bothriomys* Ameghino, 1889. Pleist.; S.A.
Irenomys Thomas, 1919. R.; S.A.
Chinchillula Thomas, 1898. R.; S.A.
Neotomys Thomas, 1894. R.; S.A.
†*Proreithrodon* Ameghino, 1908. U. Plioc.; S.A.
Reithrodon Waterhouse, 1837. Pleist.–R.; S.A.
Euneomys Coues, 1874. R.; S.A.
Chelemyscus Thomas, 1925. R.; S.A.
Holochilus Brandt, 1835. Pleist.–R.; S.A.
Sigmodon Say and Ord, 1825. U. Plioc.–R.; N.A. R.; S.A. Cotton rat.
Sigmomys Thomas, 1901. R.; S.A.
Andinomys Thomas, 1902. R.; S.A.
Neotomodon Merriam, 1898. R.; Mexico.
Neotoma Say and Ord, 1825. [Including *Teanopus* Merriam, 1903; *Hodomys* Merriam, 1894.] U. Plioc.–R.; N.A. Wood rat, pack rat.
†*Parahodomys* Gidley and Gazin, 1933. U. Plioc.–Pleist.; N.A.
Nelsonia Merriam, 1897. R.; Mexico.
Xenomys Merriam, 1892. R.; Mexico.
Ichthyomys Thomas, 1893. R.; S.A.
Anotomys Thomas, 1906. R.; S.A.
Daptomys Anthony, 1929. R.; S.A.
Rheomys Thomas, 1906. R.; S.A.
Neusticomys Anthony, 1921. R.; S.A.

†Tribe Cricetopini, new form (=†Cricetopidae Matthew and Granger, 1923a, p. 1). U. Olig.; As.
†*Cricetops* Matthew and Granger, 1923. U. Olig.; As.
†*Selenomys* Matthew and Granger, 1923. U. Olig.; As.
†*Kanisamys* Wood, 1937. L.–M. Plioc.; As.

†Tribe Cricetodontini, new form (=†Cricetodontidae Schaub, 1925, pp. 1, 5). L. Olig.–L. Plioc.; Eu. ?Olig., L. Plioc.; As. M. Olig.; N.A.
†*Cricetodon* Lartet, 1851. L. Olig.–L. Plioc.; Eu. M. Olig.; N.A. L. Olig.; ?As.
†*Paracricetodon* Schaub, 1925. L. Olig.; Eu.
†*Heterocricetodon* Schaub, 1925. L. Olig.; Eu.
†*Plesiodipus* Young, 1927 (=†*Plesiocricetodon* Schaub, 1934).[1] L. Plioc.; As.
†*Neocricetodon* Schaub, 1934. L. Plioc.; As.
†*Paracricetulus* Young, 1927. L. Plioc.; As.

?Cricetodontini *incertae sedis* (=†Melissiodontidae Schaub, 1925, p. 97; †Anomalomyidae Schaub, 1925, p. 97):
†*Melissiodon* Schaub, 1920. L. Olig.–M. Mioc.; Eu.
†*Anomalomys* Gaillard, 1900. U. Mioc.; Eu.

Tribe Cricetini, new form,[2] from Cricetinorum Fischer, 1817, p. 410 (*sensu stricto*). L. Plioc.–R.; Eu., As. R.; Af. Hamsters.

[1] Proposed because †*Plesiodipus* is not a dipodid, but such changes are not valid.
[2] It should be noted that Winge used this term in 1887, p. 109, apparently as a subfamily of the Muridae.

†*Sinocricetus* Schaub, 1930. L. Plioc.; As.
†*Nannocricetus* Schaub, 1934. L. Plioc.; As.
†*Pseudomeriones* Schaub, 1934. L. Plioc.; As.
†*Cricetinus* Zdansky, 1928. Pleist.; As.
Calomyscus Thomas, 1905. R.; As.
Phodopus Miller, 1910. [Including *Cricetiscus* Thomas, 1917.] Pleist.; Eu. R.; As.
Cricetus Leske, 1779. L. Plioc.–R.; Eu. R.; W. As.
†*Allocricetus* Schaub, 1930. Pleist.; Eu.
Cricetulus Milne Edwards, 1867. [Including *Tscherskia* Ognev, 1914; *Cansumys* Allen, 1928.] Pleist.–R.; Eu. L. Plioc.–R.; As.
Mesocricetus Nehring, 1898. R.; E. Eu., W. As.
Mystromys Wagner, 1841. R.; Af.

Tribe Myospalacini Lilljeborg, 1866, p. 25 (=Myotalpinae Miller, 1896, p. 8; Siphneinae Gill, 1872, p. 20). U. Mioc.–R.; As. "Mole" mice, sokhors.
†*Prosiphneus* Teilhard de Chardin, 1926 (=†*Myotalpavus* Miller, 1927). U. Mioc.–L. Plioc.; As.
Myospalax Laxmann, 1769 (=*Myotalpa* Kerr, 1792; *Siphneus* Brants, 1827). Plioc.–R.; As.

Cricetinae *incertae sedis:*
†*Lophocricetus* Schlosser, 1924. L. Plioc.; As.
†*Microtodon* Miller, 1927. L. Plioc.; As.
†*Anatolomys* Schaub, 1934. L. Plioc.; As.
†*Trilophomys* Depéret, 1892 (=†*Lophiomys* Depéret, 1890, *nec* Milne Edwards, 1867).

Subfam. Nesomyinae Major, 1897, p. 718. Pleist.–R.; Madagascar. Malagasy rats.
Macrotarsomys Milne Edwards and Grandidier, 1898. Pleist.[1] R.; Madagascar.
Nesomys Peter, 1870 (=*Hallomys* Jentink, 1879). R.; Madagascar.
†*Majoria* Thomas, 1915 (=†*Myoryctes* Major, 1908, *nec* Leuckart, 1863). Pleist.: Madagascar.
Brachytarsomys Günther, 1875. R.; Madagascar.
Eliurus Milne Edwards, 1885. R.; Madagascar.
Gymnuromys Major, 1896. R.; Madagascar.
Hypogeomys Grandidier, 1869. Pleist.–R.; Madagascar.
Brachyuromys Major, 1896. R.; Madagascar.

Subfam. Lophiomyinae Thomas, 1897, p. 1019 (=Lophiomyidae Gill, 1872, p. 20). R.; Af.
Lophiomys Milne Edwards, 1867. R.; Af. Maned rat, crested hamster.

Subfam. Microtinae Miller, 1896, p. 8 (=Microtidae Cope, 1891a, p. 90; Arvicolidae Gray, 1821, p. 303). U. Mioc.–R.; N.A. Plioc.–R.; Eu., As. R.; N. Af.

Tribe Lemmini, new form (=Lemmi Miller, 1896, p. 8). U. Plioc.–R.; N.A. Pleist.–R.; Eu., As. Lemmings.
†*Pliolemmus* Hibbard, 1938. U. Plioc.; N.A.

[1] Or sub-Recent, like the other Madagascar mammalian fossils. *Macrotarsomys* was first found fossil, but was not named until three years later when the living animals had also been found.

Dicrostonyx Gloger, 1841. Pleist.–R.; Eu., As. R.; N.A. Collared lemming, snow lemming.
Synaptomys Baird, 1857. U. Plioc.–R.; N.A. Bog lemming, lemming mouse.
Myopus Miller, 1910. R.; Eu., As.
Lemmus Link, 1795 (= *Myodes* Pallas, 1811). Pleist.–R.; Eu. R.; As., N.A. Lemming.
Tribe Microtini, new form (= Microti Miller, 1896, p. 8). U. Mioc.–R.; N.A. Plioc.–R.; Eu., As. R.; N. Af. Voles.
†*Poamys* Matthew, 1924. U. Mioc.; N.A.
†*Microtoscoptes* Schaub, 1934. U. Plioc.; As.
†*Goniodontomys* Wilson, 1937. M. Plioc.; N.A.
†*Ogmodontomys* Hibbard, 1941. U. Plioc.; N.A.
†*Sycium* Cope, 1899. Pleist.; N.A.
†*Anaptogonia* Cope, 1871. Pleist.; N.A.
Clethrionomys Tilesius, 1850 (= *Evotomys* Coues, 1874; *Hypudaeus* in Winge and various authors, but not *Hypudaeus* Illiger, 1811). [Including *Neoaschizomys* Tokuda, 1935.] Pleist.–R.; Eu., N.A., As. Red-backed mice or voles.
Aschizomys Miller, 1898. R.; As. (Bering Strait).
Eothenomys Miller, 1896. Pleist.–R.; As.
Anteliomys Miller, 1896. R.; As. (China).
Alticola Blanford, 1881. Pleist.–R.; As.
Hyperacrius Miller, 1896. R.; As. (India).
Dolomys Nehring, 1898. [Including †*Pliomys* Mehely, 1914; †*Apistomys* Mehely, 1914.] U. Plioc.–R.[1]; Eu.
†*Cosomys* Wilson, 1932. U. Plioc.; N.A.
†*Mimomys* Major, 1902. Plioc.–Pleist.; Eu. U. Plioc.; N.A. Pleist.; As.
Arvicola Lacépède, 1799. Pleist.–R.; Eu., As. Water vole, vole.
†*Pliopotamus* Hibbard, 1938 (= †*Neondatra* Hibbard, 1938). U. Plioc.; N.A.
Ondatra Link, 1795 (= *Fiber* Cuvier, 1800). U. Plioc.–R.; N.A. R.; Eu. (introduced). Muskrat.
Neofiber True, 1884. ?U. Plioc., Pleist.–R.; N.A. Round-tailed muskrat, Florida water rat.
Phenacomys Merriam, 1889. U. Plioc.–R.; N.A. "Lemming" mouse and tree mouse.
Pitymys McMurtrie, 1831. Pleist.–R.; N.A., Eu., As. Pine mouse.
Blanfordimys Argyropulo, 1933. R.; Cent. As.
†*Allophaiomys* Kormos, 1932. U. Plioc.; Eu.
Microtus Schrank, 1798. [Including *Pedomys* Baird, 1857; *Orthriomys* Merriam, 1898; *Chilotus* Baird, 1857; *Herpetomys* Merriam, 1898; *Neodon* Hodgson, 1849; *Phaiomys* Blyth, 1863; *Proedromys* Thomas, 1911; *Lasiopodomys* Lataste, 1887; etc.] Pleist.–R.; N.A., Eu. R.; N. Af. Meadow mouse, field mouse, (common) vole.
†*Tyrrhenicola* Major, 1905. Pleist.; Eu.
Lagurus Gloger, 1841. R.; N.A., As. U. Plioc.; Eu.

[1] This genus is another first known as a fossil and later found living.

Prometheomys Satunin, 1901. R.; Caucasus.

Tribe Ellobiini, new form (=Ellobii Weber, 1928, p. 284; Ellobiinae Gill, 1872, p. 20). U. Plioc.; Eu. R.; As., E. Eu.

†*Ungaromys* Kormos, 1932. U. Plioc.; Eu.

Ellobius Fischer, 1814. R.; As., E. Eu. "Mole" lemming.

Subfam. Gerbillinae Alston, 1876, p. 81 (=Gerbillina Gray, 1825, p. 342; Merionina Brandt, 1844, p. 231). Plioc.–R.; As. R.; Af., E. Eu. Gerbils, sand rats, antelope rats.

Gerbillus Desmarest, 1804. [Including *Dipodillus* Lataste, 1881; *Microdillus* Thomas, 1910.] Plioc.–R.; As. R.; Af.

Tatera Lataste, 1882. R.; Af., As.

Taterillus Thomas, 1910. R.; Af.

Desmodillus Thomas and Schwann, 1904. [Including *Desmodilliscus* Wettstein, 1917.] R.; Af.

Pachyuromys Lataste, 1880. R.; Af.

Ammodillus Thomas, 1904. R.; Af.

Meriones Illiger, 1811. R.; As., E. Eu., N. Af.

Brachiones Thomas, 1925. R.; As.

Psammomys Cretschmar, 1828. R.; N. Af., W. As. Sand rats.

Rhombomys Wagner, 1841. R.; As., E. Eu.

Fam. Spalacidae Gray, 1821, p. 303. U. Plioc.–R.; Eu. R.; W. As., Af. "Mole" rats.

†*Pliospalax* Kormos, 1932. Plioc.; Eu.

†*Prospalax* Mehely, 1908. U. Plioc.; Eu.

Spalax Gueldenstaedt, 1770. R.; E. Mediterranean region.

Fam. Rhizomyidae Miller and Gidley, 1918, p. 437 (=Rhizomyinae Thomas, 1897, p. 1021; Rhizomyini Winge, 1887, pp. 109, 125). U. Olig.; Eu. U. Mioc.–R.; As. Pleist.–R.; Af. Bamboo rats.

†*Rhizospalax* Miller and Gidley, 1919. U. Olig.; Eu.

†*Bramus* Pomel, 1892. Pleist.; N. Af.

Tachyoryctes Rüppell, 1835. R.; Af.

†*Tachyorctoides* Bohlin, 1937. U. Olig.; As.

†*Protachyoryctes* Hinton, 1933. U. Plioc.; As.

†*Pararhizomys* Teilhard de Chardin and Young, 1931. L. Plioc.; As.

Rhizomys Gray, 1831. [Including *Nyctocleptes* Temminck, 1832.] U. Mioc., ?M. Plioc.–R.; As.

Cannomys Thomas, 1915. R.; As.

Fam. Muridae Gray, 1821, p. 303 (=Rattidae Burnett, 1830a, p. 350). Plioc.–R.; Eu., As. Pleist.–R.; Aus. R.; native in Old World, introduced everywhere.

Subfam. Murinae Murray, 1866, p. 359 (=Murina Illiger, 1811, p. 84). Plioc.–R.; Eu., As. Pleist.–R.; Aus. R.; native in Eu., As., Af., Aus., introduced everywhere.

Hapalomys Blyth, 1859. R.; S. As.

Vandeleuria Gray, 1842. R.; As. Asiatic tree mice.

†*Rhagamys* Major, 1905. Pleist.; Mediterranean.

Micromys Dehne, 1841. Pleist.–R.; As. R.; Eu. Dwarf mouse.

†*Parapodemus* Schaub, 1938. L. Plioc.–Pleist.; Eu. L. Plioc.; ?As.

†*Anthracomys* Schaub, 1938. L. Plioc.; Eu.

†*Progonomys* Schaub, 1938. L. Plioc.; Eu., ?As.

†*Stephanomys* Schaub, 1938. M. Plioc.; Eu. ?L. Plioc., Pleist.; As.

Apodemus Kaup, 1829. Pleist.–R.; Eu., As., N. Af. (Old World) field mice.

Thamnomys Thomas, 1907. R.; Af.

Grammomys Thomas, 1915. R.; Af.

Carpomys Thomas, 1895. R.; Philippines. Fruit rat.

Batomys Thomas, 1895. R.; Philippines. Bush rat.

Pithecheir[1] Cuvier, 1838. R.; E. Indies.

Hyomys Thomas, 1903. R.; New Guinea.

Conilurus Ogilby, 1838 (=*Hapalotis* Lichtenstein, 1829, *nec* Hübner, 1816). R.; Aus. "Jerboa" rat.

Zyzomys Thomas, 1909. R.; Aus.

Laomys Thomas, 1909. R.; Aus.

Mesembriomys Thomas, 1909. R.; Aus.

Oenomys Thomas, 1904. R.; Af.

Ammomys Thomas, 1906. R.; Aus.

Mylomys Thomas, 1906. R.; Af.

Dasymys Peters, 1875. R.; Af. Shaggy-haired rats.

Arvicanthis Lesson, 1842. R.; Af. Striped mouse, kusu.

Hadromys Thomas, 1911. R.; S.E. As.

Golunda Gray, 1837. R.; As.

Pelomys Peters, 1852.[2] R.; Af.

Lemniscomys Trouessart, 1881. R.; Af.

Rhabdomys Thomas, 1916. R.; Af.

Hybomys Thomas, 1910. R.; Af.

Millardia Thomas, 1911. [Including *Grypomys* Thomas, 1911.] R.; As.

Pyromys Thomas, 1911. R.; S. As.

Dacnomys Thomas, 1916. R.; S. As.

Eropeplus Miller and Hollister, 1921. R.; E. Indies.

Stenocephalemys Frick, 1914. R.; Abyssinia.

Aethomys Thomas, 1915. R.; Af.

Thallomys Thomas, 1920. R.; Af.

Rattus Frisch, 1775[3] (=*Epimys* Trouessart, 1881). [Including *Lenothrix* Miller, 1903; *Tarsomys* Mearns, 1905; *Limnomys* Mearns, 1905; *Bullimus* Mearns, 1905; *Bunomys* Thomas, 1910; *Stenomys* Thomas, 1910; *Cremnomys* Wroughton, 1912; *Dephomys* Thomas, 1926; *Hylomyscus* Thomas, 1926; *Mastomys* Thomas, 1915; and others.] ?Plioc., Pleist.–R.; As. R.; native to the Old World, world wide by introduction. Common rats, the house rat, etc. (This is the most varied genus of mammals, with more than 550 named forms currently recognized.)

[1] Numerous attempts, such as "*Pithecochirus*," have been made to smooth out this somewhat uncouth name, but its original spelling is valid.

[2] Often and perhaps better included in *Golunda*.

[3] *Rattus* was used more or less in the present sense by Frisch in 1775 and by Zimmermann in 1777, but it is uncertain whether either of these should be considered valid. *Rattus* was applied to a species of *Arvicanthis* by Donovan in 1827, and it has sometimes been supposed that *Rattus* should, therefore, apply to that genus and not to the house rat and its allies. On this basis Trouessart gave the name *Epimys* to the latter, and this name was widely used. Most recent authors, however, consider that *Rattus* as applied to the true common rats can be dated at least from Fischer in 1803 if not from Frisch, and hence is valid, with *Epimys* as a true synonym and *Arvicanthis* as the valid name for a quite distinct genus.

Nilopegamys Osgood, 1928. R.; Af.
Tryphomys Miller, 1910. R.; Philippines.
Gyomys Thomas, 1910. R.; Aus.
Leporillus Thomas, 1906. R.; Aus.
Pseudomys Gray, 1832. R.; Aus.
Apomys Mearns, 1905. R.; Philippines.
Melomys Thomas, 1922. [Including *Solomys* Thomas, 1922.] R.; E. Indies, Aus.
Uromys Peters, 1867. [Including *Cyromys* Thomas, 1910.] R.; E. Indies, Aus.
Coelomys Thomas, 1915. R.; Ceylon.
Malacomys Milne Edwards, 1877. R.; Af.
Haeromys Thomas, 1911. R.; E. Indies.
Chiromyscus Thomas, 1925. R.; S.E. As.
Zelotomys Osgood, 1910. R.; Af.
Muriculus Thomas, 1902. R.; Af.
✓ *Mus* Linnaeus, 1758. [Including *Leggada* Gray, 1837; *Tautatus* Kloss, 1917; and others.] ?Plioc., Pleist.–R.; Eu. Pleist.–R.; As. R.; world wide as introduced, native to the Old World. Common mice, the house mouse, etc.
Mycteromys Robinson and Kloss, 1918. R.; E. Indies.
Leggadina Thomas, 1910. R.; Aus.
Colomys Thomas and Wroughton, 1907. R.; Af.
Nesoromys Thomas, 1922. R.; E. Indies.
Crunomys Thomas, 1897. R.; Philippines.
Macruromys Stein, 1933. R.; E. Indies.
Lorentzimys Jentink, 1911. R.; E. Indies.
Lophuromys Peters, 1874 (=*Lasiomys* Peters, 1866, *nec* Burmeister, 1854). R.; Af.
Leimacomys Matschie, 1893. R.; Af.
Notomys Lesson, 1842. [Including *Ascopharynx* Waite, 1900 =*Thylacomys* Waite, 1898, *nec* Owen, 1840.] R.; Aus. "Jerboa" rat (one of several genera so called).
Mastacomys Thomas, 1882. Pleist.–R.; Aus. "Jerboa" rat.
Echiothrix Gray, 1867 (=*Craurothrix* Thomas, 1896). R.; E. Indies.
✓ *Acomys* Geoffroy, 1838 (=*Acanthomys* Lesson, 1842). Plioc.; Eu. R.; Af., W. As., Mediterranean. Spiny mouse.
Uranomys Dollman, 1909. R.; Af.
✓ *Bandicota* Gray, 1873. [Including *Gunomys* Thomas, 1907.] R.; As. "Bandicoot" rat.
Nesokia Gray, 1842 (=*Spalacomys* Peters, 1861). Pleist.–R.; As. Pest rat.
Beamys Thomas, 1909. R.; Af.
Saccostomus Peters, 1846 (=*Eosaccomys* Palmer, 1903). R.; Af.
✓ *Cricetomys* Waterhouse, 1840. R.; Af. "Hamster" rat.
Anisomys Thomas, 1903. R.; New Guinea.

Subfam. Dendromurinae Allen, 1939a, p. 349 (=Dendromyinae Alston, 1876, p. 82; Deomyinae Lydekker, 1889, p. 1418). R.; Af. African tree mice.

Dendromus[1] Smith, 1829. R.; Af.
Malacothrix Wagner, 1843. R.; Af.
Prionomys Dollman, 1910. R.; Af.
Petromyscus Thomas, 1926. R.; Af.
Steatomys Peters, 1846. R.; Af.
Deomys Thomas, 1888. R.; Af.
Subfam. Otomyinae Thomas, 1897, p. 1017. R.; Af.
Otomys Cuvier, 1823. [Including *Oreomys* Heuglin, 1877; *Myotomys* Thomas, 1918.] R.; Af.
Parotomys Thomas, 1918. R.; Af.
Subfam. Phloeomyinae Alston, 1876, p. 81. Pleist.–R.; E. Indies. R.; As.
†*Coryphomys* Schaub, 1937. Pleist.; E. Indies.
Lenomys Thomas, 1898. R.; E. Indies.
Pogonomys Milne Edwards, 1877. [Including *Chiroromys* Thomas, 1888.] R.; New Guinea.
Chiropodomys Peters, 1868. [Including *Insulaemus* Taylor, 1934.] R.; As.
Mallomys Thomas, 1898. R.; New Guinea.
Phloeomys[2] Waterhouse, 1839. R.; Philippines. Rind rat.
Crateromys Thomas, 1895. R.; Philippines.
Subfam. Rhynchomyinae Thomas, 1897, p. 1017. R.; E. Indies.
Rhynchomys Thomas, 1895. R.; Philippines. "Shrew" rat.
Subfam. Hydromyinae Alston, 1876, p. 80 (=Hydromina Gray, 1825, p. 341). R.; Aus., Philippines. Water rats.
Chrotomys Thomas, 1895. R.; Philippines.
Celaenomys Thomas, 1898. R.; Philippines.
Crossomys Thomas, 1907. R.; New Guinea.
Xeromys Thomas, 1889. R.; Aus.
Hydromys Geoffroy, 1805. R.; Aus. Australian water rat.
Parahydromys Poche, 1906 (=*Drosomys* Thomas, 1906; *Limnomys* Thomas, 1906, *nec* Mearns, 1905). R.; Aus.
Leptomys Thomas, 1897. R.; New Guinea.
Pseudhydromys Rummler, 1934. R.; New Guinea.
?Muroidea *incertae sedis:*
†*Palustrimus* Wood, 1935. L. Mioc.; N.A.
Superfam. Gliroidea, new name? (=Myoxoidea Gill, 1872, p. 21).
Fam. Gliridae Thomas, 1897, p. 1016 (=Myoxidae Waterhouse, 1839b, p. 184; Myosidae Gray, 1821, p. 303; Muscardinidae Palmer, 1899, p. 413).[3] ?Eoc., ?Olig., Mioc.–R.; Eu. R.; As., Af.
Subfam. Glirinae Thomas, 1897, p. 1016 (=Myoxinae Huxley, 1872,

[1] Smith spelled this *Dendromus*, but it soon acquired the spelling *Dendromys* (and for the subfamily name, the spelling Dendromyinae). In recent literature the original spelling has been generally followed.

[2] Usually, but incorrectly, spelled *Phlaeomys*.

[3] Older authors usually called this family Myoxidae, and most recent authors call it Muscardinidae. Myoxidae is invalid because *Myoxus* is a synonym of *Glis*. Muscardinidae was proposed to replace Gliridae Thomas, 1897, on grounds of preoccupation by Gliridae Ogilby, 1837. But in my opinion Gliridae Ogilby, being based on "*Cheiromys*" (*Daubentonia*), never had any standing in nomenclature and cannot preoccupy an otherwise valid later name. Moreover preoccupation is not strictly deterrent for family names. Gliridae in the literature of the last 40 years is always Gliridae Thomas. Gliridae Ogilby, as far as I can discover, has never been used by any later author and is virtually forgotten now. *Glis*, not the relatively aberrant *Muscardinus*, is the truly typical member of the family as it has always been considered by students. I therefore return to the name Gliridae.

p. 369; Muscardininae Palmer, 1904, p. 859). ?Eoc., ?Olig., Mioc.–R.; Eu. R.; As., N. Af.

†*Caenomys* Lydekker, 1885, *ex* Bravard. L. Mioc.; Eu.

†*Brachymys* Meyer, 1847 (=†*Micromys* Meyer, 1846, *nec* Dehne, 1841). Mioc.; Eu.

†*Leithia* Lydekker, 1896. Pleist.; Malta.

†*Hypnomys* Bate, 1918. Pleist.; Balearics.

Glis Brisson, 1762 (=*Myoxus* Zimmermann, 1780). ?Eoc., ?Olig., Mioc.–R.; Eu. (Common) dormouse.

Muscardinus Kaup, 1829. Pleist.–R.; Eu. R.; W. As. Dormouse, hazel "mouse."

Eliomys Wagner, 1843. Mioc.–R.; Eu. R.; N. Af., W. As. Lerot, garden dormouse.

Dryomys Thomas, 1906 (=*Dyromys* Thomas, 1907).[1] R.; As., E. Eu. Asiatic dormouse, tree dormouse.

Glirulus Thomas, 1905. R.; Japan. Japanese dormouse.

Myomimus Ognev, 1924. R.; As.

Subfam. Graphiurinae Palmer, 1899, p. 413 (=Graphiurini Winge, 1887, pp. 109, 123; Graphiuridae Miller and Gidley, 1918, p. 440). R.; Af. African dormice.

Graphiurus Smuts, 1832. [Including *Claviglis* Jentink, 1888; *Gliriscus* Thomas and Hinton, 1925; *Aethoglis* Allen, 1936.] R.; Af.

Fam. Platacanthomyidae Miller and Gidley, 1918, p. 437 (=Platacanthomyinae Alston, 1876, p. 81). R.; As. Spiny dormice.

Platacanthomys Blyth, 1859. R.; As.

Typhlomys Milne Edwards, 1877. R.; As.

Fam. Seleviniidae Argyropulo and Vinogradov, 1939, p. 82. R.; As.

Selevinia Argyropulo and Vinogradov, 1939. R.; As.

Superfam. Dipodoidea Weber, 1904, pp. 490, 500.

Fam. Zapodidae Coues, 1875b, p. 253. [Including Sminthidae Schulze, 1890, p. 24=Sicistidae Weber, 1928, p. 279.] Olig., Pleist.–R.; Eu. L. Plioc.–R.; As. M. Plioc.–R.; N.A. Jumping "mice."

Subfam. Sicistinae Allen, 1901, p. 185 (=Sminthinae Murray, 1866, p. 360). Olig., Pleist.–R.; Eu. L. Plioc.–R.; As.

†*Plesiosminthus* Viret, 1926. Olig.; Eu.

†*Heterosminthus* Schaub, 1930. L. Plioc.; As.

Sicista Gray, 1827 (=*Sminthus* Nordmann, 1839, *ex* Nathusius). Pleist.–R.; Eu., As. Striped "mouse," birch "mouse."

Subfam. Zapodinae Trouessart, 1880, p. 168. M. Plioc.–R.; N.A. R.; As.

†*Pliozapus* Wilson, 1936. M. Plioc.; N.A.

Zapus Coues, 1875. [Including *Eozapus* Preble, 1899.] Pleist.–R.; N.A. R.; As. (China). Jumping "mouse," kangaroo "mouse."

Napaeozapus Preble, 1899. Pleist.–R.; N.A. (American) jumping "mouse."

[1] Thomas proposed *Dyromys* on grounds of preoccupation of the prior name by *Dryomys* Philippi, 1900, but on his own showing and by any possible reasonable interpretation, there is no such genus or name as *Dryomys* Philippi, 1900. The reference in Philippi is to *Drymomys* Tschudi (itself invalid), for which "*Dryomys*" Philippi is an obvious and unmistakable misprint with no standing under any rules or usages of nomenclature. *Dryomys* Thomas, 1906, is therefore valid.

Fam. Dipodidae Waterhouse, 1842, p. 203 (=Dipodina Bonaparte, 1838, p. 111; Dipsidae Gray, 1821, p. 303; Jaculidae Gill, 1872, p. 20; Jaculini Brandt, 1855, pp. 230, 310). L. Plioc.–R.; As. Pleist.–R.; Eu. R.; Af. Jerboas.

Subfam. Dipodinae Murray, 1866, p. 361 (=Jaculinae Alston, 1876, p. 89). L. Plioc.–R.; As. Pleist.–R.; Eu. R.; Af.

†*Sminthoides* Schlosser, 1924. L. Plioc.; As.

†*Brachyscirtetes* Schaub, 1934. Plioc.; As.

†*Paralactaga* Young, 1927. Plioc.; As.

†*Protalactaga* Young, 1929. U. Mioc.–L. Plioc.; As.

Dipus Zimmerman, 1780 (=*Dipodipus* Trouessart, 1910). Pleist.–R.; As. R.; E. Eu. (True) jerboa, three-toed jerboa.

Paradipus Vinogradov, 1930. R.; As.

Eremodipus Vinogradov, 1930. R.; As.

Jaculus Erxleben, 1777. R.; Af. (African) jerboa.

Scirtopoda Brandt, 1844. [Including *Stylodipus* Allen, 1925.] R.; Af. (African) jerboa.

Scarturus Gloger, 1841. R.; N. Af. (African) jerboa.

Allactaga[1] Cuvier, 1836 (=*Scirtetes*[1] Wagner, 1841). U. Plioc.–R.; As. Pleist.–R.; Eu. Allactaga, five-toed jerboa.

Alactagulus[1] Nehring, 1897. R.; As.

Pygeretmus Gloger, 1841 (=*Platycercomys* Brandt, 1844). R.; As. Flat-tailed jerboa.

Subfam. Cardiocraniinae Vinogradov, 1930, pp. 332, 336.

Cardiocranius Satunin, 1903. R.; As.

Salpingotus Vinogradov, 1923. R.; As.

Subfam. Euchoreutinae Lyon, 1901, p. 666. R.; As.

Euchoreutes Sclater, 1891. R.; As.

?MYOMORPHA *incertae sedis:*

†*Ruscinomys* Depéret, 1890. Plioc.; Eu.

†*Pauromys* Troxell, 1923. M. Eoc.; N.A.

†*Simimys* Wilson, 1935. U. Eoc.; N.A.

Suborder HYSTRICOMORPHA Brandt, 1855, p. 294.

Superfam. Hystricoidea Gill, 1872, p. 22.

Fam. Hystricidae Burnett, 1830a, p. 350 (=Histricidae Gray, 1821, p. 304; Hystricini Fischer, 1817, p. 372). Olig.; Eu. M. Plioc.–R.; As. R.; Af. Old World porcupines.

Subfam. Hystricinae Murray, 1866, pp. xiv, 351. Olig.–R.; Eu. M. Plioc.–R.; As. R.; Af. (True, Old World) porcupines.

†*Sivacanthion* Colbert, 1933. L. Plioc.; As.

Acanthion Cuvier, 1822. R.; As.

Thecurus Lyon, 1907. R.; As.

Hystrix Linnaeus, 1758. M. Plioc.–R.; As. R.; Af. ?Olig.–Pleist.; Eu. R.; Italy (perhaps introduced). (Some of the fossil forms certainly *Hystrix* only *sensu lato*.)

Subfam. Atherurinae Lyon, 1907, pp. 576, 584. R.; Af., As. Brush-tailed porcupines.

Atherurus Cuvier, 1829. R., Af., As.

Trichys Günther, 1876. R.; As.

[1] Double "l" in *Allactaga* and single in *Alactagulus* are correct. *Scirtetes* has no standing, being proposed only because *Allactaga* is "barbarous."

Superfam. Erethizontoidea, new form?
Fam. Erethizontidae Thomas, 1897, p. 1025 (=Erethyzonina Bonaparte, 1845, p. 5). [Including Coendidae Trouessart, 1897, p. 619=Cercolabina Gray, 1843, pp. xxiv, 123.] Olig.–R.; S.A. U. Plioc.–R.; N.A. New World porcupines, tree porcupines.
†Subfam. Acaremyinae Ameghino, 1902b, p. 111. Olig.–I. Mioc.; S.A.
†*Asteromys* Ameghino, 1897. Olig.; S.A.
†*Protacaremys* Ameghino, 1902. Olig.; S.A.
†*Acaremys* Ameghino, 1887. U. Olig.–L. Mioc.; S.A.
†*Sciamys* Ameghino, 1887. L. Mioc.; S.A.
Subfam. Erethizontinae Thomas, 1897, p. 1025. [Including †Steiromyinae Ameghino, 1902b, p. 109; Coendinae Pocock, 1922b, p. 422=Sphingurinae Alston, 1876, p. 93.] Olig.–R.; S.A. U. Plioc.–R.; N.A.
†*Eosteiromys* Ameghino, 1902. Olig.; S.A.
†*Parasteiromys* Ameghino, 1904. Olig.; S.A.
†*Steiromys* Ameghino, 1887. U. Olig.–Plioc.; S.A.
Erethizon Cuvier, 1822. U. Plioc.–R.; N.A. (North American) porcupine.
Coendou Lacépède, 1799 (=*Cercolabes* Brandt, 1835). [Including *Sphiggurus* Cuvier, 1825=*Sphingurus*, *Sphingura*, etc., of authors; *Sinoetherus* Cuvier, 1825=*Syntheres*, etc., of authors.] R.; S.A., Cent. A. Cuandu, couiy, (South American) tree porcupine.
Echinoprocta Gray, 1865. R.; S.A.
Subfam. Chaetomyinae Thomas, 1897, p. 1026. R.; S.A.
Chaetomys Gray, 1843. R.; S.A. Thin-spined porcupine.
Superfam. Cavioidea Kraglievich, 1930c, p. 60.
†Fam. Cephalomyidae Ameghino, 1897b, p. 493. Olig.; S.A.
†*Cephalomys* Ameghino, 1897. Olig.; S.A.
†*Litodontomys* Loomis, 1914. Olig.; S.A.
†Fam. Eocardiidae[1] Ameghino, 1891a, p. 145. U. Olig.–L. Mioc.; S.A.
†*Archaeocardia* Ameghino, 1902. U. Olig.; S.A.
†*Luantus*[2] Ameghino, 1899. U. Olig.; S.A.
†*Eocardia* Ameghino, 1887. [Including †*Dicardia* Ameghino, 1891; †*Tricardia* Ameghino, 1891; etc.] L. Mioc.; S.A.
†*Schistomys* Ameghino, 1887. [Including †*Procardia* Ameghino, 1891.] L. Mioc.; S.A.
†*Phanomys* Ameghino, 1887. L. Mioc.; S.A.
Fam. Caviidae Waterhouse, 1839b, p. 91 (=Caviadae Gray, 1821, p. 304). [Including Coelogenyidae Burmeister, 1854, p. 227=Coelogenina Gervais, 1849, p. 204.] Plioc.–R.; S.A.
†Subfam. Cardiomyinae Kraglievich, 1930c, p. 61. Plioc.; S.A.
†*Cardiomys* Ameghino, 1885. [Including †*Caviodon* Ameghino, 1885; †*Diocartherium* Ameghino, 1888; †*Lelongia* Kraglievich, 1930; etc.] Plioc.; S.A.
†*Parodimys* Kraglievich, 1932. Plioc.; S.A.
Subfam. Caviinae Murray, 1866, pp. xiv, 350. Plioc.–R.; S.A. Guinea pigs, cavies.

[1] Eocardidae in original publication.
[2] Usually cited as "*Luanthus*," but the original spelling was intentionally *Luantus*.

†*Palaeocavia* Ameghino, 1889. Plioc.; S.A.
†*Neocavia* Kraglievich, 1932. Plioc.; S.A.
†*Macrocavia* Rusconi, 1933. U. Plioc.; S.A.
✓*Cavia* Pallas, 1766. R.; S.A. Common (including domestic) guinea pigs, perea, cavies.
Kerodon Cuvier, 1825. R.; S.A. Moco.
Galea Meyen, 1831. R.; S.A. Cuy.
Microcavia Gervais and Ameghino, 1880. [Including *Caviella* Osgood, 1915; *Monticavia* Thomas, 1916; *Nanocavia* Thomas, 1916.] Pleist.–R.; S.A. Cuys, mountain guinea pigs, etc.
Subfam. Dolichotinae Pocock, 1922b, p. 426. Plioc.–R.; S.A.
†*Orthomyctera* Ameghino, 1889. Plioc.; S.A.
†*Prodolichotis* Kraglievich, 1932. Plioc.; S.A.
†*Pliodolichotis* Kraglievich, 1927. Plioc.; S.A.
†*Dolicavia* Ameghino, 1916. Plioc.; S.A.
Dolichotis Desmarest, 1820. [Including *Paradolichotis* Kraglievich, 1927.] Pleist.–R.; S.A. Mara, Patagonian "hare."
Fam. Hydrochoeridae Gill, 1872, p. 22 (=Hydrocharina Gray, 1825, p. 341). Plioc.–R.; S.A. Pleist.; N.A. R.; Cent. A.
†Subfam. Cardiatheriinae[1] Kraglievich, 1930d, p. 241. Plioc.; S.A.
†*Cardiatherium*[2] Ameghino, 1883. Plioc.; S.A.
†*Procardiatherium* Ameghino, 1885. Plioc.; S.A.
†*Anchimys* Ameghino, 1886. Plioc.; S.A.
†*Plexochoerus* Ameghino, 1886. Plioc.; S.A.
†*Eucardiodon* Ameghino, 1891 (=†*Cardiodon* Ameghino, 1885, *nec* Owen, 1841). Plioc.; S.A.
†*Anchimysops* Kraglievich, 1927. Plioc.; S.A.
Subfam. Hydrochoerinae Weber, 1928, p. 290. [Including †Protohydrochoerinae Kraglievich, 1930d, p. 240.] Plioc.–R.; S.A. Pleist.; N.A. R.; Cent. A.
†*Protohydrochoerus* Rovereto, 1914. Plioc.; S.A.
†*Nothydrochoerus* Rusconi, 1935. U. Plioc.; S.A.
†*Hydrochoeropsis* Kraglievich, 1930. U. Plioc.; S.A.
†*Neochoerus* Hay, 1926. Pleist.; N.A., S.A.
✓*Hydrochoerus* Brisson, 1762. Pleist.–R.; S.A. Pleist.; N.A. R.; Cent. A. Capybara, carpincho.
Fam. Dinomyidae Alston, 1876, p. 96 (=Dinomyina Troschel, 1874, p. 132). R.; S.A.
Dinomys Peters, 1873. R.; S.A. Long-tailed paca, false paca, pacarana.
†Fam. Heptaxodontidae Miller and Gidley, 1918, p. 447 (=†Heptaxodontinae Anthony, 1917a, p. 186). [Including †Eumegamyidae Kraglievich, 1926b, p. 121=†Megamyidae[3] (invalid); †Neoepiblemidae Kraglievich, 1926b, p. 128; Potamarchidae Kraglievich, 1926b, p. 129.] Mioc.–Plioc.; S.A. Pleist.–sub-R.; W. Indies.

[1] Hitherto spelled "Cardiotheriinae."
[2] Almost always spelled *Cardiotherium* by authors (including Ameghino in later papers), but the first spelling does not appear to be a misprint.
[3] In the preceding reference, Kraglievich mentioned Megamyidae as having been used previously, but no such reference has been found.

†Subfam. Potamarchinae, new form (=†Potamarchidae Kraglievich, 1926b, p. 129). Mioc.–Plioc.; S.A.
†*Simplimus* Ameghino, 1904. Mioc.; S.A.
†*Potamarchus* Burmeister, 1885. Plioc.; S.A.
†Subfam. Eumegamyinae Kraglievich, 1932b, p. 318. [Including †Tetrastylinae Kraglievich, 1931, p. 255; †Gyriabrinae Kraglievich, 1930b, p. 220; †Phoberomyinae Kraglievich, 1926b, p. 127.] Plioc.; S.A.
†*Telodontomys* Kraglievich, 1931. Plioc.; S.A.
†*Rusconia* Kraglievich, 1931. Plioc.; S.A.
†*Diaphoromys* Kraglievich, 1931. Plioc.; S.A.
†*Protomegamys* Kraglievich, 1932. Plioc.; S.A.
†*Eumegamys* Kraglievich, 1926 (=†*Megamys* of almost all authors but not †*Megamys* D'Orbigny and Laurillard, 1842, which Kraglievich has shown to be a litoptern). Plioc.; S.A.
†*Isostylomys* Kraglievich, 1926. Plioc.; S.A.
†*Tetrastylopsis* Kraglievich, 1931. Plioc.; S.A.
†*Tetrastylus* Ameghino, 1886. Plioc.; S.A.
†*Gyriabrus* Kraglievich, 1930. Plioc.; S.A.
†*Pseudosigmomys* Kraglievich, 1931. Plioc.; S.A.
†*Phoberomys* Kraglievich, 1926. Plioc.; S.A.
†*Carlesia* Kraglievich, 1926. Plioc.; S.A.
†*Telicomys* Kraglievich, 1926. Plioc.; S.A.
†Subfam. Neoepibleminae, new form (=†Neoepiblemidae Kraglievich, 1926b, p. 128). Plioc.; S.A.
†*Neoepiblema* Ameghino, 1889. Plioc.; S.A.
†*Dabbenea* Kraglievich, 1926. Plioc.; S.A.
†Subfam. Heptaxodontinae Anthony, 1917a, p. 186. [Including †Elasmodontomyinae Anthony, 1917a, p. 186.] Pleist.–sub-R.; W. Indies. ?Plioc.; S.A.
†*Heptaxodon* Anthony, 1917. Pleist.[1]; W. Indies.
†*Elasmodontomys* Anthony, 1916. Pleist.; W. Indies.
†*Clidomys* Anthony, 1920. Pleist.; W. Indies.
†*Spirodontomys* Anthony, 1920. Pleist.; W. Indies.
†*Speoxenus* Anthony, 1920. Pleist.; W. Indies.
†*Amblyrhiza* Cope, 1868. Pleist.; W. Indies.
?†Heptaxodontinae *incertae sedis:*
†*Tetrastylomys* Kraglievich, 1926. Plioc.; S.A.
†*Pentastylomys* Kraglievich, 1926. Plioc.; S.A.
Fam. Dasyproctidae Smith, 1842, p. 307 (=Dasyporcina [*sic*] Gray, 1825, p. 341; Coelogenyidae Burmeister, 1854, p. 227 [Coelogenina Gervais, 1849, p. 204]; Agoutidae Gray, 1821, p. 304—all invalid names). R.; S.A.
Subfam. Cuniculinae, new form (=Cuniculidae Miller and Gidley, 1918, p. 446). R.; Cent. A., S.A.
Cuniculus Brisson, 1762 (=*Agouti*[2] Lacépède, 1799; *Coelogenus*

[1] Throughout this section "Pleist." is used for brevity in referring to the age of the extinct West Indian genera. Doubtless all did live in the Pleistocene, but some, at least, also lived into post-Pleistocene times and it is even possible, although improbable, that some are still living.

[2] Note that *Agouti*, a name still often used, although it is antedated by *Cuniculus*, is not applicable to the agoutis (agutis) but to the pacas.

Cuvier, 1807 [*Coelogenys* of most authors]). R.; S.A., Cent. A. Lowland pacas.

Stictomys Thomas, 1924. R.; S.A. Mountain pacas.

Subfam. Dasyproctinae Murray, 1866, pp. xiv, 351.

Dasyprocta Illiger, 1811. R.; S.A., Cent. A., W. Indies.

Myoprocta Thomas, 1903. R.; S.A. Acushi (acuchi, acuschy, etc.).

Superfam. Chinchilloidea Kraglievich, 1940, p. 756.

Fam. Chinchillidae Bennett, 1833, p. 58. [Including Lagostomidae Bonaparte, 1838, p. 113.] Olig.–R.; S.A.

†*Scotamys* Loomis, 1914. Olig.; S.A.

†*Perimys* Ameghino, 1887. U. Olig.–L. Mioc.; S.A.

†*Prolagostomus* Ameghino, 1887. L. Mioc.; S.A.

†*Pliolagostomus* Ameghino, 1887. L. Mioc.; S.A.

†*Scotaeumys* Ameghino, 1887. L. Mioc.; S.A.

†*Sphodromys* Ameghino, 1887. L. Mioc.; S.A.

†*Euphilus* Ameghino, 1889. Plioc.; S.A.

Lagostomus Brookes, 1828 (*Viscaccia* of some authors, in error). Pleist.–R.; S.A. Plains vizcacha, vizcachón.

Lagidium Meyen, 1833 (= *Viscaccia* Oken, 1816).[1] R.; S.A. Mountain vizcacha, chinchillón.

Chinchilla Bennett, 1829. R.; S.A. Chinchilla.

Superfam. Octodontoidea, new form?

Fam. Capromyidae Smith, 1842, p. 308 (=Ondatrina Gray, 1825, p. 341). Mioc.–R.; S.A. R.; Cent. A., W. Indies.

†*Neoreomys* Ameghino, 1887. L. Mioc.; S.A.

†*Scleromys* Ameghino, 1887. L. Mioc.; S.A.

†*Lomomys* Ameghino, 1891. L. Mioc.; S.A.

†*Olenopsis* Ameghino, 1889. Mioc.–Plioc.; S.A.

†*Eumysops* Ameghino, 1888. Plioc.; S.A.

†*Isomyopotamus* Rovereto, 1914. Plioc.; S.A.

†*Paramyocastor* Ameghino, 1904. Mioc.; S.A.

Capromys Desmarest, 1822. R.; W. Indies. Hutia, jutia.

Geocapromys Chapman, 1901. R.; W. Indies. Hutia.

Procapromys Chapman, 1901. R.; S.A. Hutia.

Plagiodontia Cuvier, 1836. R.; Cent. A., W. Indies.

Myocastor Kerr, 1792 (= *Myopotamus* Geoffroy, 1805). Plioc.–R.; S.A. Nutria, coypu.

Fam. Octodontidae Waterhouse, 1839a, p. 172. [Including Spalacopodidae Lilljeborg, 1866, p. 44.] U. Olig.–R.; S.A. Pleist.; W. Indies. Degus.

†*Eoctodon* Ameghino, 1902. U. Olig.; S.A.

†*Pithanotomys* Ameghino, 1887. Plioc.–Pleist.; S.A.

†*Palaeoctodon* Rovereto, 1914. Plioc.; S.A.

†*Alterodon* Anthony, 1920. Pleist.; W. Indies.

Octodon Bennett, 1832. R.; S.A. Degu.

Octodontomys Palmer, 1903 (= *Neoctodon* Thomas, 1902, *nec* Bedel, 1892). R.; S.A. Chozchori.

Spalacopus Wagler, 1832. R.; S.A.

Aconaemys Ameghino, 1891 (= *Schizodon* Waterhouse, 1842, *nec* Agassiz, 1829). R.; S.A.

[1] The use of the later name, *Lagidium*, has been validated by suspension of the Rules.

Octomys Thomas, 1920. R.; S.A.

Fam. Ctenomyidae Tate, 1935, p. 295 (=Ctenomydae Gervais, 1849, p. 203; Ctenomysideae Lesson, 1842, p. 105). Plioc.–R.; S.A.

†*Actenomys* Burmeister, 1888 (hitherto generally called †*Dicoelophorus* Ameghino, 1888).[1] Plioc.; S.A.

†*Eucelophorus* Ameghino, 1909. ?Plioc.; S.A.

†*Xenodontomys* Kraglievich, 1927. Plioc.; S.A.

†*Megactenomys* Rusconi, 1930. Plioc.; S.A.

Ctenomys De Blainville, 1826. Pleist.–R.; S.A. Tucu tucu.

Fam. Abrocomidae Miller and Gidley, 1918, p. 447. Plioc.–R.; S.A.

†*Protabrocoma* Kraglievich, 1927. Plioc.; S.A.

Abrocoma Waterhouse, 1837. R.; S.A. "Rat chinchilla."

Fam. Echimyidae Miller and Gidley, 1918, p. 445 (=Echymyidae Bonaparte, 1850; Echimyda Pictet, 1843, p. 202; Echymina Gray, 1825, p. 341; Loncheridae Burmeister, 1850, p. 17; Loncherini Giebel, 1847, p. 93; all incorrect forms). U. Olig.–R.; S.A. Pleist.–R.; W. Indies, Cent. A. Spiny "rats," "porcupine rats," urares.

Subfam. Echimyinae Murray, 1866, pp. xiv, 350 (=Loncherinae Thomas, 1897, p. 1024; Loncherini Giebel, 1847, p. 93). U. Olig.–R.; S.A. Pleist.–R.; W. Indies, Cent. A.

†*Protadelphomys* Ameghino, 1902. U. Olig.; S.A.

†*Stichomys* Ameghino, 1887. L. Mioc.; S.A.

†*Adelphomys* Ameghino, 1887. L. Mioc.; S.A.

†*Gyrignophus* Ameghino, 1891. L. Mioc.; S.A.

†*Prospaniomys* Ameghino, 1902. L. Mioc.; S.A.

†*Spaniomys* Ameghino, 1887. U. Olig.–L. Mioc.; S.A.

†*Graphimys* Ameghino, 1891. L. Mioc.; S.A.

†*Isolobodon* Allen, 1916. Pleist.; W. Indies.

†*Heteropsomys* Anthony, 1916. Pleist.; W. Indies.

†*Homopsomys* Anthony, 1917. Pleist.; W. Indies.

†*Aphaetreus* Miller, 1922. Pleist.; W. Indies.

†*Ithydontia* Miller, 1922. Pleist.; W. Indies.

†*Brotomys* Miller, 1916. Sub–R.; Cent. A.

†*Boromys* Miller, 1916. Sub–R.; Cent. A.

Proëchimys Allen, 1889. R.; S.A., Cent. A.

Hoplomys Allen, 1908. R.; S.A., Cent. A.

Euryzygomatomys Goeldi, 1901. R.; S.A.

Clyomys Thomas, 1916. R.; S.A.

Carterodon Waterhouse, 1848. Pleist.[2]–R.; S.A.

Cercomys Cuvier, 1832. R.; S.A.

Mesomys Wagner, 1845. R.; S.A.

[1] *Dicoelophorus* has priority, but the animal to which it should be applied is debated. Rusconi has proposed two nomenclatural solutions and Miller one, the three proposals mutually exclusive so that only one of them (if any) can be correct, but all concluding that this important Pliocene genus is properly called *Dicoelophorus*. The situation is too complicated to summarize here, but all three of Rusconi's and Miller's arguments essentially depend on accepting certain specimens as types of *Dicoelophorus*. But under the Rules (which both these authors accept) the type of a genus is a species, not a specimen. The type of this genus is "*Dicoelophorus*" *latidens*. It is agreed that this species belongs in *Ctenomys*. Therefore *Dicoelophorus* is a synonym of *Ctenomys* and the valid name of the Pliocene genus is *Actenomys*.

[2] This is another of the very few instances of an animal's being found first as a fossil and later discovered to be still living.

Lonchothrix Thomas, 1920. R.; S.A.
Isothrix Wagner, 1845. R.; S.A.
Diplomys Thomas, 1916. R.; S.A., Cent. A.
Echimys Cuvier, 1809 (=*Echinomys* Wagner, 1840; *Loncheres* Illiger, 1811).[1] R.; S.A., Cent. A.
Subfam. Dactylomyinae Tate, 1935, p. 295. R.; S.A.
Dactylomys Geoffroy, 1833. R.; S.A.
Kannabateomys Jentink, 1891. [Including *Lachnomys* Thomas, 1916.] R.; S.A.
Thrinacodus Günther, 1879. R.; S.A.
Fam. Thryonomyidae[2] Pocock, 1922b, p. 423 (=Aulacodina Bonaparte, 1845, p. 5). L. Mioc.; ?Af. Plioc.; E. As. R.; Af.
†*Paraulacodus* Hinton, 1933. Plioc.; As.
Thryonomys Fitzinger, 1867 (=*Aulacodus* Temminck, 1827, *nec* Eschscholtz, 1822). [Including *Choeromys* Thomas, 1922.] R.; Af. Cane "rat," bamboo "rat."[3]
?Thryonomyidae *incertae sedis:*
†*Neosciuromys* Stromer, 1922. L. Mioc.; Af.
†*Phiomyoides* Stromer, 1926. L. Mioc.; Af.
†*Sayimys* Wood, 1937. M. Plioc.; As.
Fam. Petromyidae Tullberg, 1899, p. 147. R.; Af.
Petromys[4] Smith, 1831. R.; Af. Rock "rat."
?HYSTRICOMORPHA *incertae sedis:*
Superfam. Bathyergoidea Osborn, 1910, p. 538 (=Bathyergomorphi Tullberg, 1899, p. 357).
Fam. Bathyergidae Waterhouse, 1841b, p. 81 (=Georychidae Anon., 1897, p. 14; Georychina Gravenhorst, 1843, facing p. 502). ?L. Mioc., Pleist.–R.; Af.
†*Gypsorhychus* Broom, 1934. Pleist.; Af.
Georychus Illiger, 1811. R.; Af. Blesmol.
Cryptomys Gray, 1864. R.; Af.
Heliophobius Peters, 1846[5] (=*Myoscalops* Thomas, 1890). R.; Af.
Bathyergus Illiger, 1811. R.; Af. "Mole rat."
Heterocephalus Rüppell, 1842. [Including *Fornarina* Thomas.] R.; Af. Sand "rat," naked "rat," naked "mole."
?Bathyergidae *incertae sedis:*
†*Bathyergoides* Stromer, 1926. L. Mioc.; Af.
?HYSTRICOMORPHA or ?MYOMORPHA *incertae sedis:*
Superfam. Ctenodactyloidea, new form? (=Ctenodactyloidei Tullberg, 1899, p. 387).
Fam. Ctenodactylidae Zittel, 1893, p. 542 (=Ctenodactylina Gervais, 1853, p. 245). L. Plioc.; ?As. R.; Af. Gundis.
✓*Ctenodactylus* Gray, 1830. R.; Af.

[1] *Echinomys* is simply an (invalid) emendation of *Echimys*. Many authors maintain that *Echimys* and *Loncheres* are distinct genera, making *Echimys* what is here called *Proëchimys*, or *Euryzygomatomys*, or both, and calling the present genus *Loncheres*. I have followed Tate, who makes the two names strict synonyms.

[2] Spelled "Thrynomyidae" by Pocock.

[3] The same vernacular names are applied to some other distantly related or unrelated rodents.

[4] This is *Petromus* in the original publication and perhaps that was intended, but it may well have been a misprint (correctable under the Rules), and I have assumed this rather than depart from universal usage without absolute necessity.

[5] Not preoccupied by *Heliophobus* Boisduval, 1829.

Pectinator Blyth, 1856. L. Plioc.; ?As. R.; Af.
Massouteria Lataste, 1885. R.; Af.
Felovia Lataste, 1886. R.; Af.

Cohort MUTICA Linnaeus, 1766, p. 24.

Order CETACEA Brisson, 1762, pp. 3, 227 (=Cete Linnaeus, 1758, p. 75).

†Suborder ARCHAEOCETI Flower, 1883, p. 182 (=Zeuglodontia Gill, 1871a, p. 122).

†Fam. Protocetidae Stromer, 1908, p. 148. M. Eoc.; Af., N.A.
†*Protocetus* Fraas, 1904. M. Eoc.; Egypt, ?N.A.
†*Pappocetus* Andrews, 1920. M. Eoc.; Nigeria.
†*Eocetus* Fraas, 1904 (=†*Mesocetus* Fraas, 1904, *nec* Moreno, 1892, *nec* Van Beneden, 1880). M. Eoc.; Egypt.

†Fam. Dorudontidae Miller, 1923, p. 40. U. Eoc.; N.A., Eu., Af. L. Mioc.; Eu., New Zealand.
†*Dorudon* Gibbes, 1845. U. Eoc.; N.A., Egypt.
†*Zygorhiza* True, 1908. U. Eoc.; N.A., England.
†*Phococetus* Gervais, 1876. L. Mioc.; France.
†*Kekenodon* Hector, 1881. L. Mioc.; New Zealand.

†Fam. Basilosauridae Cope, 1867, p. 144 (=†Zeuglodontidae Bonaparte, 1849, p. 618, invalid). U. Eoc.; N.A., Af. L. Olig.; Eu.
†*Prozeuglodon* Andrews, 1906. U. Eoc.; Egypt.
†*Basilosaurus* Harlan, 1834 (=†*Zeuglodon* Owen, 1839). U. Eoc.; N.A.
†*Platyosphys* Kellogg, 1936. L. Olig.; Ukraine.

?†ARCHAEOCETI *incertae sedis:*
†*Microzeuglodon* Stromer, 1903. L. Mioc.; Eu.
†*Archaeodelphis* Allen, 1921. U. Eoc.; N.A.
†*Patriocetus* Abel, 1914. U. Olig.; Eu.
†*Agriocetus* Abel, 1914. U. Olig.; Eu.

Suborder ODONTOCETI Flower, 1867, pp. 110, 115 (=Odontocete Flower, 1864, p. 388). Toothed whales.

†Superfam. Squalodontoidea, new.

†Fam. Agorophiidae Abel, 1913b, p. 720. U. Eoc.; N.A.
†*Agorophius* Cope, 1895. U. Eoc.; N.A.
†*Xenorophus* Kellogg, 1923. U. Eoc.; N.A.

†Fam. Squalodontidae Brandt, 1873, p. 576. U. Olig.–U. Mioc.; Eu. L. Mioc.; S.A., Aus., New Zealand. M.–U. Mioc., N.A.
†*Microcetus* Kellogg, 1923. U. Olig.; Eu.
†*Microsqualodon* Abel, 1905. L. Mioc.; Eu.
†*Neosqualodon* Dal Piaz, 1904. L. Mioc.; Eu.
†*Rhytisodon* Paolo, 1897. L. Mioc.; Eu.
†*Squalodon* Grateloup, 1840. L.–U. Mioc.; Eu. M.–U. Mioc.; N.A.
†*Trirhizodon* Cope, 1890. L.–M. Mioc.; Eu.
†*Phoberodon* Cabrera, 1926. L. Mioc.; S.A.
†*Prosqualodon* Lydekker, 1894. L. Mioc.; S.A., New Zealand.
†*Metasqualodon* Hall, 1911. L. Mioc.; Aus.
†*Parasqualodon* Hall, 1911. L. Mioc.; Aus.
†*Colophonodon* Leidy, 1853. U. Mioc.; N.A.
†*Saurocetus* Agassiz, 1848. U. Mioc.; N.A.

Superfam. Platanistoidea, new. River dolphins.

Fam. Platanistidae Gray, 1863b, p. 199. M. Mioc., L.–M. Plioc., Pleist.; N.A. L. Mioc.–R.; S.A. U. Mioc.; Eu. R.; As.

Subfam. Platanistinae Flower, 1867, p. 114 (=Platanistina Gray, 1846, p. 45). M. Mioc.; N.A. U. Mioc.; Eu. R.; S. As.
†*Zarhachis* Cope, 1868. M. Mioc.; N.A.
†*Pachyacanthus* Brandt, 1871. U. Mioc.; Eu.
Platanista Wagler, 1830. R.; S. As. Susu, Ganges dolphin.
Subfam. Iniinae Flower, 1867, p. 114 (=Iniina Gray, 1846, pp. 25, 45). L. Mioc.–R.; S.A. L. Plioc.; N.A. R.; As.
†*Proinia* True, 1910. L. Mioc.; S.A.
†*Hesperocetus* True, 1912. L. Plioc.; N.A.
†*Saurodelphis* Burmeister, 1891 (=†*Saurocetes* Burmeister, 1871, *nec Sauro-cetus* Agassiz, 1848; †*Pontoplanodes* Ameghino, 1891).[1] Plioc.; S.A.
†*Anisodelphis* Rovereto, 1915. Plioc.; S.A.
†*Ischyorhynchus* Ameghino, 1891. Plioc.; S.A.
Inia D'Orbigny, 1834. R.; S.A. Amazon dolphin.
Lipotes Miller, 1918. R.; China.
Subfam. Stenodelphininae Miller, 1923, p. 40. M. Plioc., Pleist.; N.A. Plioc., R.; S.A.
†*Lonchodelphis* Allen, 1924. M. Plioc.; N.A.
†*Pontistes* Burmeister, 1885. Plioc.; S.A.
†*Pontivaga* Ameghino, 1891. Plioc.; S.A.
Stenodelphis Gervais, 1847 (=*Pontoporia* Gray, 1846, *nec* Kroyer, 1842, *emend.* Agassiz, 1846). Pleist.; N.A. R.; S.A.
Superfam. Physeteroidea Gill, 1872, p. 15.
Fam. Ziphiidae Gray, 1865c, p. 528 (=Ziphiina Gray, 1850, pp. 59, 61, *fide* Palmer, 1904, p. 776). [Including Squalodelphidae Dal Piaz, 1916, p. 32.] L. Mioc.; S.A. L. Mioc.–M. Plioc.; Eu. U. Mioc.; N.A. R.; all oceans. Beaked whales.
†*Notocetus* Moreno, 1892 (=†*Diochotichus* Ameghino, 1894[2]; †*Argyrodelphis* Lydekker, 1894; *nec* †*Notiocetus* Ameghino, 1891). L. Mioc.; S.A.
†*Squalodelphis* Dal Piaz, 1916. L. Mioc.; Eu.
†*Cetorhynchus* Gervais, 1861. M.–U. Mioc.; Eu.
†*Ziphioides* Probst, 1886. M. Mioc.; Eu.
†*Anoplonassa* Cope, 1869. U. Mioc.; N.A.
†*Belemnoziphius* Huxley, 1864. U. Mioc.; N.A., Eu.
†*Choneziphius* Duvernoy, 1851. U. Mioc.; N.A. U. Mioc.–M. Plioc.; Eu.
†*Eboroziphius* Leidy, 1876. U. Mioc.; N.A.
Mesoplodon Gervais, 1850. U. Mioc.; N.A. U. Mioc.–M. Plioc.; Eu. R.; Atlantic, Pacific, Indian oceans. "Cow fish."
†*Palaeoziphius* Abel, 1905. U. Mioc.; Eu.
†*Proroziphius* Leidy, 1876. U. Mioc.; N.A.

[1] This genus is usually and perhaps correctly called †*Pontoplanodes*, yet †*Saurocetes* may be the correct name after all. The questions are (1) whether *Sauro-cetus* really preoccupies *Saurocetes*, and (2) whether appearance of *Saurodelphis* in a newspaper was valid publication. Cabrera, 1926, answers both these affirmatively, and I follow his excellent authority in the hope of promoting uniformity, although my own tendency would be to answer both negatively.

[2] †*Diochotichus*, now the name most frequently employed for this genus, was given on the grounds that †*Notocetus* is preoccupied by †*Notiocetus*. Cabrera, 1926, does not consider this as preoccupation, and I follow him, although with great reluctance because of the probable confusion of having such similar names for allied but distinct animals.

Ziphius Cuvier, 1823. R.; all oceans. Two-toothed whale.
†*Ziphirostrum* Du Bus *ex* Van Beneden, 1868 (=†*Mioziphius* Abel, 1905).[1] U. Mioc.; Eu.
†*Berardiopsis* Portis, 1886. M. Plioc.; Eu.
Tasmacetus Oliver, 1937. R.; S. Pacific.
Berardius Duvernoy, 1851. R.; Pacific.
Hyperoodon Lacépède, 1804. R.; N. Atlantic, Mediterranean, S. Pacific, Antarctic. Bottle-nosed whale.

Fam. Physeteridae Gray, 1821, p. 310. [Including Kogiinae Gill, 1871b, p. 732 (Kogiidae auct.); Physodontidae Lydekker, 1894b, p. 4.] L. Mioc.; S.A. L.–U. Mioc., M. Plioc.; Eu. M. Mioc.–L. Plioc., Pleist.; N.A. L. Plioc.; Aus. R.; Atlantic, Pacific, Indian oceans. Sperm whales.

†Subfam. Hoplocetinae Cabrera, 1926, p. 408. L. Mioc.; S.A. ?L., M.–U. Mioc.; Eu. M. Mioc.; N.A. ?L. Plioc.; ?Aus.
†*Apenophyseter* Cabrera, 1926. L. Mioc.; S.A.
†*Diaphorocetus* Ameghino, 1892 (=†*Mesocetus* Moreno, 1892, *nec* Van Beneden, 1879). L. Mioc.; S.A.
†*Idiorophus* Kellogg, 1925. L. Mioc.; S.A.
†*Hoplocetus* Gervais, 1848–1852. M. Mioc.; Eu.
†*Aulophyseter* Kellogg, 1927. M. Mioc.; N.A.
†*Scaldicetus* Du Bus, 1867. ?L. Mioc., U. Mioc.; Eu. ?L. Plioc.; ?Aus.

Subfam. Physeterinae Flower, 1867, p. 114. M.–U. Mioc., Pleist.; N.A. L.–U. Mioc., M. Plioc.; Eu. L. Plioc.; Aus. R.; all oceans.
†*Ontocetus* Leidy, 1859. M.–U. Mioc.; N.A. M. Mioc.; Japan.
†*Idiophyseter* Kellogg, 1925. M. Mioc.; N.A.
†*Orycterocetus* Leidy, 1853. M. Mioc.; N.A.
†*Dinoziphius* Van Beneden, 1880. U. Mioc.; N.A.
†*Physeterula* Van Beneden, 1877. U. Mioc.; Eu.
†*Prophyseter* Abel, 1905. U. Mioc.; Eu.
†*Thalassocetus* Abel, 1905. U. Mioc.; Eu.
†*Physetodon* McCoy, 1879. L. Plioc.; Aus.
†*Balaenodon* Owen, 1846. M. Plioc.; Eu.
†*Priscophyseter* Portis, 1886. M. Plioc.; Eu.
Physeter Linnaeus, 1758. U. Mioc., Pleist.; N.A. L.–M. Mioc.; Eu. R.; all oceans. Sperm whale, cachalot.

Subfam. Kogiinae Gill, 1871b, p. 732. L. Plioc.; N.A. R.; Atlantic, Pacific, Indian oceans.
†*Kogiopsis* Kellogg, 1929. L. Plioc.; N.A.
Kogia Gray, 1846. R.; Atlantic, Pacific, Indian oceans. Pygmy sperm whale.

Superfam. Delphinoidea Flower, 1864, p. 389.

†Fam. Eurhinodelphidae Abel, 1901, p. 60. L. Mioc.; S.A. L.–U. Mioc.; Eu. M. Mioc.; N.A. U. Mioc.; Japan.
†*Argyrocetus* Lydekker, 1894. L. Mioc.; S.A.
†*Ziphiodelphis* Dal Piaz, 1909. L. Mioc.; Eu.
†*Eurhinodelphis* Du Bus, 1867. M. Mioc.; N.A. U. Mioc.; Eu., Japan.

†Fam. Hemisyntrachelidae Slijper, 1936, p. 550. M. Mioc.; N.A. L. Plioc.; Eu.

[1] Many, perhaps most, recent authors use Abel's name, which is antedated by at least three properly established generic names and is certainly invalid. †*Ziphirostrum* appears to be the oldest name for the genus.

†*Lophocetus* Cope, 1867. M. Mioc.; N.A.
†*Hemisyntrachelus* Brandt, 1873. L. Plioc.; Eu.
†Fam. Acrodelphidae Abel, 1905, p. 41. L.–U. Mioc.; Eu. M. Mioc.–L. Plioc.; N.A.
†*Acrodelphis* Abel, 1900. L.–U. Mioc.; Eu. M. Mioc.; N.A.
†*Schizodelphis* Gervais, 1861 (=†*Cyrtodelphis* Abel, 1900). L. Mioc.–L. Plioc.; Eu. L. Mioc.; Af. M. Mioc., L. Plioc.; N.A.
†*Eoplatanista* Dal Piaz, 1916. L. Mioc.; Eu.
†*Champsodelphis* Gervais, 1848–1852. M.–U. Mioc.; Eu.
†*Heterodelphis* Brandt, 1873. M.–U. Mioc.; Eu.
†*Pomatodelphis* Allen, 1921. M. Mioc.; Eu. L. Plioc.; N.A.
Fam. Monodontidae Gray, 1821, p. 310. [Including Delphinapteridae Weber, 1904, pp. 577, 579 = Delphinapterinae Gill, 1871a, p. 124.] Pleist.; Eu., N.A. R.; N. oceans.
Delphinapterus Lacépède, 1804. Pleist.; N.A. R.; N. oceans. Beluga, white whale.
Monodon Linnaeus, 1758. Pleist.; Eu., N.A. R.; Arctic, N. Atlantic. Narwhal.
Fam. Delphinidae Gray, 1821, p. 310. L. Mioc.–R.; Eu., N.A. R.; all seas.
†*Delphinavus* Lull, 1914. L. Mioc.; N.A.
†*Protodelphinus* Dal Piaz, 1922. L. Mioc.; Eu.
†*Iniopsis* Lydekker, 1893. L. Mioc.; Eu.
†*Kentriodon* Kellogg, 1927. M. Mioc.; N.A.
†*Delphinodon* Leidy, 1869. M. Mioc.; N.A.
†*Delphinopsis* Müller, 1853. U. Mioc.; Eu.
†*Agabelus* Cope, 1875. M. Mioc.; N.A.
†*Belosphys* Cope, 1875. M. Mioc.; N.A.
†*Ixacanthus* Cope, 1868. M. Mioc.; N.A.
†*Tretosphys* Cope, 1868. M. Mioc.; N.A.
†*Liolithax* Kellogg, 1931. M. Mioc.; N.A.
†*Oedolithax* Kellogg, 1931. M. Mioc.; N.A.
†*Lamprolithax* Kellogg, 1931. M. Mioc.; N.A.
†*Nannolithax* Kellogg, 1931. M. Mioc.; N.A.
†*Platylithax* Kellogg, 1931. M. Mioc.; N.A.
†*Loxolithax* Kellogg, 1931. M. Mioc.; N.A.
†*Grypolithax* Kellogg, 1931. M. Mioc.; N.A.
†*Ceterhinops* Leidy, 1877. U. Mioc.; N.A.
†*Stereodelphis* Gervais, 1848–1852. M. Mioc.; Eu.
†*Macrochirifer* Brandt, 1874. U. Mioc.; Eu.
†*Pithanodelphis* Abel, 1905. U. Mioc.; Eu.
Steno Gray, 1846. L.–M. Plioc.; Eu. R.; oceans except polar. Long-beaked dolphin.
Sotalia Gray, 1866. R.; Indian Ocean, W. Af., eastern S.A. White dolphin.
Prodelphinus Gervais, 1880. R.; Atlantic. Spotted dolphin.
Delphinus Linnaeus, 1758. L.–M. Plioc.; Eu. R.; all seas. (Common) dolphin.
Grampus Gray, 1828. R.; seas except polar. Grampus,[1] Risso's dolphin.

[1] Like several other names among Cetacea, and indeed like most truly vernacular mammal names, "grampus" is applied to several different animals. It is merely a corruption of the French for "big fish."

Tursiops Gervais, 1855 (=*Tursio* Gray, 1843, *nec* Fleming, 1822). U. Plioc.; Eu. R.; all seas except polar. Bottle-nosed dolphin or porpoise.

Lagenorhynchus Gray, 1846. R.; seas except polar. Spectacled dolphin, striped dolphin.

Cephalorhynchus Gray, 1846. R.; S. seas.

Orcinus Fitzinger, 1860 (=*Orca* Gray, 1846, *nec* Wagler, 1830). M. Plioc.; Eu. R.; all seas. Killer "whale."

Pseudorca Reinhardt, 1862. U. Plioc.; Eu., Japan. R.; all seas. Lesser killer, false killer.

Orcaella[1] Gray, 1866. R.; S. As. Irrawaddy River dolphin.

Globicephala Lesson, 1828. Pleist.; N.A. R.; seas except polar. Ca'ing whale, "blackfish."

Lissodelphis Gloger, 1841 (=*Tursio* Wagler, 1830, *nec* Fleming, 1822). R.; all oceans. "Right whale" dolphin.

Fam. Phocaenidae Bravard, 1885, p. 144 (=Phocaenina Gray, 1825, p. 340). U. Mioc.; Eu. Pleist.; New Zealand. R.; oceans except polar. Porpoises.

†*Palaeophocaena* Abel, 1905. U. Mioc.; Eu.

†*Protophocaena* Abel, 1905. U. Mioc.; Eu.

†*Phocaenopsis* Huxley, 1859. Pleist.; New Zealand.

Phocaena Cuvier, 1817. [Including *Phocaenoides* Andrews, 1911; etc.] R.; seas except polar. (Common) porpoises.

Neophocaena Palmer, 1899 (=*Neomeris* Gray, 1846, *nec* Lamouroux, 1816). R.; Indian Ocean, W. Pacific.

Suborder MYSTICETI Flower, 1864, p. 388.[2] Whale-bone whales.

†Fam. Cetotheriidae Cabrera, 1926, p. 369 (=Cetotheriinae Brandt, 1872, p. 116). M. Olig.–L. Plioc.; Eu. L. Mioc.; S.A. M.–U. Mioc.; N.A.

†*Pachycetus* Van Beneden, 1883. M. Olig.; Eu.

†*Cetotheriopsis* Brandt, 1871. U. Olig.; Eu. L. Mioc.; S.A.

†*Aglaocetus* Kellogg, 1934. L. Mioc.; S.A.

†*Cophocetus* Packard and Kellogg, 1934. M. Mioc.; N.A.

†*Mauicetus* Benham, 1939. L. Mioc.; New Zealand.

†*Peripolocetus* Kellogg, 1931. M. Mioc.; N.A.

†*Tiphyocetus* Kellogg, 1931. M. Mioc.; N.A.

†*Cephalotropis* Cope, 1896. U. Mioc.; N.A.

†*Cetotheriomorphis* Brandt, 1873. U. Mioc.; Eu.

†*Cetotherium* Brandt, 1843. U. Mioc.; Eu.

†*Eucetotherium* Brandt, 1873. U. Mioc.; Eu.

†*Herpetocetus* Van Beneden, 1872. U. Mioc.; Eu.

†*Isocetus* Van Beneden, 1880. U. Mioc.; Eu.

†*Mesocetus* Van Beneden, 1880. M.–U. Mioc.; Eu.

†*Metopocetus* Cope, 1896. U. Mioc.; N.A.

†*Mixocetus* Kellogg, 1934. U. Mioc.; N.A.

†*Parietobalaena* Kellogg, 1924. ?M.–U. Mioc.; N.A.

†*Plesiocetopsis* Brandt, 1873. U. Mioc.; N.A. L. Plioc.; Eu.

†*Rhegnopsis* Cope, 1896. U. Mioc.; N.A.

†*Siphonocetus* Cope, 1895. U. Mioc.; N.A.

†*Tretulias* Cope, 1895. U. Mioc.; N.A.

[1] Usually written "*Orcella*," which is better etymology but incorrect zoological nomenclature.

[2] Spelled Mysticete by Flower. According to Hay, 1930, p. 571, Cope first used Mysticeti, 1891a, p. 69.

†*Ulias* Cope, 1895. U. Mioc.; N.A.
†*Amphicetus* Van Beneden, 1880. L. Plioc.; Eu.
†*Heterocetus* Van Beneden, 1880. L. Plioc.; Eu.
Fam. Rhachianectidae Weber, 1904, p. 575. R.; N. Pacific.
Rhachianectes Cope, 1869. R.; N. Pacific. Gray whale.
Fam. Balaenopteridae Gray, 1864a, p. 203. U. Mioc.–Pleist.; N.A. L.–M. Plioc.; Eu. R.; all oceans.
†*Mesoteras* Cope, 1870. U. Mioc.; N A.
†*Megapteropsis* Van Beneden, 1872. L. Plioc.; Eu.
†*Plesiocetus* Van Beneden, 1859. L. Plioc.; Eu.
†*Burtinopsis* Van Beneden, 1872. M. Plioc.; Eu.
†*Palaeocetus* Seeley, 1865. M. Plioc.; Eu.
†*Idiocetus* Capellini, 1876. M. Plioc.; Eu.
†*Notiocetus* Ameghino, 1891. Plioc.; S.A.
Balaenoptera Lacépède, 1804. [Including †*Cetotheriophanes* Brandt, 1873.] L. Plioc.–Pleist.; N.A. L.–M. Plioc.; Eu. R.; all oceans. Rorqual, fin whale, finback.
Megaptera Gray, 1846. L. Plioc., Pleist.; N.A. M. Plioc.; Eu. R.; all oceans. Hump-backed whale.
Sibbaldus Gray, 1864. R.; all oceans. Sulphur-bottom whale, blue whale.
Fam. Balaenidae Gray, 1825, p. 340 (=Balanadae Gray, 1821, p. 310). [Including Neobalaenidae Miller, 1923, p. 21.] L. Mioc., Pleist.; S.A. L.–U. Plioc.; Eu. R.; Arctic, Atlantic, Pacific oceans.
†*Morenocetus* Cabrera, 1926. L. Mioc.; S.A.
†*Protobalaena* Du Bus, 1867. L. Plioc.; Eu.
†*Balaenotus* Van Beneden, 1872. M. Plioc.; Eu.
†*Balaenula* Van Beneden, 1872. M. Plioc.; Eu.
Balaena Linnaeus, 1758. L.–U. Plioc.; Eu. R.; Arctic. Greenland right whale, bowhead.
Eubalaena Gray, 1864. Pleist.; S.A. R.; oceans except Arctic. Right whale.
Neobalaena Gray, 1870. R.; S. Pacific.

Cohort FERUNGULATA, new.
Superorder FERAE Linnaeus, 1758, p. 37.
Order CARNIVORA Bowdich, 1821, p. 33 (=Carnivori Vicq d'Azyr, 1792, p. civ).
†Suborder CREODONTA Cope, 1875b, p. 444.
†Superfam. Arctocyonoidea Trouessart, 1885, p. 7 (=†Arctocyonoidae Hay, 1930, p. 459; †Procreodi Matthew, 1915, p. 5).
†Fam. Arctocyonidae Murray, 1866, p. 117. [Including †Oxyclaenidae Scott, 1892, p. 294; †Chriacidae Osborn and Earle, 1895, p. 20; †Triisodontidae Scott, 1892, p. 300.] L. Paleoc.–L. Eoc.; N.A. U. Paleoc., ?U. Eoc.; Eu. ?U. Paleoc.; ?As.
†Subfam. Oxyclaeninae Matthew, 1937, p. 38 (=†Oxyclaenidae Scott, 1892, p. 294). [Including †Chriacinae Matthew, 1937, p. 64=†Chriacidae Osborn and Earle, 1895, p. 20.] L. Paleoc.–L. Eoc.; N.A. U. Paleoc.; Eu.
†*Oxyclaenus* Scott, 1892. L. Paleoc.; N.A.
†*Loxolophus* Cope, 1885. L. Paleoc.; N.A.
†*Carcinodon* Scott, 1892. L. Paleoc.; N.A.
†*Protogonodon* Scott, 1892. L. Paleoc.; N.A.

†*Deuterogonodon* Simpson, 1935. M. Paleoc.; N.A.
†*Tricentes* Cope, 1883. M. Paleoc.; N.A.
†*Mimotricentes* Simpson, 1937. M. Paleoc.; N.A.
†*Prothryptacodon* Simpson, 1935. M. Paleoc.; N.A.
†*Thryptacodon* Matthew, 1915. U. Paleoc.–L. Eoc.; N.A.
†*Arctocyonides* Lemoine, 1891. U. Paleoc.; Eu.
†*Chriacus* Cope, 1883. L. Paleoc.–L. Eoc.; N.A.
†*Metachriacus* Simpson, 1935. M. Paleoc.; N.A.
†*Spanoxyodon* Simpson, 1935. M. Paleoc.; N.A.
†*Deltatherium* Cope, 1881. M. Paleoc.; N.A.

†Subfam. Arctocyoninae Giebel, 1855, p. 755 (= †Arctocyonidae of most authors, not *sensu lato* as here). M. Paleoc.–L. Eoc.; N.A. U. Paleoc.; Eu.
†*Claenodon* Scott, 1892. [Including †*Neoclaenodon* Gidley, 1919.] M. Paleoc.; N.A.
†*Arctocyon* De Blainville, 1841. U. Paleoc.; Eu.
†*Anacodon* Cope, 1882. L. Eoc.; N.A.

†Subfam. Triisodontinae Trouessart, 1904, p. 161 (= †Triisodontidae Scott, 1892, p. 300). L.–M. Paleoc.; N.A.
†*Baioconodon* Gazin, 1941. L. Paleoc.; N.A.
†*Eoconodon* Matthew and Granger, 1921. L. Paleoc.; N.A.
†*Triisodon* Cope, 1881. M. Paleoc.; N.A.
†*Goniacodon* Cope, 1888. M. Paleoc.; N.A.

?†Arctocyonoidea *incertae sedis:*
†*Paroxyclaenus* Teilhard de Chardin, 1921. U. Eoc.; Eu.
†*Hyracolestes* Matthew and Granger, 1925. U. Paleoc.; As.
†*Didymoconus* Matthew and Granger, 1924. L. Olig.; As.
†*Ardynictis* Matthew and Granger, 1925. L. Olig.; As.

†Superfam. Mesonychoidea Osborn, 1910,[1] p. 527 (= †Acreodi Matthew, 1909a, p. 327).

†Fam. Mesonychidae Cope, 1875b, p. 444. M. Paleoc.–U. Eoc.; N.A. U. Paleoc.–L. Eoc.; Eu. U. Eoc.; As.
†*Microclaenodon* Scott, 1892. M. Paleoc.; N.A.
†*Dissacus* Cope, 1881. M. Paleoc.–L. Eoc.; N.A. U. Paleoc.–L. Eoc.; Eu.
†*Hapalodectes* Matthew, 1909. L. Eoc.; N.A. ?U. Eoc.; ?As.
†*Pachyaena* Cope, 1874. L. Eoc.; N.A., Eu.
†*Synoplotherium* Cope, 1872. [Including †*Dromocyon* Marsh, 1876.] M. Eoc.; N.A.
†*Mesonyx* Cope, 1872. M.–?U. Eoc.; N.A.
†*Harpagolestes* Wortman, 1901. M.–U. Eoc.; N.A.
†*Andrewsarchus* Osborn, 1924. U. Eoc.; As.

†Superfam. Oxyaenoidea Osborn, 1910, p.]527 (= †Pseudocreodi Matthew, 1909a, p. 327).

†Fam. Oxyaenidae Cope, 1877, p. 89. U. Paleoc.–M. Eoc.; N.A. L.–U. Eoc.; Eu. U. Eoc.; As.

†Subfam. Oxyaeninae Trouessart, 1885, p. 15. U. Paleoc.–M. Eoc.; N.A. U. Eoc.; As.

[1] The assignment of authorship in this classification (in Osborn's "Age of mammals") is seldom clear. The section in which the word Mesonychoidea occurs is said to be "chiefly by Matthew," but as Matthew does not appear subsequently ever to have used this term in his independent studies it may perhaps be assumed to have been an insertion by Osborn, and is in any case usually assigned to him as responsible for the work as a whole.

†*Oxyaena* Cope, 1874. [Including †*Dipsalidictis* Matthew, 1915.] U. Paleoc.–L. Eoc.; N.A.
†*Dipsalidictides* Denison, 1938. L. Eoc.; N.A.
†*Protopsalis* Cope, 1880. L. Eoc.; N.A.
†*Patriofelis* Leidy, 1870. M. Eoc.; N.A.
†*Sarkastodon* Granger, 1938. U. Eoc.; As.

†Subfam. Palaeonictinae Denison, 1938, p. 174. U. Paleoc.–L. Eoc.; N.A. L.–U. Eoc.; Eu.
†*Dipsalodon* Jepsen, 1930. U. Paleoc.; N.A.
†*Palaeonictis* De Blainville, 1842. L. Eoc.; Eu., N.A.
†*Ambloctonus* Cope, 1875. L. Eoc.; N.A.
†*Paroxyaena* Martin, 1906. U. Eoc.; Eu.

†Fam. Hyaenodontidae Leidy, 1869, pp. 38, 369. [Including †Proviverridae Schlosser, 1886b, p. 293.] L. Eoc.–M. Olig.; N.A. M. Eoc.–M. Olig.; Eu. U. Eoc.–L. Olig., L. Plioc.; As. L. Olig., L. Mioc.; Af.

†Subfam. Proviverrinae Matthew, 1909a, p. 465 (=†Proviverridae Schlosser, 1886b, p. 293, *sensu stricto*). L.–M. Eoc.; N.A. M. Eoc.–L. Olig.; Eu. L. Olig.; Af. L. Plioc.; As.
†*Sinopa* Leidy, 1871. L.–M. Eoc.; N.A. M. Eoc.; Eu.
†*Tritemnodon* Matthew, 1906. L.–M. Eoc.; N.A.
†*Prorhyzaena* Rütimeyer, 1891. M. Eoc.; Eu.
†*Proviverra* Rütimeyer, 1862. L.–M. Eoc.; Eu.
†*Quercytherium* Filhol, 1882. U. Eoc.; Eu.
†*Galethylax* Gervais, 1848–1852. U. Eoc.; Eu.
†*Cynohyaenodon* Filhol, 1873. ?U. Eoc.–?L. Olig.; Eu.
†*Paracynohyaenodon* Martin, 1906. U. Eoc.; Eu., As.
†*Metasinopa* Osborn, 1909. L. Olig.; Egypt.
†*Dissopsalis* Pilgrim, 1910. L. Plioc.; As.

†Subfam. Hyaenodontinae Trouessart 1885, p. 9 (=†Hyaenodontidae, *sensu stricto*). M. Eoc.–M. Olig.; Eu. U. Eoc.–M. Olig.; N.A. U. Eoc.–L. Olig.; As. L. Olig., L. Mioc.; Af.
†*Propterodon* Martin, 1906. M. Eoc.; Eu. U. Eoc.; As.
†*Apterodon* Fischer, 1881. L. Olig.; Eu., Af.
†*Pterodon* De Blainville, 1839. U. Eoc.–L. Olig.; Eu. U. Eoc.; N.A., As. L. Olig.; Egypt.
†*Hemipsalodon* Cope, 1885. L. Olig.; N.A.
†*Dasyurodon* Andreae, 1887. M. Olig.; Eu.
†*Hyaenodon* Laizer and Parieu, 1838. U. Eoc.–M. Olig.; Eu., N.A. L. Olig.; As., Af.
†*Metapterodon* Stromer, 1926. L. Mioc.; Af.

†Subfam. Limnocyoninae Wortman, 1902, p. 128. L.–U. Eoc.; N.A. U. Eoc.; Eu.
†*Prolimnocyon* Matthew, 1915. L. Eoc.; N.A.
†*Limnocyon* Marsh, 1872. M.–U. Eoc.; N.A.
†*Thinocyon* Marsh, 1872. M. Eoc.; N.A.
†*Oxyaenodon* Matthew, 1899. U. Eoc.; N.A.
†*Thereutherium* Filhol, 1876. U. Eoc.; Eu.

†Subfam. Machaeroidinae Matthew, 1909a, p. 330.[1] M.–U. Eoc.; N.A.

[1] Matthew used this name without definition at one point in his memoir (1909, p. 330) but in another (p. 461) he placed †*Machaeroides* in the †Limnocyoninae. The subfamily name there appears as "Machairodontinae," but this is clearly a misprint since Matthew always spelled the generic name *Machaeroides*. Denison (1938) first definitely diagnosed the subfamily and correctly spelled its name, yet I think he is correct in ascribing it to Matthew.

†*Machaeroides* Matthew, 1909. M. Eoc.; N.A.
†*Apataelurus* Scott, 1937. U. Eoc.; N.A.
?†Hyaenodontidae *incertae sedis:*
†*Opisthopsalis* Matthew, Granger, and Simpson, 1929. U. Paleoc.; As.
†CREODONTA *incertae sedis:*
†Fam. Creotarsidae[1] Hay, 1930, p. 487.
†*Creotarsus* Matthew, 1918. L. Eoc.; N.A.
Suborder FISSIPEDA Blumenbach, 1791.[2]
†Superfam. Miacoidea Simpson, 1931a, pp. 263, 276 (=†Miacoidae Teilhard de Chardin, 1915, p. 188[3]; Eucreodi Matthew, 1909a, p. 327).
†Fam. Miacidae Cope, 1880, p. 78 (=†Uintacyonidae Hay, 1902, p. 759). [Including †Viverravidae Wortman and Matthew, 1899, p. 136.] M. Paleoc.–U. Eoc.; N.A. U. Eoc.; Eu. U. Eoc., ?L. Olig.; As.
†Subfam. Viverravinae Matthew, 1909a, p. 345 (=†Viverravidae Wortman and Matthew, 1899, p. 136). M. Paleoc.–U. Eoc.; N.A. U. Eoc.; Eu. ?L. Olig.; ?As.
†*Didymictis* Cope, 1875. M. Paleoc.–L. Eoc.; N.A.
†*Ictidopappus* Simpson, 1935. M. Paleoc.; N.A.
†*Viverravus* Cope, 1872. L.–M. Eoc.; N.A. ?L. Olig.; ?As. U. Eoc.; Eu.
†*Plesiomiacis* Stock, 1935. U. Eoc.; N.A.
†Subfam. Miacinae Trouessart, 1885, p. 18. L.–U. Eoc.; N.A. U. Eoc.; As., Eu.
†*Uintacyon* Leidy, 1871. L.–U. Eoc.; N.A.
†*Miacis* Cope, 1872. [Including †*Mimocyon* Peterson, 1919.] L.–U. Eoc.; N.A. U. Eoc.; As., Eu.
†*Tapocyon* Stock, 1934. U. Eoc.; N.A.
†*Vulpavus* Marsh, 1871. L.–M. Eoc.; N.A.
†*Vassacyon* Matthew, 1909. L. Eoc.; N.A.
†*Oödectes* Wortman, 1901. M. Eoc.; N.A.
†*Palaearctonyx* Matthew, 1909. M. Eoc.; N.A.
†*Pleurocyon* Peterson, 1919. U. Eoc.; N.A.
Superfam. Canoidea Simpson, 1931a, p. 276 (=Arctoidea Flower, 1869, p. 15, plus Cynoidea Flower, 1869, p. 24; Arctoidea of most later authors; Ursoidae Hay, 1930, p. 488).
Fam. Canidae Gray, 1821, p. 301 (=Canini Fischer, 1817, p. 372). [Including Amphicyonidae Trouessart, 1885, p. 57; Lycaonidae Rochebrune, 1883, p. 133; Megalotidae Gray, 1869a, p. 210; Otocyonidae Trouessart, 1885, p. 51; etc.] U. Eoc.–R.; N.A., Eu. L. Olig.–R.; As. Pleist.–R.; S.A., Af. R.; Aus. Dogs, wolves, foxes, etc.
Subfam. Caninae Gill, 1872, p. 63. U. Eoc.–R.; N.A., Eu. Pleist.–R.; As., S.A. R.; Af., Aus.
†*Procynodictis* Wortman and Matthew, 1899. U. Eoc.; N.A.

[1] This family and genus are placed here, following Camp, Taylor, and Welles, 1942.
[2] This name is generally spelled "Fissipedia" and credited to Fischer von Waldheim, 1813. Blumenbach's prior use seems valid. It included much extraneous material, but that is true of almost all old names. Both Blumenbach and Fischer von Waldheim spelled the word Fissipeda, and there is no good reason for the subsequent change.
[3] Hay, 1930, also used this name and credited it to Teilhard de Chardin, but it is clear that Teilhard did not mean it as the name of a superfamily in any usual sense.

†*Cynodictis* Bravard and Pomel, 1850. U. Eoc.–L. Olig.; Eu.
†*Pseudocynodictis* Schlosser, 1911. (Confused with †*Cynodictis* by many authors.) L.–U. Olig.; N.A.
†*Daphoenus* Leidy, 1850. L.–U. Olig.; N.A.
†*Nothocyon* Matthew, 1899. L. Olig.–L. Mioc.; N.A.
†*Cynodesmus* Scott, 1893. L. Mioc.; N.A.
†*Mesocyon* Scott, 1890. U. Olig.–L. Mioc.; N.A.
†*Tomarctus* Cope, 1873. L. Mioc.–L. Plioc.; N.A.
†*Alopecodon* Viret, 1933. M. Mioc.; Eu.
†*Tephrocyon* Merriam, 1906. M. Mioc.–L. Plioc.; N.A.
†*Leptocyon* Matthew, 1918. L. Plioc.; N.A.
†*Aenocyon* Merriam, 1918.[1] Pleist.; N.A.
†*Theriodictis* Mercerat, 1891 (= †*Dinocynops* Ameghino, 1898). Pleist.; S.A.
†*Sivacyon* Pilgrim, 1932. Pleist.; As.
Canis Linnaeus, 1758. [Including *Thos* Oken, 1816; *Simenia* Gray, 1868; and many proposed genera and subgenera.] U. Plioc.–R.; N.A. Pleist.–R.; E., As. R.; world wide.[2] Wolf, wild and domestic true dogs, coyotes, jackals, etc.
Alopex Kaup, 1829. R.; Arctic. Arctic (blue or white) fox.
Vulpes Frisch, 1775. ?U. Mioc., Pleist.–R.; N.A. Pleist.–R.; Eu., As. R.; N. Af. (Common) fox, red fox, kit fox, etc.
Fennecus Desmarest, 1804 (= *Megalotis* Illiger, 1811). R.; N. Af. Fennec.
Urocyon Baird, 1857. Pleist.–R.; N.A. R.; northern S.A. Gray fox.
Nyctereutes Temminck, 1838–1839. R.; E. As. Hao, "raccoon" dog.
Dusicyon H. Smith, 1839. Pleist.–R.; S.A.
Subgenera of *Dusicyon:*
Dusicyon (*Dusicyon*) H. Smith, 1839. [Including *Pseudalopex* Burmeister, 1856.] Pleist.–R.; S.A. Culpeo, South American "fox," Falkland "wolf."
Dusicyon (*Cerdocyon*) H. Smith, 1839. [Including *Atelocynus* Cabrera?[3]] R.; S.A. Maikong, crab-eating "fox," bush "fox" or "dog."
Dusicyon (*Lycalopex*) Burmeister, 1854. Pleist.–R.; S.A. (South American) field "fox."
Chrysocyon H. Smith, 1839. R.; S.A. Guara, aguará-guazú, maned "wolf."

Subfam. Simocyoninae Zittel, 1893, p. 632 (= †Simocyonidae Dawkins, 1868, p. 1). [Including Lycaonina Gray, 1868c, p. 494; Cuoninae Miller, 1924, p. 155; Speothoinae Pocock, 1914, p. 929; †Thaumastocyoninae Hürzeler, 1940a, p. 225.] M. Olig.–L. Plioc.; N.A. U. Olig.–L. Plioc.; Eu. Pleist.–R.; As., S.A. R.; Af.
†*Brachyrhynchocyon* Loomis, 1936 (= †*Brachicyon* Loomis, 1931, *nec* †*Brachycyon* Filhol, 1872). M. Olig.; N.A.

[1] Often, with considerable reason, placed as no more than a subgenus of *Canis*. Perhaps some of the supposed fossil specimens of *Canis* in South America belong here.
[2] But not wild in South America and probably introduced by man in Australia although wild or at least feral there. The genus is recorded in the Pleistocene of South America, but the references are unreliable except in a broad sense and true *Canis, sensu stricto*, seems to be a human importation there.
[3] Name for *Dusicyon* (*Cerdocyon*) *microtis* used in Cabrera and Yepes, 1940. I have not seen its formal proposal.

†*Haplocyon* Schlosser, 1901. U. Olig.–L. Mioc.; Eu.
†*Haplocyonoides* Hürzeler, 1940. L. Mioc.; Eu.
†*Temnocyon* Cope, 1878. U. Olig.–L. Mioc.; N.A.
†*Enhydrocyon* Cope, 1879. L. Mioc.; N.A.
†*Philotrox* Merriam, 1906. L. Mioc.; N.A.
†*Thaumastocyon* Stehlin and Helbing, 1925. M. Mioc.; N.A.
†*Euoplocyon* Matthew, 1924. U. Mioc.; N.A.
†*Araeocyon* Thorpe, 1922 (= †*Pliocyon* Thorpe, 1921, *nec* Matthew, 1918). L. Plioc.; N.A.
†*Simocyon* Wagner, 1858 (= †*Pseudocyon* Wagner, 1857, *nec* Lartet, 1851). L. Plioc.; Eu.
†*Metarctos* Gaudry, 1860. L. Plioc.; Eu.
†*Protocyon* Giebel, 1855 (= †*Palaeocyon* Lund, 1843, *nec* De Blainville, 1841). Pleist.; S.A.
Speothos Lund, 1839 (= *Icticyon* Lund, 1843; *Cynogale* Lund, 1842, *nec* Gray, 1837).[1] Pleist.–R.; S.A. Bush dog.
Cuon Hodgson, 1837 (= *Cyon* Agassiz, 1846, and most later authors). Pleist.–R.; As. Dhole, red dog.
Lycaon Brookes, 1827. R.; Af. Cape hunting dog.

?Simocyoninae *incertae sedis:*
†*Ischyrocyon* Matthew, 1904. U. Mioc.; N.A.

†Subfam. Amphicynodontinae, new name (= †Cynodontinae Schlosser, 1911b, p. 389). [Including †Hemicyoninae Frick, 1926, p. 12.] U. Eoc.–L. Plioc.; Eu. L. Mioc.–L. Plioc.; N.A. L. Olig., U. Mioc., ?L. Plioc.; As.
†*Plesiocyon* Schlosser, 1887. U. Eoc.; Eu.
†*Amphicynodon* Filhol, 1882 (= †*Cynodon* Aymard, 1848, *nec* Spix, 1829). [Including †*Paracynodon* Schlosser, 1899.] Olig.; Eu.
†*Pachycynodon* Schlosser, 1887. Olig.; Eu. L. Olig.; As. L. Mioc.; N.A.
†*Parictis* Scott, 1893. L. Olig.–L. Mioc.; N.A.
†*Cephalogale* Jourdan, 1862. L. Olig.–L. Plioc.; Eu. L. Mioc.; As.
†*Hemicyon* Lartet, 1851. M.–U. Mioc.; Eu. U. Mioc.–L. Plioc.; N.A. U. Mioc.; As.
†*Dinocyon* Jourdan, 1861. U. Mioc.–L. Plioc.; Eu.

?†Amphicynodontinae *incertae sedis:*
†*Allocyon* Merriam, 1930. L. Mioc.; N.A.
†*Amphicticeps* Matthew and Granger, 1924. L. Olig.; As.

†Subfam. Amphicyoninae Trouessart, 1885, p. 6. U. Eoc.–L. Plioc.; Eu. L.–U. Mioc.; N.A. U. Mioc.–L. Plioc.; As.
†*Pseudamphicyon* Schlosser, 1887. U. Eoc.–L. Olig.; Eu.
†*Amphicyon* Lartet, 1836. U. Olig.–L. Plioc.; Eu. M.–U. Mioc.; N.A. U. Mioc.–L. Plioc.; As.
†*Pseudocyon* Lartet, 1851. U. Olig.–M. Mioc.; Eu.
†*Paradaphaenus* Matthew, 1899. L. Mioc.; N.A.
†*Pericyon* Thorpe, 1922. L. Mioc.; N.A.
†*Daphoenodon* Peterson, 1909. L. Mioc.; N.A.

[1] The genus was first discovered fossil, and its living, but not generically distinct, representatives were differently named before the relationship was recognized. Many authors continue to use *Icticyon* for the living forms.

†*Mammocyon* Loomis, 1936. L. Mioc.; N.A.
†*Amphicyonopsis* Viret, 1929. M. Mioc.; Eu.
†*Pseudarctos* Schlosser, 1899. M.–U. Mioc.; Eu.
†*Vishnucyon* Pilgrim, 1932. L. Plioc.; As.
†*Arctamphicyon* Pilgrim, 1932. M. Plioc.; As.
?†Amphicyoninae *incertae sedis:*
†*Tomocyon* Viret, 1929. M. Mioc.; Eu.
†Subfam. Borophaginae, new. L. Mioc.–Pleist.; N.A. U. Mioc.; As.
†*Borocyon* Peterson, 1910. L. Mioc.; N.A.
†*Aelurodon* Leidy, 1858. U. Mioc.–L. Plioc.; N.A.
†*Gobicyon* Colbert, 1939. U. Mioc.; As.
†*Pliocyon* Matthew, 1918. U. Mioc.–L. Plioc.; N.A.
†*Osteoborus* Stirton and Vanderhoof, 1933. U. Mioc.–M. Plioc.; N.A.
†*Pliogulo* White, 1941. L. Plioc.; N.A.
†*Borophagus* Cope, 1892 (=†*Hyaenognathus* Merriam, 1903). M. Plioc.–Pleist.; N.A.
?†Borophaginae *incertae sedis:*
†*Hadrocyon* Stock and Furlong, 1926. L. Plioc.; N.A.
Subfam. Otocyoninae Trouessart, 1885, pp. 6, 51 (=Otocyonidae Trouessart, 1885, p. 51). R.; Af.
Otocyon Müller, 1836. R.; Af. "Gna-Schakal," big-eared fox, motlosi.
Fam. Ursidae Gray, 1825, p. 339 (=Ursinidae Gray, 1821, p. 301; Ursini Fischer, 1817, p. 372). M. Mioc.–R.; Eu. L. Plioc.–R.; N.A. M. Plioc.–R.; As. Pleist.–R.; S.A. Bears.
†*Agriotherium* Wagner, 1837 (=†*Hyaenarctos* Falconer and Cautley, 1845). [Including †*Lydekkerion* Frick, 1926.] L.–U. Plioc.; Eu. L.–M. Plioc.; N.A. M. Plioc.–Pleist.; As.
†*Indarctos* Pilgrim, 1913. L. Plioc.; Eu., N.A. M. Plioc.; As.
†*Ursavus* Schlosser, 1899. M. Mioc.–L. Plioc.; Eu. M. Mioc.; ?N.A.
†*Plionarctos* Frick, 1926. L. Plioc.; N.A.
†*Arctodus* Leidy, 1854. Pleist.; N.A.
†*Tremarctotherium* Kraglievich, 1926. Pleist.; N.A.
†*Arctotherium* Bravard, 1857. Pleist.; S.A.
†*Pararctotherium* Ameghino, 1904. Pleist.; S.A.
Tremarctos Gervais, 1855. R.; S.A. Spectacled bear.
Selenarctos Heude, 1901 (=*Arcticonus* Pocock, 1917). R.; As. Himalayan bear.
Ursus Linnaeus, 1758. [Including *Euarctos* Gray, 1864; *Danis* Gray, 1825, *nec* Fabricius, 1808.] L. Plioc.–R.; Eu. Pleist.–R.; N.A., As. Black bear, brown bear, blue bear, grizzly bear, (common) bear, etc.
Thalarctos Gray, 1825 (=*Thalassarctos* Gray, 1825).[1] ?Pleist.–R.; Arctic. Polar bear.
Helarctos Horsfield, 1825. M. Plioc.; Eu. Pleist.–R.; As. Sun bear, Malayan bear.
Melursus Meyer, 1793. Pleist.–R.; As. "Sloth" bear.

[1] Later than *Thalarctos*.

Fam. Procyonidae Bonaparte, 1850 (=Procyonina Gray, 1825, p. 339). [Including Cercoleptidae Bonaparte, 1838, p. 111; Nasuidae Gray, 1869a, p. 238; Bassariscidae Gray, 1869a, p. 246; Ailuridae Flower, 1869, p. 15=Ailurina Gray, 1843, p. xxi; Ailuropodidae Pocock, 1921a, p. 420=Ailuropodae Grevé, 1894, p. 217; Bassaricyonidae Coues, 1887, p. 516.] L. Mioc.–R.; N.A. U. Mioc.–L. Plioc.; Eu. L. Plioc.–R.; As. Plioc.–R.; S.A.

†Subfam. Cynarctinae McGrew, 1937, p. 444. L. Mioc.–L. Plioc.; N.A.

†*Cynarctoides* McGrew, 1938. L. Mioc.; N.A.

†*Cynarctus* Matthew, 1902. M. Mioc.–L. Plioc.; N.A.

Subfam. Procyoninae Gill, 1872, p. 6. [Including Potosinae Trouessart, 1904, p. 183; Bassaricyoninae Pocock, 1921a, p. 422; Nasuinae Gill, 1872, p. 6; Bassariscinae Pocock, 1921a, p. 421=Bassariscidae Gray, 1869a, p. 246.] L. Mioc.–R.; N.A. U. Mioc.–R.; S.A.

†*Phlaocyon* Matthew, 1899. L.–M. Mioc.; N.A.

†*Aletocyon* Romer and Sutton, 1927. L. Mioc.; N.A.

Bassariscus Coues, 1887 (=*Bassaris* Lichtenstein, 1831, *nec* Hübner, 1816–1821). [Including *Probassariscus* Merriam, 1911; *Jentinkia* Trouessart, 1904=*Wagneria* Jentink, 1886, *nec* Robineau-Desvoidy, 1830.] U. Mioc.–R.; N.A. Cacomistle, ring-tailed "cat."

Procyon Storr, 1780. [Including *Euprocyon* Gray, 1864.] U. Plioc.–R.; N.A. Pleist.–R.; S.A. Raccoon.

†*Cyonasua* Ameghino, 1885. U. Mioc.; S.A.

†*Amphinasua* Moreno and Mercerat, 1891. L. Plioc.; S.A.

†*Pachynasua* Ameghino, 1904. L.–U. Plioc.; S.A.

†*Brachynasua* Ameghino and Kraglievich, 1925. Pleist.; S.A.

Nasua Storr, 1780. Pleist.–R.; S.A. R.; Cent. A. Coati, coatimundi.

Nasuella Hollister, 1916. R.; S.A. Mountain coati.

Potos Cuvier and Geoffroy, 1795 (=*Cercoleptes* Illiger, 1811). R.; S.A., Cent. A. Kinkajou.

Bassaricyon Allen, 1876. R.; Cent. A., U.S.A.

Subfam. Ailurinae Trouessart, 1885, p. 25 (=Ailurina Gray, 1843, p. xxi). [Including Ailuropodinae=Ailuropodae Grevé, 1894, p. 217.] U. Mioc.–L. Plioc.; Eu. L. Plioc.–R.; As.

†*Sivanasua* Pilgrim, 1931 (=†*Ailuravus* Schlosser, 1916, *nec* Rütimeyer, 1891). U. Mioc.; Eu. L. Plioc.; As.

†*Parailurus* Schlosser, 1899. L. Plioc.; Eu.

Ailurus Cuvier, 1825. R.; As. Panda.

Ailuropoda Milne Edwards, 1870 (=*Ailuropus* Milne Edwards, 1871). [Including †*Aelureidopus* Smith Woodward, 1915.] Pleist.–R.; As. Giant panda.

Procyonidae *incertae sedis:*

†*Zodiolestes* Riggs, 1942. L. Mioc.; N.A.

Fam. Mustelidae Swainson, 1835, p. 321 (=Mustelini Fischer, 1817, p. 372). [Including Lutridae DeKay, 1842, pp. xv, 39=Lutrina Bonaparte, 1838, p. 111.] L. Olig.–R.; N.A., Eu., As. M. Plioc.–R.; Af. Pleist.–R.; S.A.

Subfam. Mustelinae Gill, 1872, p. 64. [Including Martinae Burmeister, 1850, p. 12 = Martina Wagner, 1841, p. 216; Potoriinae Schlosser, 1911b, p. 392; Guloninae Miller, 1912, p. 432 = Gulonina Gray, 1825, p. 339; Grisoninae Pocock, 1922a, p. 835; Tayrinae Pocock, 1922a, p. 833; Ictonychinae Pocock, 1922a, p. 835 = Zorillina Gray, 1865a, pp. 105, 150; Lyncodontinae Pocock, 1922a, p. 836.] L. Olig.–R.; N.A., Eu., As. Pleist.–R.; S.A. R.; Af.

†*Mustelavus* Clark, 1936. L. Olig.; N.A.

†*Plesictis* Pomel, 1846. L. Olig.–Mioc.; Eu.

†*Bunaelurus* Cope, 1873. L.–M. Olig.; N.A. L. Olig.; As.

†*Palaeogale* Meyer, 1846. L. Olig.–Mioc.; Eu. L. Olig.; As. M. Olig.; N.A.[1]

†*Oligobunis* Cope, 1881. L. Mioc.; N.A.

†*Promartes* Riggs, 1942. L. Mioc.; N.A.

†*Paroligobunis* Peterson, 1906. L. Mioc.; N.A.

†*Aelurocyon* Peterson, 1906. L. Mioc.; N.A.

†*Megalictis* Matthew, 1907. L. Mioc.; N.A.

†*Ischyrictis* Helbing, 1930. L.–U. Mioc.; Eu.

†*Laphyctis* Viret, 1933. M. Mioc.; Eu.

†*Plesiogulo* Zdansky, 1924. L. Plioc.; As. M. Plioc.: N.A.

†*Pseudictis* Schlosser, 1887. U. Mioc.; Eu.

†*Proputorius* Filhol, 1890. Mioc.; Eu. L. Plioc.; As.

†*Brachypsalis* Cope, 1890. U. Mioc.–M. Plioc.; N.A.

†*Plionictis* Matthew, 1924. M.–U. Mioc.; N.A.

†*Miomustela* Hall, 1930. U. Mioc.; N.A.

†*Sinictis* Zdansky, 1924. L. Plioc.–?Pleist.: As. L. Plioc.: Eu.

†*Cernictis* Hall, 1935. M. Plioc.; N.A.

†*Canimartes* Cope, 1892. U. Plioc.; N.A.

†*Trigonictis* Hibbard, 1941. U. Plioc.; N.A.

Mustela Linnaeus, 1758. [Including *Putorius* Frisch, 1775; *Lutreola* Wagner, 1841; *Kolonocus* Satunin, 1911; etc.] U. Mioc.[2]–R.; N.A., Eu. L. Plioc.[2]–R.; As. Pleist.–R.; S.A. R.; N. Af. Weasel, ferret, mink, ermine, polecat, stoat.

Vormela Blasius, 1884. R.; As., E. Eu.

Martes Frisch, 1775. L. Plioc.–R.; As., Eu. U. Plioc.–R.; N.A. Marten, sable, fisher.

Charronia Gray, 1865.[3] R.; As.

Galera Browne, 1789 (= *Tayra* Oken, 1816).[4] R.; Cent. A., S.A. Taira.

Grison Oken, 1816 (= *Galictis* Bell, 1826).[5] Pleist.; N.A. Pleist.–R.; S.A. R.; Cent. A. Grison.

[1] An unmistakable specimen of this genus has been found in the Lower Brule of South Dakota, although it has not been published.

[2] As with most living genera, pre-Pleistocene records may be viewed with doubt since they almost always use the generic name in a broader sense than among recent mammals and often prove to be erroneous when the species become better known.

[3] *Nec Charonia* Gistel, 1848. This is not considered to be true preoccupation, and the name *Charronia* is in general use, even though its slight difference in spelling from *Charonia* may be only an error.

[4] In recent years, students have been calling this genus *Tayra*, because of Allen's assertion that *Galera* dates only from Gray, 1843, but Palmer cites *Galera*, with the same type, as of Browne, 1789, long before Oken's work, and it therefore seems to be the correct name.

[5] Earlier authors and some more recent compilations use the antedated name *Galictis* and unite in it both *Grison* and *Galera*.

Grisonella Thomas, 1912. Pleist.–R.; S.A.
Lyncodon Gervais, 1844. Pleist.–R.; S.A.
Zorilla Oken, 1816[1] (=*Ictonyx* Kaup, 1835). R.; Af., W. As. Zorilla, African polecat.
Poecilictis Thomas and Hinton, 1920. R.; N. Af.
Poecilogale Thomas, 1883. R.; Af.
Gulo Frisch, 1775. Pleist.–R.; N.A., Eu. R.; As. Wolverine, carajou, glutton.

Subfam. Mellivorinae Gill, 1872, p. 64 (=Mellivorina Gray, 1865a, p. 103). L.–M. Plioc.; As. L. Plioc.; N.A. R.; Af. Ratels.
†*Eomellivora* Zdansky, 1924. L. Plioc.; As., N.A.
Mellivora Storr, 1780. M. Plioc.; As. R.; Af. Ratel, honey badger.

Subfam. Melinae Burmeister, 1850, p. 13 (=Melina Bonaparte, 1838, p. 111). [Including Taxidiinae Pocock, 1920, p. 436; Mydainae Pocock, 1922a, p. 834=Myadina Gray, 1825, p. 339; Helictidinae Gill, 1872, p. 6=Helictidina Gray, 1865a, pp. 103, 152.] M. Mioc.–R.; Eu. L. Plioc.–R.; As. U. Plioc.–R.; N.A. Badgers.
†*Trochictis* Meyer, 1842. M. Mioc.–L. Plioc.; Eu.
†*Trochotherium* Fraas, 1870. U. Mioc.; Eu.
†*Promeles* Zittel, 1890. L. Plioc.; Eu.
†*Parataxidea* Zdansky, 1924. L. Plioc.; Eu., As.
†*Melodon* Zdansky, 1924. U. Mioc.–L. Plioc.; As.
Meles Brisson, 1762. L. Plioc.–R.; As. U. Plioc.–R.; Eu. (Old World or European) badger.
Arctonyx Cuvier, 1825. R.; As. Sand badger.
Mydaus Cuvier, 1821. R.; E. Indies. Teledu.
Taxidea Waterhouse, 1839. U. Plioc.–R.; N.A. (American) badger.
Helictis Gray, 1831. R.; As. "Ferret" badger.
Melogale Geoffroy, 1834. R.; As.

Subfam. Mephitinae Gill, 1872, p. 65 (=Mephitina Bonaparte, 1845, p. 1). U. Mioc.–U. Plioc.; Eu. L. Plioc.; As. L. Plioc.–R.; N.A. Pleist.–R.; S.A. Skunks.
†*Trocharion* Major, 1903. U. Mioc.; Eu.
†*Promephitis* Gaudry, 1861. L.–U. Plioc.; Eu. L. Plioc.; As.
†*Pliogale* Hall, 1930. L. Plioc.; N.A.
†*Martinogale* Hall, 1930. L. Plioc.; N.A.
†*Brachyprotoma* Brown, 1908. U. Plioc.–Pleist.; N.A.
†*Osmotherium* Cope, 1896. [Including †*Pelycictis* Cope, 1896.] Pleist.; N.A.
Mephitis Cuvier, 1800. Pleist.–R.; N.A. Striped skunk.
Spilogale Gray, 1865. U. Plioc.–R.; N.A. Spotted skunk.
Conepatus Gray, 1837. Pleist.–R.; N.A., S.A. Hog-nosed skunk.

†Subfam. Leptarctinae Gazin, 1936a, p. 207. L. Mioc.–L. Plioc.; N.A.
†*Mephititaxus* White, 1941. L. Mioc.; N.A.
†*Leptarctus* Leidy, 1857. U. Mioc.–L. Plioc.; N.A.
†*Craterogale* Gazin, 1936. U. Mioc.; N.A.

Subfam. Lutrinae Baird, 1857, pp. 3, 183 (=Lutrina Bonaparte, 1838, p. 111). [Including Lataxinae Burmeister, 1850, p. 13

[1] It is possible that *Zorilla* is a *nomen vanum* and that *Ictonyx* should be used, as it is by some recent authors.

= Enhydrinae Gill, 1872, p. 65 = Enhydrina Gray, 1825, p. 340.] U. Olig.–R.; Eu. M. Mioc.–R.; N.A. L. Plioc.–R.; As. M. Plioc.–R.; Af. R.; S.A.

†*Potamotherium* Geoffroy, 1833. U. Olig.–L. Mioc.; Eu.

†*Paralutra* Roman and Viret, 1934. M. Mioc.; Eu.

†*Sthenictis* Peterson, 1910. M.–U. Mioc.; N.A.

†*Mionictis* Matthew, 1924. U. Mioc.; N.A.

†*Sivalictis* Pilgrim, 1932. L. Plioc.; As., Eu.

†*Vishnuonyx* Pilgrim, 1932. L. Plioc.; As.

†*Sivaonyx* Pilgrim, 1931. M. Plioc.; As.

†*Lutravus* Furlong, 1932. L.–U. Plioc.; N.A.

†*Nesolutra* Bate, 1935. Pleist.; Malta.

†*Cyrnaonyx* Helbing, 1935. Pleist.; Eu.

†*Enhydriodon* Falconer, 1868. L. Plioc.; Eu. U. Plioc.; As. M. Plioc.; Af.

Lutra Brisson, 1762. [Including *Lontra* Gray, 1843; *Hydrictis* Pocock, 1921 = *Hydrogale* Gray, 1865, *nec* Kaup, 1829; etc.] L. Plioc.–R.; Eu., As. U. Plioc.–R.; N.A. Pleist.–R.; S.A. R.; Af. (Common) otter.

Lutrogale Gray, 1865. R.; As. Simung.[1]

Pteronura Gray, 1837. R.; S.A. (Brazilian) giant otter, saro.

Amblonyx Rafinesque, 1832 (= *Micronyx* Allen, 1920; *Leptonyx* Lesson, 1842, *nec Leptonyx* Swainson, 1821). R.; S. As. (Asiatic) dwarf otter.

Aonyx Lesson, 1827. R.; Af. (African) small-clawed otter.

Paraonyx Hinton, 1921. R.; Af.

Enhydra Fleming, 1822 (= *Latax* Gloger, 1827; not preoccupied by *Enhydris* Merrem, 1820). U. Plioc.; Eu. R.; N. Pacific. Sea otter.

Superfam. Feloidea Simpson, 1931a, p. 277 (= Feloidae Hay, 1930, p. 538; Aeluroidea Flower, 1869, p. 22; Herpestoidei Winge, 1895, p. 46; Mungotoidea Pocock, 1919b, p. 515).

Fam. Viverridae Gray, 1821, p. 301.[2] [Including Cryptoproctidae Flower, 1869, p. 29 = Cryptoproctina Gray, 1864b, p. 508; Herpestidae Gray, 1869a, p. 143 = Herpestina Bonaparte, 1845, p. 1; Suricatidae Cope, 1882a, p. 474; Eupleridae Chenu, 1850–1858, p. 165, *fide* Palmer, 1904, p. 741; etc.] ?U. Eoc., L. Olig.–R.; Eu. L. Plioc.–R.; As. R.; Af., Madagascar.

†Subfam. Stenoplesictinae Schlosser, 1923, p. 473. ?U. Eoc.–M. Mioc.; Eu.

†*Stenoplesictis* Filhol, 1880. U. Eoc. or L. Olig.; Eu.

†*Palaeoprionodon* Filhol, 1880. U. Eoc. or L. Olig.; Eu. L. Olig.; As.

†*Leptoplesictis* Major, 1903. M. Mioc.; Eu.

?†Stenoplesictinae *incertae sedis:*

†*Amphicticeps* Matthew and Granger, 1924. L. Olig.; As.

Subfam. Viverrinae Gill, 1872, p. 69. [Including, among others, supposed subfamilies corresponding to the following tribes.] Mioc.–R.; Eu. U. Mioc.–R.; As. R.; Af., Madagascar.

[1] Usually believed to be the barang, rather than the simung, of Java, but Pohle has shown that this is an error.

[2] Gray spelled the name "Viveridae," an error corrected by Bonaparte, 1845.

Tribe Viverrini Winge, 1895, p. 47. Mioc.–R.; Eu. U. Mioc.–R.; As. R.; Af.
†*Semigenetta* Helbing, 1927. Mioc.; Eu.
†*Tungurictis* Colbert, 1939. U. Mioc.; As.
†*Vishnuictis* Pilgrim, 1932. M.–U. Plioc.; As.
Poiana Gray, 1864. R.; Af. African linsang.
Genetta Oken, 1816. R.; N. Af., S. Eu., W. As. Genet.
Viverricula Hodgson, 1838. R.; As. Rasse.
Osbornictis Allen, 1919. R.; Af. Water civet.
Viverra Linnaeus, 1758. R.; As. *Sensu lato* since M. Mioc. in Eu. and L. Plioc. in As. (Oriental) civet.
Civettictis Pocock, 1915. R.; Af. (African) civet.
Tribe Prionodontini, new form (=Prionodontina Gray, 1864b, p. 507). R.; As. Linsangs.
Prionodon Horsfield, 1824 (=*Linsang* Müller, 1839). R.; As. Linsang.
Pardictis Thomas, 1925. R.; As.
Subfam. Paradoxurinae Gill, 1872, p. 61 (=Paradoxurina Gray, 1864b, pp. 508, 526). R.; As., Af.
Tribe Nandiniini, new form (=Nandiniidae Pocock, 1929, p. 898). R.; Af.
Nandinia Gray, 1843. R.; Af. African palm civet, tree civet.
Tribe Arctogalidiini, new form (=Arctogalidiinae Pocock, 1933, pp. 969, 977). R.; E. Indies, S.E. As.
Arctogalidia Merriam, 1897 (=*Arctogale* Peters, 1863, *nec* Kaup, 1829). R.; E. Indies, S.E. As. (Small-toothed) palm civet.
Tribe Paradoxurini, new form (=Paradoxurina Gray, 1864b, pp. 506, 508). R.; As. Palm civets.
Paradoxurus Cuvier, 1821. R.; As. Musang.
Paguma Gray, 1831. R.; As.
Macrogalidia Schwarz, 1910. R.; As.
Arctictis Temminck, 1824. R.; As. Binturong.
Subfam. Hemigalinae Gill, 1872, pp. 4, 62 (=Hemigalina Gray, 1864b, pp. 508, 524). R.; As., Madagascar.
Tribe Fossini, new form (=Fossinae Pocock, 1915c, p. 350). R.; Madagascar.
Fossa Gray, 1864. R.; Madagascar. Fanaloka, Malagasy civet.[1]
Tribe Hemigalini, new form (=Hemigalina Gray, 1864b, p. 508). Asiatic palm civets.[2]
Hemigalus Jourdan, 1837. R.; As.
Chrotogale Thomas, 1912. R.; As.
Diplogale Thomas, 1912. R.; As.
Tribe Cynogalini, new form (=Cynogalina Gray, 1864b, p. 507). R.; As.
Cynogale Gray, 1837. R.; As. Mampalon, "otter" civet.
Tribe Euplerini, new form (=Eupleridae Chenu, 1850–1858, p. 165, *fide* Palmer, 1904, p. 741). R.; Madagascar.
Eupleres Doyère, 1835. R.; Madagascar. Falanouc.
Subfam. Galidiinae Gill, 1872, p. 61 (=Galidiina Gray, 1864b, pp. 508, 522; Galidictinae Mivart, 1882, p. 143). R.; Madagascar. Malagasy mongooses.

[1] Note that *Cryptoprocta*, and not the genus *Fossa*, is the fossa.
[2] The paradoxures and some other viverrids are also called palm civets.

Galidia Geoffroy, 1837. R.; Madagascar.
Galidictis Geoffroy, 1839. R.; Madagascar.
Mungotictis Pocock, 1915. R.; Madagascar.
Salanoia Gray, 1864 (=*Hemigalidia* Mivart, 1882). R.; Madagascar.

Subfam. Herpestinae Gill, 1872, p. 61 (=Herpestina Bonaparte, 1845, p. 3; Mungosina Gray, 1864b, p. 509=Mungotidae Pocock, 1919b, p. 515). [Including Suricatinae Thomas, 1882, p. 59, footnote.] U. Olig.–R.; Eu. R.; As., Af.

Tribe Suricatini, new form (=Suricatinae Thomas, 1882, p. 59, footnote=Suricatidae Cope, 1882a, p. 474). R.; Af.
Suricata Desmarest, 1804 (=*Ryzaena* Illiger, 1811). R.; Af. Suricate, mierkat.

Tribe Herpestini Winge, 1895, p. 47 (=Herpestina Bonaparte, 1845, p. 3). U. Olig.–R.; Eu. R.; Af., As. Mongooses.
Herpestes Illiger, 1811.[1] [Including *Galerella* Gray, 1864; *Myonax* Thomas, 1865.] R.; Af., As., Spain; introduced in the W. Indies; in a broad sense, in Eu. since U. Olig. Common mongoose, ichneumon.
Helogale Gray, 1861. [Including *Dologale* Thomas, 1926.] R.; Af. Dwarf mongooses.
Atilax Cuvier, 1826. R.; Af. Marsh mongooses.
Mungos Geoffroy and Cuvier, 1795 (=*Ariela* Gray, 1864).[2] R.; Af. Striped mongoose.
Crossarchus Cuvier, 1825. R.; Af. Cusimanse.
Ichneumia Geoffroy, 1837 (=*Lasiopus* Geoffroy, 1835, *nec* Dejean, 1833). R.; Af. White-tailed mongoose.
Bdeogale Peters, 1852. [Including *Galeriscus* Thomas, 1894.] R.; Af.
Rhynchogale Thomas, 1894 (=*Rhinogale* Gray, 1864, *nec* Gloger, 1841). R.; Af.
Cynictis Ogilby, 1833. [Including *Paracynictis* Pocock, 1916.] R.; Af. Mierkat.
Xenogale Allen, 1919. R.; Af.

Subfam. Cryptoproctinae Trouessart, 1885, pp. 6, 91 (=Cryptoproctina Gray, 1864b, p. 508). R.; Madagascar.
Cryptoprocta Bennett, 1833. R.; Madagascar. Fossa.

Fam. Hyaenidae Gray, 1869a, pp. vi, 211 (=Hyaenadae Gray, 1821, p. 302). [Including Protelidae Flower, 1869, p. 37=Protelina Geoffroy, 1851, p. xiv.]

†Subfam. Ictitheriinae Trouessart, 1897, p. 320.[3]
†*Ictitherium* Wagner, 1848 (=†*Galeotherium* Wagner, 1839, *nec* Jäger, 1839). [Including †*Palhyaena* Gervais, 1859; †*Thalassictis* Gervais, 1850, *ex* Nordmann.] L. Plioc.; Eu., As.

Subfam. Protelinae Mivart, 1882, p. 43 (=Protelina Geoffroy, 1851, p. xiv). R.; Af.

[1] Pocock believed the prior name *Mungos* to be a synonym of *Herpestes*, so used the former in this sense and made the corresponding changes in family and subfamily names, but Allen maintains that *Mungos* antedates *Ariela*, not *Herpestes*, and acceptance of this permits the maintenance of the more familiar and elegant *Herpestes*.

[2] Allen is followed in taking *Herpestes fasciatus* as the type of *Mungos* and Pocock in maintaining "*Ariela*" as distinct from *Herpestes* or *Crossarchus*. Contrary to Pocock's own opinion (also to Thomas and many who have followed Thomas and Pocock), this makes *Herpestes* valid in the usual sense and *Mungos* also valid but in a different sense. If Thomas were followed in making "*Ariela*"=*Crossarchus*, then "*Crossarchus*" would become *Mungos*.

[3] Spelled "Ictitherinae" by Trouessart, "Ictitheriinae" by Dietrich, 1927.

Proteles Geoffroy, 1824. R.; Af. Aard-"wolf."

Subfam. Hyaeninae Mivart, 1882, p. 143. L. Plioc.–Pleist.; Eu. U. Mioc.–R.; As. R.; Af. Hyenas.

†*Hyaenictis* Gaudry, 1861. L. Plioc.; Eu. ?U. Plioc.; ?As.

†*Lycyaena* Henel, 1862.[1] L.–M. Plioc.; Eu., As.

Crocuta Kaup, 1828. L. Plioc.–Pleist.; Eu. U. Mioc.–Pleist.; As. R.; Af. Spotted hyena.

Hyaena Brisson, 1762. U. Plioc.–Pleist.; Eu. Pleist.–R.; As. R.; Af. Striped hyena.

Fam. Felidae Gray, 1821, p. 302 (=Felini Fischer, 1817, p. 372). [Including Guepardidae Gray, 1869a, pp. v, 39; Lyncidae Schulze, 1900, p. 222=Lyncina Gray, 1867, p. 276; †Nimravidae Cope, 1881a, p. 167; †Machaerodontidae Woodward, 1898, p. 399; †Ailuromachairodontidae Kretzoi, 1929a, p. 1336; †Megantereontidae Kretzoi, 1929a, p. 1337.]

†Subfam. Proailurinae Zittel, 1893, p. 665.[2] U. Eoc. or L. Olig.–Mioc.; Eu. L.–M. Plioc.; As.

†*Proailurus* Filhol, 1879. U. Eoc. or L. Olig.–Mioc.; Eu.

†*Stenogale* Schlosser, 1887. U. Eoc. or L. Olig.–Mioc.; Eu.

†*Mellivorodon* Lydekker, 1884. M. Plioc.; As.

†*Vinayakia* Pilgrim, 1932. L.–M. Plioc.; As.

?†Proailurinae *incertae sedis:*

†*Aeluropsis* Lydekker, 1884. M. Plioc.; As.

†Subfam. Nimravinae Trouessart, 1885, pp. 6, 92 (=†Nimravidae Cope, 1881a, p. 167). [Including †Pogonodontinae Kretzoi, 1929a, p. 1334; †Dinictinae Kretzoi, 1929a, p. 1334; †Dinailurictinae Kretzoi, 1929a, p. 1337; †Pseudaelurinae Kretzoi, 1929a, p. 1330.] U. Eoc.–U. Mioc.; Eu. L. Olig.–M. Plioc.; N.A. L. Mioc.; Af. L. Plioc.; As. False sabertooths.

†*Ailurictis* Trouessart, 1885 (=†*Aelurogale* Filhol, 1872, *nec* †*Ailurogale* Fitzinger, 1869). U. Eoc.–M. Olig., ?M. Mioc.; Eu.

†*Dinictis* Leidy, 1854. [Including †*Metadeiniktis* Kretzoi, 1929.] L. Olig.–L. Mioc.; N.A.

†*Dinailurictis* Helbing, 1922. M. Olig.; Eu.

†*Nimravus* Cope, 1879. U. Olig.–L. Mioc.; N.A.

†*Dinaelurus* Eaton, 1922. L. Mioc.; N.A.

†*Archaelurus* Cope, 1879. L. Mioc.; N.A.

†*Pogonodon* Cope, 1880. L. Mioc.; N.A.

†*Pseudaelurus* Gervais, 1848–1852. [Including †*Afrosmilus* Kretzoi, 1929; †*Parapseudailurus* Kretzoi, 1929; †*Hyperailurictis* Kretzoi, 1929; †*Pratifelis* Hibbard, 1934; †*Adelphailurus* Hibbard, 1934.] L.–U. Mioc.; Eu. L. Mioc.; Af. U. Mioc.–M. Plioc.; N.A.

†*Metailurus* Zdansky, 1924. U. Mioc.–L. Plioc.; As.

Subfam. Felinae Trouessart, 1885, pp. 6, 92 (=Felini Fischer, 1817, p. 372). [Including Pantherinae Pocock, 1917, p. 332;

[1] Possibly a synonym of *Agnotherium* Kaup, 1833, and *Agnocyon* Kaup, 1862, but those names are almost indeterminate, and change from the well-known †*Lycyaena* is not advisable without better evidence.

[2] "†Proaelurinae" in Zittel, †Proailurinae in Pilgrim, 1931, p. 125.

Acinonychinae Pocock, 1917, p. 332=Guepardina Gray, 1867, p. 277; Neofelinae Kretzoi, 1929a, p. 1338.] L. Plioc.–R.; As., Eu. ?Plioc., Pleist.–R.; N.A. Pleist.–R.; S.A. R.; Af.; also now world wide by introduction. Cats.

†*Sivaelurus* Pilgrim, 1913. L. Plioc.; As.

†*Vishnufelis* Pilgrim, 1932. L. Plioc.; As.

†*Dinofelis* Zdansky, 1926. L. Plioc.; As.

Felis Linnaeus, 1758. [Including the subgenera and their synonyms listed below, all given generic rank by some extreme students.] ?Plioc., Pleist.–R.; N.A. Pleist.–R.; S.A. L. Plioc.–R.; Eu. U. Plioc.–R.; As. R.; Af.; now world wide by introduction.

Subgenera and synonyms of *Felis:*

Felis (*Felis*) Linnaeus, 1758. [Including *Catolynx* Severtzov, 1858[1]; *Chaus* Gray, 1843.] R.; Eu., As., Af.[2]; world wide by introduction. Domestic cat, Old World wild cat.

Felis (*Microfelis*) Roberts, 1926. R.; Af. Blackfooted cat.

Felis (*Lynx*) Kerr, 1792. [Including *Pardina* Kaup, 1829; *Caracal* Gray, 1843.] R.; Eu., As., Af., N.A. Lynx, bobcat, caracal.

Felis (*Otocolobus*) Brandt, 1842 (=*Trichaelurus* Satunin, 1905).[3] R.; As. Manul.

Felis (*Leptailurus*) Severtzov, 1858. R.; As. Serval.

Felis (*Prionailurus*) Severtzov, 1858. R.; As. Dwarf "tiger" cat.

Felis (*Pardofelis*) Severtzov, 1858. R.; As. Marble cat.

Felis (*Badiofelis*) Pocock, 1932. R.; Borneo. (Borneo) marble cat.

Felis (*Profelis*) Severtzov, 1858. [Including *Catopuma* Severtzov, 1858.] R.; As., Af. Golden cat.

Felis (*Zibethailurus*) Severtzov, 1858. R.; As. Fishing cat.

Felis (*Ictailurus*) Severtzov, 1858. R.; S. As.

Felis (*Leopardus*) Gray, 1842. Pleist.–R.; S.A. R.; southern N.A. Ocelot.

Felis (*Noctifelis*) Severtzov, 1858. [Including *Margay* Gray, 1869; *Oncilla* Allen, 1919.] R.; S.A. Margay, guiña.

Felis (*Herpailurus*) Severtzov, 1858. [Including *Oncifelis* Severtzov, 1858.] Pleist.–R.; S.A. R.; southern N.A. Eyra, jaguarundi.

Felis (*Dendrailurus*) Severtzov, 1858. [Including *Lynchailurus* Severtzov, 1858.] R.; S.A. Kodkod, pampa cat, grass cat ("gato pajero").

Felis (*Puma*) Jardine, 1834. Pleist.–R.; N.A. R.; S.A. Puma, cougar, mountain "lion," (American) "panther."

[1] Some (e.g., Pocock) take *Catolynx* to be strictly equal to *Felis* (*Felis*), others of *Chaus*. In either case I take it to be a synonym of *Felis* (*Felis*), since *Chaus* seems not to merit subgeneric, let alone generic, rank.

[2] Distributions given for subgenera and synonyms are for recent forms only. Few fossil records can be surely assigned to these moot subgenera and all are here included under *Felis* as a genus.

[3] Satunin thought that *Otocolobus* dated from Severtzov, 1858, and was preoccupied by Brandt's use of the name in 1844 for a rodent, and he therefore proposed *Trichaelurus*, accepted by many recent authors, such as Pocock or Allen. The fact appears to be, as Birula pointed out (see Brongersma, 1935), that Brandt used *Otocolobus* for the manul in 1842, his use of the same name for a rodent being later, therefore not pertinent, and (incidentally) a mere misprint. Thus *Otocolobus* is the correct name of this subgenus.

Panthera Oken, 1816. [Including the subgenera, synonyms, and supposed genera listed below.] L. Plioc.–Pleist.; Eu. L. Plioc.–R.; As. Pleist.–R.; N.A., S.A., Af.

Subgenera and synonyms of *Panthera:*

Panthera (*Panthera*) Oken, 1816. R.; Af., As. Panther, leopard.

Panthera (*Leo*) Oken, 1816. R.; Af., As. Lion.[1]

Panthera (*Tigris*) Oken, 1816. R.; As. Tiger.

Panthera (*Jaguarius*) Severtzov, 1858 (=*Pardotigris* Kretzoi, 1929). R.; S.A. Jaguar. (Perhaps merits subgeneric rank.)

Panthera (*Neofelis*) Gray, 1867. R.; As. Clouded leopard.

Panthera (*Uncia*) Gray, 1867. R.; As. Irbis, snow leopard, "ounce."[2]

†*Sivapanthera* Kretzoi, 1929 (=†*Sivafelis* Pilgrim, 1932).[3] Pleist.; As.

Acinonyx Brookes, 1828 (=*Cynailurus* Wagler, 1830). U. Plioc.; Eu. R.; Af., As. Cheetah, guepard, hunting "leopard."

†Subfam. Machairodontinae Gill, 1872, p. 59.[4] [Including †Hoplophoneinae Kretzoi, 1929a, p. 1334; †Epimachairodontinae Kretzoi, 1929a, p. 1335; †Smilodontinae Kretzoi, 1929a, p. 1336; †Ailuromachairodontinae Kretzoi, 1929a, p. 1336; †Megantereontinae Kretzoi, 1929a, p. 1337.] L. Olig.–Pleist.; N.A., Eu. L.–U. Plioc.; As. L. Plioc.; Af. Pleist.; S.A. Saber-tooths.

†*Hoplophoneus* Cope, 1874. L. Olig.–L. Mioc.; N.A.

†*Eusmilus* Gervais, 1875. [Including †*Pareusmilus* Kretzoi, 1929.] L.–U. Olig.; Eu. M.–U. Olig.; N.A.

†*Sansanosmilus* Kretzoi, 1929. [Including †*Albanosmilus* Kretzoi, 1929.[5]] M. Mioc.; Eu. L. Plioc.; As.

†*Ailuromachairodus* Kretzoi, 1929. M. Mioc.; Eu.

†*Machairodus* Kaup, 1833. [Including †*Amphimachairodus* Kretzoi, 1929; †*Heterofelis* Cook, 1922.] U. Mioc.–L. Plioc.; Eu. L. Plioc.; N.A., As., Af.

†*Ischyrosmilus* Merriam, 1918. L.–U. Plioc.; N.A.

†*Megantereon* Croizet and Jobert, 1828. [Including †*Toscanius* Kretzoi, 1929[6]; †*Telosmilus* Kretzoi, 1929.] M.–U. Plioc.; As. U. Plioc.; Eu.

[1] Most students who think *Leo* valid include the tiger in it also, but a few separate them. Kretzoi did not separate the two, but, as Haltenorth remarks, this was undoubtedly pure forgetfulness.

[2] "Ounce," originally the lynx and later, broadly, any medium-sized cat, lynx, panther, etc., has now somehow become attached more or less exclusively to the irbis. "Ounce" is equivocal in this sense, and irbis is a better name.

[3] †*Sivapanthera* was one of many names that Kretzoi based on the work of others. When Pilgrim returned to the subject, he agreed as to the validity of a separate genus for these cheetah-like fossils, but not as to the scope of the genus. Because of this disagreement he proposed a new name and placed †*Sivapanthera* as a synonym of it. Of course †*Sivafelis* was thus a synonym, not †*Sivapanthera*, and †*Sivafelis* was invalid on the face of it as proposed and has no standing.

[4] Spelled "Machaerodontinae" by Gill, Machairodontinae by Hay, 1930, p. 340.

[5] †*Sansanosmilus* was proposed at the same time as †*Albanosmilus* but on the next page. Unless other things are equal, insistence on page (*a fortiori*, line) priority is a ridiculous fetish, and I select †*Sansanosmilus* for preservation because its type is better known and because it has been used as valid since Kretzoi's paper and (so far as I know) †*Albanosmilus* has not.

[6] Kretzoi supposes †*Drepanodon* Bronn, 1853, to be the correct name for this genus, but proposes †*Toscanius* in case this should prove incorrect. Scott and Jepsen (1936) used †*Drepanodon* for †*Hoplophoneus*. The status of †*Drepanodon* is dubious and disputed, owing in part to the rarity of some early publications involved, but it is likely

†*Paramachaerodus* Pilgrim, 1913. [Including †*Pontosmilus* Kretzoi, 1929; †*Propontosmilus* Kretzoi, 1929; †*Sivasmilus* Kretzoi, 1929; †*Protamphimachairodus* Kretzoi, 1929.] L.–M. Plioc.; As. L. Plioc.; Eu.

†*Homotherium* Fabrini, 1890. [Including †*Epimachairodus* Kretzoi, 1929.] U. Plioc.–Pleist.; Eu.

†*Smilodon* Lund, 1842. [Including †*Trucifelis* Leidy, 1868; †*Dinobastis* Cope, 1893; †*Smilodontopsis* Brown, 1908.] Pleist.; N.A., S.A.

?Felidae *incertae sedis:*

†Subfam. Hyainailourinae, new form (=†Hyaenaelurinae Pilgrim, 1932, p. 166). L.–M. Mioc.; Eu. U. Mioc.; As.

†*Hyainailouros*[1] Biedermann, 1863. L.–M. Mioc.; Eu. U. Mioc.; As.

?Felidae *incertae sedis:*

†*Ailuraena* Stirton and Christian, 1940. U. Plioc.; N.A.

Suborder PINNIPEDIA Illiger, 1811, p. 138.

†Fam. Semantoridae Orlov, 1931, p. 69. L. Plioc.; As.

†*Semantor* Orlov, 1931. L. Plioc.; As. (W. Siberia).

Fam. Otariidae Gill, 1866, pp. 7, 10 (=Otariina Gray, 1825, p. 340). [Including Desmatophocidae Hay, 1930, p. 557; Allodesmidae Kellogg, 1931, p. 227.] L. Mioc.–R.; Pacific N.A. Plioc.–R.; S.A. Pleist.–R.; Aus., New Zealand, Japan. R.; Pacific, Antarctic. Eared seals.

†*Allodesmus* Kellogg, 1922. L. Mioc.; Pacific N.A.

†*Neotherium* Kellogg, 1931. L. Mioc.; Pacific N.A.

†*Desmatophoca* Condon, 1906. L. Mioc.; Pacific N.A.

†*Pithanotaria* Kellogg, 1925. L. Mioc.; Pacific N.A.

†*Dusignathus* Kellogg, 1927. U. Mioc.; Pacific N.A.

†*Pontolis* True, 1905 (=†*Pontoleon* True, 1905, *nec Pontoleo* Gloger, 1841).[2] M.–U. Plioc.; Pacific N.A.

†*Pliopedia* Kellogg, 1921. U. Plioc.; Pacific N.A.

Arctocephalus Geoffroy and Cuvier, 1826. Plioc.; S.A. Pleist.; New Zealand. R.; Antarctic regions to southern S.A., Af., Aus., and New Zealand. Southern fur seals.

Callorhinus Gray, 1859 (=*Callotaria* Palmer, 1892).[3] R.; N. Pacific. (Northern) fur seal.

Zalophus Gill, 1866. Pleist.; Pacific N.A., Aus., New Zealand. R.; Cent. Pacific, California to New Zealand, Aus., Japan. (California) sea "lion."

Eumetopias Gill, 1866. Pleist.; Pacific N.A., Atlantic S.A. R.; N. Pacific. (Northern) sea "lion."

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that †*Drepanodon* (which apparently dates from Nesti, 1826, not Bronn, 1853, as Kretzoi has it, or Leidy, 1857, as Scott and Jepsen concluded) is not available for any cat but is a synonym of *Ursus* and can be forgotten. This validates †*Hoplophoneus* and also †*Toscanius*, if the latter be supposed really separable from †*Megantereon*, which I think very improbable.

[1] This non-Latinized transliteration appears uncouth to some who prefer Stehlin's emendation to "*Hyaenaelurus*," but, regardless of etymology, the original spelling is correct in zoology.

[2] I question whether *Pontoleo* preoccupies †*Pontoleon*, but the change to †*Pontolis* has generally been accepted, and the similarity, if not identity, of the two names would lead to confusion, especially as *Pontoleo* is also a name for an otariid (=*Otaria*).

[3] *Callorhinus* said by Palmer to be preoccupied by *Callirhinus* Blanchard, 1850, and Girard, 1857, but this is not undoubted preoccupation, is not confusing, and the change is not generally accepted.

Otaria Peron, 1816. [Including *Phocarctus* Peters, 1866.] R.; coasts and islands around southern S.A. (Southern) sea "lion."

Fam. Odobenidae Allen, 1880, pp. 5, 17[1] (=Trichecidae Gray, 1821, p. 302; Rosmaridae Gill, 1866, pp. 7, 11; both invalid). U. Mioc., Pleist.; Atlantic N.A. M. Plioc.–Pleist.; Eu. R.; Arctic regions.

†*Prorosmarus* Berry and Gregory, 1906. U. Mioc.; Atlantic N.A.

†*Trichecodon* Lankester, 1865. M. Plioc.–Pleist.; Eu.

†*Alachtherium* Du Bus, 1867. M. Plioc.; Eu.

Odobenus Brisson, 1762 (=*Trichechus* Linnaeus, 1766, *nec* Linnaeus, 1758; *Rosmarus* Brünnich, 1772). [Including †*Odobenotherium* Gratiolet, 1858.[2]] Pleist.; Atlantic N.A., Eu. R.; Arctic regions. Walrus.

Fam. Phocidae Gray, 1825, p. 340 (=Phocadae Gray, 1821, p. 302). M. Mioc.–R.; N.A. U. Plioc.; Egypt. R.; virtually all seas and coasts. True seals.

Subfam. Phocinae Gill, 1866, pp. 5, 8. M. Mioc.–R.; N.A., Eu. R.; all northern seas.

†*Miophoca* Zapfe, 1937. M. Mioc.; Eu.

†*Leptophoca* True, 1906. M. Mioc.; Atlantic N.A.

†*Prophoca* Van Beneden, 1876. U. Mioc.; Eu.

†*Callophoca* Van Beneden, 1876. M. Plioc.; Eu.

†*Gryphoca* Van Beneden, 1876. M. Plioc.; Eu.

†*Platyphoca* Van Beneden, 1876. M. Plioc.; Eu.

†*Phocanella* Van Beneden, 1876. M. Plioc.; Eu.

Phoca Linnaeus, 1758. [Including *Pusa* Scopoli, 1777; *Histriophoca* Gill, 1873; *Pagophoca* Trouessart, 1904=*Pagophilus* Gray, 1844, *nec Pagophila* Kaup, 1829.] M. Mioc.–R.; Eu. L. Plioc.–R.; N.A. R.; Arctic, N. Atlantic, N. Pacific, Lake Baikal, etc. Common seal, harbor seal, hair seal, ringed seal, ribbon seal, Greenland seal, harp seal, saddleback seal.

Halichoerus Nilsson, 1820. R.; N. Atlantic. Gray seal.

Erignathus Gill, 1866. R.; N. Polar seas. Bearded seal.

Subfam. Lobodontinae Hay, 1930, p. 562 (=Lobodoninae Kellogg, 1922, p. 89; Lobodontina Gray, 1869b, p. 342). [Including Stenorhynchinae Gill, 1866, pp. 6, 10; Stenorhyncina Gray, 1825, p. 340.] R.; Antarctic, S. Pacific.

Lobodon Gray, 1844. R.; Antarctic. Crab-eating seal.

Ommatophoca Gray, 1844. R.; Antarctic. Ross seal.

Hydrurga Gistel, 1848 (=*Stenorhinchus* Cuvier, 1826, *nec Stenorhynchus* Lamarck, 1819; *Ogmorhinus* Peters, 1875). R.; Antarctic to S. Aus., S.A., New Zealand. "Leopard" seal.

Leptonychotes Gill, 1872 (=*Leptonyx* Gray, 1837, *nec* Swainson, 1821; *Poecilophoca* Lydekker, 1891). R.; Antarctic. Weddell seal.

[1] Spelled Odobaenidae by Allen, emended to Odobenidae by Palmer, 1904, p. 833.

[2] The older literature almost always used *Trichechus* for the walrus, but this name belongs to the manatee, as now generally accepted.

Subfam. Monachinae Trouessart, 1904, p. 283 (=Monachina Gray, 1869b, p. 345). U. Mioc.–R.; Eu. U. Plioc.; Egypt. R.; tropical and subtropical seas.

†*Monotherium* Van Beneden, 1876. U. Mioc.; Eu.

†*Paleophoca* Van Beneden, 1859. M. Plioc.; Eu.

†*Pristiphoca* Gervais, 1852–1853. U. Plioc.; Eu., Egypt.

Monachus Fleming, 1822. R.; tropical and subtropical seas, W. Indies, Mediterranean, Cent. Pacific. Monk seal.

Subfam. Cystophorinae Gill, 1866, pp. 6, 9 (=Cystophorina Gray, 1837, p. 582). M. Plioc.–R.; Eu. R.; N. Atlantic, Arctic, S. Pacific, Antarctic, Indian Ocean, Pacific N.A.

†*Mesotaria* Van Beneden, 1876. M. Plioc.; Eu.

Cystophora Nilsson, 1820. R.; Arctic, N. Atlantic, W. Indies. Hooded seal.

Mirounga Gray, 1827 (=*Macrorhinus* Cuvier, 1826, *nec* Latreille, 1825; *Rhinophoca* Wagler, 1830). R.; Antarctic, S. Pacific, Indian Ocean, Pacific N.A.[1] "Elephant" seal.

Superorder PROTUNGULATA Weber, 1904, p. 587.[2]

†Order CONDYLARTHRA Cope, 1881e, p. 1018.

†Fam. Hyopsodontidae Lydekker, 1889, p. 1465 (=†Hyopsodinae Trouessart, 1879, p. 229). [Including †Mioclaenidae Osborn and Earle, 1895, p. 48.] L. Paleoc.–U. Eoc.; N.A.

†Subfam. Mioclaeninae Matthew, 1937, pp. vi, 195 (=†Mioclaenidae Osborn and Earle, 1895, p. 48). L.–M., ?U. Paleoc.; N.A.

†*Tiznatzinia* Simpson, 1936. L. Paleoc.; N.A.

†*Choeroclaenus* Simpson, 1937. L. Paleoc.; N.A.

†*Mioclaenus* Cope, 1881. M. Paleoc.; N.A.

†*Ellipsodon* Scott, 1892. ?L., M. Paleoc.; N.A.

†*Litaletes* Simpson, 1935. M. Paleoc.; N.A.

†*Jepsenia* Gazin, 1939. M. Paleoc.; N.A.

?†Mioclaeninae *incertae sedis:*

†*Phenacodaptes* Jepsen, 1930. U. Paleoc.; N.A.

†Subfam. Hyopsodontinae Trouessart, 1879, p. 229.[3] L. Paleoc.–U. Eoc.; N.A.

†*Oxyacodon* Osborn and Earle, 1895. L. Paleoc.; N.A.

†*Oxytomodon* Gazin, 1941. M. Paleoc.; N.A.

†*Litomylus* Simpson, 1935. M. Paleoc.; N.A.

†*Haplaletes* Simpson, 1935. M. Paleoc.; N.A.

†*Dracoclaenus* Gazin, 1939. M. Paleoc.; N.A.

†*Protoselene* Matthew, 1897. M. Paleoc.; N.A.

†*Litolestes* Jepsen, 1930. U. Paleoc.; N.A.

†*Haplomylus* Matthew, 1915. U. Paleoc.–L. Eoc.; N.A.

†*Hyopsodus* Leidy, 1870. L.–U. Eoc.; N.A.

†Fam. Phenacodontidae Cope, 1881e, p. 1018. L. Paleoc.–L. Eoc.; N.A. L. Eoc.; Eu.

†*Desmatoclaenus* Gazin, 1941. L.–M. Paleoc.; N.A.

†*Tetraclaenodon* Scott, 1892 (=†*Euprotogonia* Cope, 1893; †*Protogonia* Cope, 1881, *nec Protogonius* Hübner, 1816). M. Paleoc.; N.A.

[1] Formerly in California, now only on Guadalupe Island.

[2] The propriety of so assigning the authorship is questionable. See p. 233.

[3] Spelled Hyopsodinae by Trouessart; Hyopsodontinae in Matthew, 1937, p. 194.

†*Gidleyina* Simpson, 1935. U. Paleoc.; N.A.
†*Phenacodus* Cope, 1873. U. Paleoc.–L. Eoc.; N.A. L. Eoc.; Eu.
†*Ectocion* Cope, 1882. U. Paleoc.–L. Eoc.; N.A.
†Fam. Didolodontidae Scott, 1913, p. 489[1] (="Bunolitopternidae" Schlosser, 1823, p. 525). U. Paleoc.–Eoc.; S.A.
†*Didolodus* Ameghino, 1897. Eoc.; S.A.
†*Argyrolambda* Ameghino, 1904. Eoc.; S.A.
†*Paulogervaisia* Ameghino, 1901. Eoc.; S.A.
†*Proectocion* Ameghino, 1904. Eoc.; S.A.
†*Enneoconus* Ameghino, 1901. Eoc.; S.A.
†*Asmithwoodwardia* Ameghino, 1901. Eoc.; S.A.
†*Ernestokokenia* Ameghino, 1901. U. Paleoc.–Eoc.; S.A.
†*Archaeohyracotherium* Ameghino, 1906. Eoc.; S.A.
†Fam. Periptychidae Cope, 1882c, p. 832. L.–U. Paleoc.; N.A.
†Subfam. Anisonchinae Osborn and Earle, 1895, p. 58. L.–M. Paleoc.; N.A.
†*Hemithlaeus* Cope, 1882. L. Paleoc.; N.A.
†*Conacodon* Matthew, 1897. L. Paleoc.; N.A.
†*Anisonchus* Cope, 1881. L.–M. Paleoc.; N.A.
†*Coriphagus* Douglass, 1908. [Including †*Mixoclaenus* Matthew and Granger, 1921.] M. Paleoc.; N.A.
†*Haploconus* Cope, 1882. M. Paleoc.; N.A.
†Subfam. Periptychinae Osborn and Earle, 1895, p. 53. L.–U. Paleoc.; N.A.
†*Ectoconus* Cope, 1884. L. Paleoc.; N.A.
†*Carsioptychus* Simpson, 1936 (= †*Plagioptychus* Matthew, 1936, *nec* Matheron, 1843). L. Paleoc.; N.A.
†*Periptychus* Cope, 1881. M.–U. Paleoc.; N.A.
†Fam. Meniscotheriidae Cope, 1882b, p. 334. U. Paleoc.–L. Eoc.; N.A. U. Paleoc.; Eu.
†Subfam. Meniscotheriinae Simpson, 1937a, p. 224. U. Paleoc.–L. Eoc.; N.A.
†*Meniscotherium* Cope, 1874. U. Paleoc.–L. Eoc.; N.A.
†Subfam. Pleuraspidotheriinae, new form? (= †Pleuraspidotheridae Zittel, 1892, p. 222). U. Paleoc.; Eu.
†*Pleuraspidotherium* Lemoine, 1878. U. Paleoc.; Eu.
†*Orthaspidotherium* Lemoine, 1885. U. Paleoc.; Eu.
?†CONDYLARTHRA *incertae sedis:*
†*Phenacolophus* Matthew and Granger, 1925. U. Paleoc.; As.
†Fam. Tricuspiodontidae Simpson, 1929e, p. 16. U. Paleoc.; Eu.
†*Tricuspiodon* Lemoine, 1885. U. Paleoc.; Eu.
†Order LITOPTERNA Ameghino, 1889, p. 492.
†Fam. Proterotheriidae Ameghino, 1887a, p. 19.[2] U. Paleoc.–L. Plioc.; S.A.
†Subfam. Polymorphinae, new. U. Paleoc.–Olig.; S.A.
†*Wainka* Simpson, 1935. U. Paleoc.; S.A.
†*Josepholeidya* Ameghino, 1901. U. Paleoc.–Eoc.; S.A.
†*Ricardolydekkeria* Ameghino, 1901. U. Paleoc.–Eoc.; S.A.
†*Guilielmofloweria* Ameghino, 1901. Eoc.; S.A.

[1] Spelled Didolodidae in Scott, 1913; Didolodontidae in Simpson, 1934, p. 6.
[2] Proterotheridae in original publication; Proterotheriidae in Cope, 1889c, p. 876.

†*Anisolambda* Ameghino, 1901. Eoc.; S.A.
†*Polymorphis* Roth, 1899. ?U. Eoc.; S.A.
†*Megacrodon* Roth, 1899. ?U. Eoc.; S.A.
†*Xesmodon* Berg, 1899 (= †*Glyphodon* Roth, 1899, *nec* Günther, 1858). ?U. Eoc.; S.A.
†*Polyacrodon* Roth, 1899. ?U. Eoc.; S.A.
†*Decaconus* Ameghino, 1901. ?U. Eoc.; S.A.
†*Protheosodon* Ameghino, 1897. L. Olig.; S.A.

†Subfam. Proterotheriinae, new. Olig.–Plioc.; S.A.
†*Eoproterotherium* Ameghino, 1904. L. Olig.; S.A.
†*Deuterotherium* Ameghino, 1895. L. Olig.; S.A.
†*Prolicaphrium* Ameghino, 1902. U. Olig.; S.A.
†*Prothoatherium* Ameghino, 1902. U. Olig.; S.A.
†*Licaphrops* Ameghino, 1904. U. Olig.–L. Mioc.; S.A.
†*Licaphrium* Ameghino, 1887. L. Mioc.; S.A.
†*Thoatherium* Ameghino, 1887. L. Mioc.; S.A.
†*Diadiaphorus* Ameghino, 1887. L. Mioc.–L. Plioc.; S.A.
†*Proterotherium* Ameghino, 1883. L. Mioc.–L. Plioc.; S.A.
†*Brachytherium* Ameghino, 1883. [Including †*Epitherium* Ameghino, 1889.] L.–M. Plioc.; S.A.
†*Diplasiotherium* Rovereto, 1914. Plioc.; S.A.
†*Chapalmatherium* Ameghino, 1908. Plioc.; S.A.

†Fam. Macraucheniidae Gill, 1872, p. 12. U. Paleoc.–Pleist.; S.A.
†Subfam. Macraucheniinae Bordas, 1939, p. 416 (= †Macraucheniidae of many authors). [Including †Theosodontinae Ameghino, 1902b, p. 90; †Cramaucheniinae Ameghino, 1902b; p. 90.] U. Paleoc.–Pleist.; S.A.
†*Victorlemoinea* Ameghino, 1901. U. Paleoc.–Eoc.; S.A.
†*Notodiaphorus* Loomis, 1914. L. Olig.; S.A.
†*Cramauchenia* Ameghino, 1902. U. Olig.; S.A.
†*Paramacrauchenia* Bordas, 1939. U. Olig.; S.A.
†*Theosodon* Ameghino, 1887. U. Olig.–U. Mioc.; S.A.
†*Cullinia* Cabrera and Kraglievich, 1931. U. Mioc.; S.A.
†*Scalabrinitherium* Ameghino, 1883. ?U. Mioc.; S.A.
†*Oxyodontherium* Ameghino, 1883. [Including †*Mesorhinus* Ameghino, 1885.] ?U. Mioc.; S.A.
†*Paranauchenia* Ameghino, 1904. ?U. Mioc.; S.A.
†*Promacrauchenia* Ameghino, 1904. M. Plioc.; S.A.
†*Windhausenia* Kraglievich, 1930. U. Plioc. or Pleist.; S.A.
†*Macrauchenia* Owen, 1840. Pleist.; S.A.

†Subfam. Adianthinae Patterson, 1940a, p. 13 (= †Adiantinae Bordas, 1939, p. 417; †Adianthidae Ameghino, 1891a, p. 134). L. Olig.–L. Mioc.; S.A.[1]
†*Proadiantus* Ameghino, 1897. L. Olig.; S.A.
†*Proheptoconus* Bordas, 1939. U. Olig.; S.A.
†*Adianthus* Ameghino, 1891. U. Olig.–L. Mioc.; S.A.

?†Macraucheniidae *incertae sedis:*
†*Ernestohaeckelia* Ameghino, 1901. Eoc.; S.A.
†*Rütimeyeria* Ameghino, 1901. Eoc.; S.A.

[1] †*Pseudadiantus* Ameghino, 1901, usually mentioned as a possible or established Eocene (Casamayor) forerunner of this group, is based on a typothere and is probably synonymous with †*Notopithecus* (unpublished personal observation).

†*Amilnedwardsia* Ameghino, 1901. Eoc.; S.A.

†Order NOTOUNGULATA Roth, 1903, pp. 11, 12 (=†Toxodontia Owen, 1858, p. 26, *sensu* Lydekker, 1894c, p. 2, Scott, 1904b, p. 590, etc., *nec* †Toxodontia Ameghino, e.g., 1906, or of many other authors).

†Suborder NOTIOPROGONIA Simpson, 1934, pp. 7, 10.

†Fam. Arctostylopidae Schlosser, 1923, p. 614. U. Paleoc.; As. L. Eoc.; N.A.

†*Palaeostylops* Matthew and Granger, 1925. U. Paleoc.; As.

†*Arctostylops* Matthew, 1915. L. Eoc.; N.A.

†Fam. Henricosborniidae Ameghino, 1901, p. 357 (=†Pantostylopidae Ameghino, 1901, p. 423; †Selenoconidae Ameghino, 1902a, p. 20).

†*Henricosbornia* Ameghino, 1901 (=or including †*Selenoconus* Ameghino, 1901; †*Pantostylops* Ameghino, 1901; †*Prohyracotherium* Ameghino, 1902; †*Hemistylops* Ameghino, 1904; and other proposed genera). Paleoc.–L. Eoc.; S.A.

†*Othnielmarshia* Ameghino, 1901. L. Eoc.; S.A.

†*Peripantostylops* Ameghino, 1904. ?Paleoc., L. Eoc.; S.A.

?†Henricosborniidae *incertae sedis:*

†*Seudenius* Simpson, 1935. Paleoc.; S.A.

†Fam. Notostylopidae Ameghino, 1897b, p. 488. Eoc.; S.A.

†*Homalostylops* Ameghino, 1901 (=†*Acrostylops* Ameghino, 1901). L. Eoc.; S.A.

†*Notostylops* Ameghino, 1897 (=or including †*Anastylops* Ameghino, 1897; †*Catastylops* Ameghino, 1901; †*Eostylops* Ameghino, 1901; and many other proposed genera). L. Eoc.; S.A.

†*Otronia* Roth, 1901. U. Eoc.; S.A.

†Suborder TOXODONTA Scott, 1904b, p. 590 (emended; approximately =†Toxodontia Owen, 1858, p. 26, as used by some but not all later authors). [Including †Entelonychia Ameghino, 1894, p. 312.]

†Fam. Oldfieldthomasiidae, new name (=†Acœlodidae Ameghino, 1901, p. 364).[1] U. Paleoc.–Eoc.; S.A.

†*Kibenikhoria* Simpson, 1935. Paleoc.; S.A.

†*Oldfieldthomasia* Ameghino, 1901. L. Eoc.; S.A.

†*Maxschlosseria* Ameghino, 1901. [Including †*Paracoelodus* Ameghino, 1904.] L. Eoc.; S.A.

†*Ultrapithecus* Ameghino, 1901. L. Eoc.; S.A.

†*Tsamnichoria* Simpson, 1936. U. Eoc.; S.A.

?†Oldfieldthomasiidae *incertae sedis* (=†Acœlodidae *sensu stricto*):

†*Acoelodus* Ameghino, 1897. L. Eoc.; S.A.

†Fam. Archaeopithecidae Ameghino, 1897b, p. 422. L. Eoc.; S.A.

†*Archaeopithecus* Ameghino, 1897. L. Eoc.; S.A.

†*Acropithecus* Ameghino, 1904. L. Eoc.; S.A.

†Fam. Archaeohyracidae Ameghino, 1897b, p. 431. ?Paleoc., L. Eoc.–Olig.; S.A.

[1] The genus †*Acoelodus* is based on a single senile specimen, apparently unlike anything discovered since and of doubtful pertinence to the family that has borne its name. It is practically *incertae sedis*. Ameghino's own idea of the family and all definitions of it are really based almost entirely on the abundant, well-known genus †*Oldfieldthomasia*. Specimens of this genus make up the hypodigm of Ameghino's family, to which †*Acoelodus* may or may not belong. Clarity can be obtained only by changing the name.

†*Eohyrax* Ameghino, 1901. ?Paleoc., L. Eoc.; S.A.
†*Acoelohyrax* Ameghino, 1902. L. Eoc.; S.A.
†*Degonia* Roth, 1901 (= †*Pseudopithecus* Roth, 1901). U. Eoc.; S.A.
†*Archaeohyrax* Ameghino, 1897. ?U. Eoc., Olig.; S.A.

†Fam. Isotemnidae Ameghino, 1897b, p. 479. Paleoc.–L. Olig.; S.A.
†*Isotemnus* Ameghino, 1897. [Including †*Prostylops* and other proposed genera.] Paleoc.–L. Eoc.; S.A.
†*Eochalicotherium* Ameghino, 1901. [Including †*Dimerostephanus* Ameghino, 1902; †*Amphitemnus* Ameghino, 1904.] L. Eoc.; S.A.
†*Pleurostylodon* Ameghino, 1897. [Including †*Paratemnus* Ameghino, 1904; etc.] L. Eoc.; S.A.
†*Edvardotrouessartia* Ameghino, 1901. L. Eoc.; S.A.
†*Thomashuxleya* Ameghino, 1901. L. Eoc.; S.A.
†*Periphragnis* Roth, 1899 (= †*Proasmodeus* Ameghino, 1902). U. Eoc.; S.A.
†*Rhyphodon* Roth, 1899. U. Eoc.; S.A.
†*Trimerostephanos* Ameghino, 1895. U. Eoc.–L. Olig.; S.A.
†*Pleurocoelodon* Ameghino, 1895. L. Olig.; S.A.

?†Isotemnidae *incertae sedis:*
†*Brandmayria* Cabrera, 1935. U. Paleoc.; S.A.

†Fam. Homalodotheriidae Gregory, 1910, p. 466 (= †Homalodontotheridae Ameghino, 1889, pp. 523, 551). L. Olig.–U. Mioc.; S.A.
†*Asmodeus* Ameghino, 1895. L. Olig.; S.A.
†*Homalodotherium* Flower, 1873 (= †*Homalodontotherium* Flower, 1874). L.–M. Mioc.; S.A.
†*Chasicotherium* Cabrera and Kraglievich, 1931. U. Mioc.; S.A.

†Fam. Leontiniidae Ameghino, 1895, p. 646. [Including †Colpodontidae Ameghino, 1906, p. 469.] Olig.; S.A.
†*Ancylocoelus* Ameghino, 1895. L. Olig.; S.A.
†*Leontinia* Ameghino, 1895. [Including †*Stenogenium* Ameghino, 1895; †*Scaphops* Ameghino, 1895.] L. Olig.; S.A.
†*Scarrittia* Simpson, 1934. L. Olig.; S.A.
†*Colpodon* Burmeister, 1885. U. Olig.; S.A.

†Fam. Notohippidae Ameghino, 1894, p. 283. [Including †Rhynchippidae Loomis, 1914, p. 88.] U. Eoc.–L. Mioc.; S.A.
†Subfam. Rhynchippinae, new rank (= †Rhynchippidae Loomis, 1914, p. 88). U. Eoc.–L. Olig.; S.A.
†*Pseudostylops* Ameghino, 1901. U. Eoc.; S.A.
†*Morphippus* Ameghino, 1897. L. Olig.; S.A.
†*Rhynchippus* Ameghino, 1897. L. Olig.; S.A.
†*Eurygenium* Ameghino, 1895, *nec Eurygenius* La Ferté, 1849[1] (= †*Eurygeniops* Ameghino, 1897). L. Olig.; S.A.
†Subfam. Notohippinae, new rank (= †Notohippidae Ameghino, 1894, p. 283, *emend.* Loomis, 1914, p. 88). U. Eoc.–L. Mioc.; S.A.
†*Interhippus* Ameghino, 1904. U. Eoc.–L. Olig.; S.A.
†*Nesohippus* Ameghino, 1904. L. Olig.; S.A.
†*Argyrohippus* Ameghino, 1901. U. Olig.; S.A.
†*Stilhippus* Ameghino, 1904. U. Olig.; S.A.

[1] This is not preoccupation.

†*Perhippidium* Ameghino, 1904. U. Olig.; S.A.
†*Notohippus* Ameghino, 1891. L. Mioc.; S.A.
†Fam. Toxodontidae Gervais, 1847, p. 221. [Including †Nesodontidae Murray, 1866, pp. xiii, 168, 388; †Xotodontidae Ameghino, 1889, pp. 375, 402; †Haplodontidae Ameghino, 1906, p. 481 = †Haplodontheriidae Ameghino, 1907, p. 89.] L. Olig.–Pleist.; S.A.
†Subfam. Nesodontinae, new rank (= †Nesodontidae Murray, 1866, pp. xiii, 168). L. Olig.–M. Mioc.; S.A.
†*Proadinotherium* Ameghino, 1895. [Including †*Pronesodon* Ameghino, 1895; †*Coresodon* Ameghino, 1895.] L.–U. Olig.; S.A.
†*Nesodon* Owen, 1846. L.–M. Mioc.; S.A.
†*Adinotherium* Ameghino, 1887. L.–M. Mioc.; S.A.
†Subfam. Toxodontinae Trouessart, 1898, p. 688 (= †Toxodontidae Gervais, 1847, p. 221, *sensu stricto*, or *emend.* Ameghino, 1906, p. 481, etc.). [Including †Xotodontidae Ameghino, 1889, pp. 375, 402.] M. Mioc.–Pleist.; S.A.
†*Stereotoxodon* Ameghino, 1904. M. Mioc.; S.A.
†*Palaeotoxodon* Ameghino, 1904. U. Mioc.; S.A.
†*Hemitoxodon* Cabrera and Kraglievich, 1931. U. Mioc.; S.A.
†*Stenotephanos* (*nec* †*Stenostephanos*) Ameghino, 1886. ?L. Mioc., U. Mioc.; S.A.
†*Xotodon* Ameghino, 1887. U. Mioc.–M. Plioc.; S.A.
†*Gyrinodon* Hopwood, 1928. U. Mioc. or L. Plioc.; S.A. (Venezuela).
†*Eutomodus* Ameghino, 1889 (= †*Tomodus* Ameghino, 1886, *nec* Trautschold, 1879). U. Mioc.; S.A.
†*Alitoxodon* Rovereto, 1914. M. Plioc.; S.A.
†*Chapalmalodon* Mercerat, 1917.[1] U. Plioc.; S.A.
†*Toxodon* Owen, 1840. Pleist.; S.A.
†Subfam. Haplodontheriinae Kraglievich, 1934, p. 95 (= †Haplodontidae Ameghino, 1906, p. 481; †Haplodontheriidae Ameghino, 1907, p. 89). M. Mioc.–M. Plioc.; S.A.
†*Prototrigodon* Kraglievich, 1930. M. Mioc.; S.A.
†*Paratrigodon* Cabrera and Kraglievich, 1931. U. Mioc.; S.A.
†*Dinotoxodon* Mercerat, 1895. U. Mioc.; S.A.
†*Haplodontherium* Ameghino, 1885 (= †*Haplodontotherium* Sclater, 1886). U. Mioc.; S.A.
†*Pachynodon* Burmeister, 1891. U. Mioc.; S.A.
†*Toxodontherium* Ameghino, 1883. U. Mioc.–L. Plioc.; S.A.
†*Trigodon* Ameghino, 1882. M. Plioc.; S.A.
†*Trigodonops* Kraglievich, 1930. ?Plioc.; S.A. (Brazil).
†Suborder TYPOTHERIA Zittel, 1892, pp. 62, 212.
†Fam. Interatheriidae[2] Ameghino, 1887b, p. 63. [Including †Protypotheridae Ameghino, 1891d, p. 393; †Notopithecidae Ameghino, 1897b, p. 418.] L. Eoc.–M. Plioc.; S.A.
†Subfam. Notopithecinae, new rank (= †Notopithecidae Ameghino, 1897b, p. 418). Eoc.; S.A.
†*Notopithecus* Ameghino, 1897 (=or including †*Adpithecus*

[1] A very dubious genus. Based originally on a femur and a skull, Kraglievich selected the femur as type, and this is doubtful as to origin and affinities.
[2] Spelled †Interatheridae in original reference.

Ameghino, 1901; †*Infrapithecus* Ameghino, 1901; †*Pseudadiantus* Ameghino, 1901; †*Patriarchippus* Ameghino, 1901; and other proposed genera). L. Eoc.; S.A.

†*Transpithecus* Ameghino, 1901. L. Eoc.; S.A.

†*Guilielmoscottia* Ameghino, 1901. U. Eoc.; S.A.

†Subfam. Interatheriinae, new rank (= †Interatheriidae, *sensu stricto*, of previous students). L. Olig.–M. Plioc.; S.A.

†*Archaeophylus* Ameghino, 1897.[1] L. Olig.; S.A.

†*Plagiarthrus* Ameghino, 1896 (= †*Argyrohyrax* Ameghino, 1897). L. Olig.; S.A.

†*Cochilius* Ameghino, 1902. L.–U. Olig.; S.A.

†*Phanophilus* Ameghino, 1903. L. Olig.; S.A.

†*Paracochilius* Bordas, 1939. U. Olig.; S.A.

†*Protypotherium* Ameghino, 1887 (= †*Patriarchus* Ameghino, 1889). U. Olig.–M. Plioc.[2]; S.A.

†*Interatherium* Ameghino, 1887, *ex* Moreno, 1882 (= †*Icochilus* Ameghino, 1889). L. Mioc.; S.A.

†*Epipatriarchus* Ameghino, 1903. M. Mioc.; S.A.

†*Caenophilus* Ameghino, 1903. M. Mioc.; S.A.

†Fam. Mesotheriidae Alston, 1876, pp. 75, 98 (= †Typotheriidae Lydekker, 1886, p. 170). [Including †Trachytheridae Ameghino, 1894, p. 276; †Eutrachytheriidae Ameghino, 1897b, p. 427.] L. Olig.–Pleist.; S.A.

†Subfam. Trachytheriinae, new rank (= †Trachytheridae Ameghino, 1894, p. 276). Olig.; S.A.

†*Trachytherus* Ameghino, 1889, *nec Trachytherium* Gervais, 1849[3] (= †*Eutrachytherus* Ameghino, 1897). L. Olig.; S.A.

†*Proedium* Ameghino, 1895, *nec Proedrus* Foerster, 1888[3] (= †*Proedrium* Ameghino, 1897; †*Isoproedrium* Ameghino, 1904). L. Olig.; S.A.

†Subfam. Mesotheriinae, new rank (= †Typotheriidae of most authors). M. Mioc.–Pleist.; S.A.

†*Typothericulus* Kraglievich, 1930. U. Mioc.; S.A.

†*Acrotypotherium* Rusconi, 1936. U. Mioc.; S.A.

†*Eutypotherium* Roth, 1901[4] (= †*Tachytypotherium* Roth, 1903). U. Mioc.; S.A.

†*Typotheriopsis* Cabrera and Kraglievich, 1931. L. Plioc.; S.A.

†*Pseudotypotherium* Ameghino, 1904. U. Plioc.; S.A.

†*Typotheriodon* C. Ameghino, 1919. U. Plioc.–L. Pleist.; S.A.

†*Mesotherium* Serres, 1857 or 1867 (= †*Typotherium* Gervais, 1859, *ex* Bravard, or Gervais, 1867, or Bravard, 1858).[5] Pleist.; S.A.

[1] †*Progaleopithecus* Ameghino, 1904, may be mentioned because of its misleading name. It is hardly determinate but belongs to this subfamily and may be synonymous with †*Archaeophylus* (see Patterson, 1940).

[2] It is unlikely that a single genus really has such a range. The type is from the Upper Miocene.

[3] This is not preoccupation.

[4] Rejected by most students, including Roth himself, on grounds of preoccupation by *Eutypotherium* Haeckel, 1895, but, as Patterson has pointed out, the latter name was given to a purely hypothetical "genus," hence has no standing in nomenclature and cannot preoccupy a name based on a real animal.

[5] As I have shown elsewhere, this is a knotty nomenclatural problem, but whatever criteria are used to solve it, †*Mesotherium* has priority and is the correct name of this well-known genus. "†*Typotherium* Bravard, 1857," usually given, is a *nomen nudum* with no standing. The earliest possible date for valid publication of †*Typotherium* is 1858, and by the same criteria †*Mesotherium* was published in 1857. By the strictest criteria both names date from 1867, but †*Mesotherium* earlier in that year.

†*Typotheridion* Cabrera, 1939. Pleist.; S.A.
†*Bravardia* Cattoi, 1941. Pleist.; S.A.

†Suborder HEGETOTHERIA, new.

†Fam. Hegetotheriidae[1] Ameghino, 1894, p. 275. U. Eoc.–Pleist.; S.A.

†Subfam. Hegetotheriinae Ameghino, 1894, p. 277. U. Eoc.–L. Plioc.; S.A.

†*Eohegetotherium* Ameghino, 1901. U. Eoc.; S.A.
†*Prohegetotherium* Ameghino, 1897. L. Olig.; S.A.
†*Hegetotherium* Ameghino, 1887 (= †*Selatherium* Ameghino, 1894). U. Olig.–L. Mioc.; S.A.
†*Pseudhegetotherium* Cabrera and Kraglievich, 1931. U. Mioc.; S.A.
†*Hemihegetotherium* Rovereto, 1914. L. Plioc.; S.A.

†Subfam. Pachyrukhinae Kraglievich, 1934, p. 96 (= †Pachyrucidae Lydekker, 1894c, p. 3). U. Eoc.–Pleist.; S.A.

†*Eopachyrucos* Ameghino, 1901. U. Eoc.; S.A.
†*Propachyrucos* Ameghino, 1897. L. Olig.; S.A.
†*Pachyrukhos* Ameghino, 1885 (= †*Pachyrucos* Ameghino, 1889). U. Olig.–M. Mioc.; S.A.
†*Paedotherium* Burmeister, 1888. U. Mioc.–Pleist.; S.A.
†*Prosotherium* Ameghino, 1897. L. Olig.; S.A.
†*Tremacyllus* Ameghino, 1891. L.–U. Plioc.; S.A.

†Subfam. Muñiziinae[2] Kraglievich, 1931a, p. 261. U. Mioc.; S.A.

†*Muñizia* Kraglievich, 1930. U. Mioc.; S.A.

†Order ASTRAPOTHERIA Lydekker, 1894c, p. 42.

†Suborder TRIGONOSTYLOPOIDEA Simpson, 1934, pp. 4, 19.

†Fam. Trigonostylopidae Ameghino, 1901, p. 390. Eoc.; S.A.

†*Trigonostylops* Ameghino, 1897. [Including †*Chiodon* Berg, 1899 = †*Staurodon* Roth, 1899, *nec* Lowe, 1854.] Eoc.; S.A.

?†TRIGONOSTYLOPOIDEA *incertae sedis:*

†*Shecenia* Simpson, 1935. Paleoc.; S.A.

†Suborder ASTRAPOTHERIOIDEA Ameghino, 1894, p. 303.[3]

†Fam. Astrapotheriidae Ameghino, 1887a, p. 19.[4] Eoc.–Mioc.; S.A.

†Subfam. Albertogaudryinae, new form (= †Albertogaudryidae Ameghino, 1901, p. 398). Eoc.; S.A.

†*Albertogaudrya* Ameghino, 1901. [Including †*Scabellia* Ameghino, 1901.] L. Eoc.; S.A.
†*Astraponotus* Ameghino, 1901. [Including †*Notamynus* Roth, 1903.] U. Eoc.; S.A.

†Subfam. Astrapotheriinae, new. Olig.–Mioc.; S.A.

†*Parastrapotherium* Ameghino, 1895. Olig.; S.A.
†*Astrapothericulus* Ameghino, 1901. U. Olig.; S.A.
†*Astrapotherium* Burmeister, 1879. U. Olig.–U. Mioc.; S.A.
†*Uruguaytherium* Kraglievich, 1927. Mioc.; S.A.
†*Xenastrapotherium* Kraglievich, 1928. Mioc.; S.A.

[1] †Hegetotheridae in original publication.
[2] †Muñizinae in the original publication.
[3] †Astrapotheroidea in Ameghino; †Astrapotherioidea in Simpson, 1934, p. 7.
[4] Spelled †Astrapotheridae in Ameghino.

Order TUBULIDENTATA Huxley, 1872, p. 288.
Fam. Orycteropodidae Bonaparte, 1850 (=Orycteropidae Gray, 1821, p. 305). Plioc.; Eu., As. R.; Af.
✓*Orycteropus* Geoffroy, 1795. Plioc.; Eu., As. R.; Af. Aardvark.
?TUBULIDENTATA *incertae sedis:*
†*Tubulodon* Jepsen, 1932. L. Eoc.; N.A.
Superorder PAENUNGULATA, new.
†Order PANTODONTA Cope, 1873b, pp. 40, 67 (=†Coryphodontia Marsh, 1884, p. 193, included in †Amblypoda Cope, 1875a, pp. 24, 28 =†Amblydactyla Marsh, 1884, pp. 177, 193). [Including †Taligrada Cope, 1883b, p. 406.]
†Fam. Coryphodontidae Marsh, 1876, p. 428. [Including †Pantolambdidae Cope, 1883b, p. 406.] M. Paleoc.–L. Eoc.; N.A. L. Eoc.; Eu. U. Eoc.–M. Olig.; As.
†*Pantolambda* Cope, 1883. M. Paleoc.; N.A.
†*Sparactolambda* Patterson, 1939. U. Paleoc.; N.A.
†*Titanoides* Gidley, 1917. U. Paleoc.; N.A.
†*Coryphodon* Owen, 1845. U. Paleoc.–L. Eoc.; N.A. L. Eoc.; Eu.
†*Eudinoceras* Osborn, 1924. U. Eoc.; As.
†*Hypercoryphodon* Osborn and Granger, 1932. M. Olig.; As.
†Fam. Barylambdidae Patterson, 1939, pp. 361, 372 (=†Barylambdinae Patterson, 1937a, p. 229). U. Paleoc.; N.A.
†*Barylambda* Patterson, 1937. U. Paleoc.; N.A.
†*Haplolambda* Patterson, 1939. U. Paleoc.; N.A.
†Fam. Pantolambdodontidae Granger and Gregory, 1934, p. 6. U. Eoc.; As.
†*Pantolambdodon* Granger and Gregory, 1934. U. Eoc.; As.
†Order DINOCERATA Marsh, 1873a, pp. 117, 118 (=†Dinocerea Marsh, 1872b, p. 344).
†Fam. Uintatheriidae Flower, 1876, p. 387 (=†Eobasileidae Cope, 1873a, p. 563; †Tinoceridae Marsh, 1872a, p. 323; †Dinoceratidae Zittel, 1893, p. 429). [Including †Bathyopsidae Osborn, 1898b, p. 182.] U. Paleoc.–U. Eoc.; N.A., As.
†*Prodinoceras* Matthew, Granger, and Simpson, 1929. U. Paleoc.; As.
†*Probathyopsis* Simpson, 1929. U. Paleoc.–L. Eoc.; N.A.
†*Bathyopsoides* Patterson, 1939. U. Paleoc.; N.A.
†*Bathyopsis* Cope, 1881. L. Eoc.; N.A.
†*Elachoceras* Scott, 1886. M. Eoc.; N.A.
†*Uintatherium* Leidy, 1872. (Many probable synonyms, see p. 242.) M. Eoc.; N.A.
†*Eobasileus* Cope, 1872. [Including †*Uintacolotherium* Cook, 1926.] M.–U. Eoc.; N.A.
†*Gobiatherium* Osborn and Granger, 1932. U. Eoc.; As.
†Order PYROTHERIA Ameghino, 1895, p. 608.
†Fam. Pyrotheriidae Ameghino, 1889, p. 894. [Including †Carolozittelidae Ameghino, 1901, pp. 387, 388.] Eoc.–Olig.; S.A.
†*Carolozittelia* Ameghino, 1901. L. Eoc.; S.A.
†*Propyrotherium* Ameghino, 1901. U. Eoc.; S.A.
†*Pyrotherium* Ameghino, 1888. L. Olig.; S.A.
†*Griphodon* Anthony, 1924. Eoc. or Olig.; S.A.

?†PYROTHERIA *incertae sedis:*
†*Carodnia* Simpson, 1935. Paleoc.; S.A.
†*Ctalecarodnia* Simpson, 1935. Paleoc.; S.A.
Order PROBOSCIDEA Illiger, 1811, p. 96.
†Suborder MOERITHERIOIDEA Osborn, 1921a, p. 2.
†Fam. Moeritheriidae Andrews, 1906b, p. 99. U. Eoc.–L. Olig.; Af.
†*Moeritherium* Andrews, 1901. U. Eoc.–L. Olig.; Af. (Egypt).
Suborder ELEPHANTOIDEA Osborn, 1921a, p. 2. [Including †Mastodontoidea Osborn, 1921a, p. 2; †Stegodontoidea Osborn, 1936, p. 25, 1942, p. 805.]
†Fam. Gomphotheriidae Cabrera, 1929, p. 74 (=†Bunomastodontidae Osborn, 1921a, p. 2; †Trilophodontidae Simpson, 1931a, p. 281). [Including †Bunomastodontidae Osborn, 1921a, p. 2; †Humboldtidae Osborn, 1936, pp. 575, 687, 722; †Serridentidae Osborn, 1936, pp. 30, 287, 381; †Palaeomastodontidae Andrews, 1906b, p. 130[1]; †Dibunodontidae Hopwood, 1935, pp. 11, 85.] L. Olig.–Mioc.; Af. L. Mioc.–Pleist.; As. L. Mioc.–M. Plioc.; Eu. U. Mioc.–Pleist.; N.A. Pleist.; S.A.
†Subfam. Gomphotheriinae Hay, 1922, p. 101 (=†Longirostrinae Osborn, 1918a, p. 136). [Including †Tetralophodontinae Maarel, 1932, p. 126; †Palaeomastodontinae Osborn, 1936, p. 691; ?† Gnathabelodontinae Barbour and Sternberg, 1935, p. 396; †Serridentinae Osborn, 1921c, p. 232.] L. Olig.–L. Mioc.; Af. L. Mioc.–M. Plioc.; As. L. Mioc.–L. Plioc.; Eu. U. Mioc.–M. Plioc., ?Pleist.; N.A.
†*Palaeomastodon* Andrews, 1901. L. Olig.; Af. (Egypt).
†*Phiomia* Andrews and Beadnell, 1902. L. Olig., ?U. Olig.; Af.
†*Gomphotherium* Burmeister, 1837[2] (=†*Trilophodon* Falconer and Cautley, 1857[3]; †*Bunolophodon* Vacek, 1877; †*Tetrabelodon* Cope, 1884). [Subgenera: †*Megabelodon* Barbour, 1914; †*Choerolophodon* Schlesinger, 1917; †*Genomastodon* Barbour, 1917; and †*Tatabelodon* Frick, 1933.] L. Mioc.–M. Plioc.; As. L. Mioc.–L. Plioc.; Eu. L. Mioc.; Af. U. Mioc.–L. Plioc.; N.A.
†*Serridentinus* Osborn, 1923. [Subgenera: †*Ocalientinus* Frick, 1933; †*Serbelodon* Frick, 1933; †*Trobelodon* Frick, 1933.] L. Mioc.–L. Plioc.; As. L.–M. Mioc.; Eu. U. Mioc.–L. Plioc., ?U. Plioc.; N.A.
†*Tetralophodon* Falconer and Cautley, 1857.[4] [Subgenera: †*Morrillia* Osborn, 1924; †*Lydekkeria* Osborn, 1924.] U. Mioc.–L. Plioc.; As. L.–M. Plioc., ?Pleist.; N.A. L. Plioc.; Eu.
?†Gomphotheriinae *incertae sedis:*
†*Gnathabelodon* Barbour and Sternberg, 1935. M. Plioc.; N.A.

[1] †Palaeomastodontidae appears to be the oldest name available for the family, but (availing myself of the privilege of not following priority regardless of all other considerations for supergeneric groups) I reject it because the typical genus intended is really †*Gomphotherium* and some authors would not place †*Palaeomastodon* in this family at all. The other proposed family names are not based on valid generic names and so are themselves invalid.
[2] Or (misprinted as †*Gamphotherium*) Gloger, 1841.
[3] Or, with doubtful propriety, 1846.
[4] Or perhaps 1847.

†*Eubelodon* Barbour, 1914. M. Plioc.; N.A.

†Subfam. Anancinae Hay, 1922, p. 101 (=†Brevirostrinae Osborn, 1918a, p. 136; †Dibunodontidae Hopwood, 1935, p. 55). [Including †Humboldtinae Osborn, 1934a, p. 180, and 1936, p. 667.] L.–M. Plioc.; Eu. U. Plioc.–Pleist.; N.A., As. Pleist.; S.A.

†*Anancus* Aymard, 1855 (=†*Dibunodon* Schlesinger, 1917). [Subgenus: †*Pentalophodon* Falconer, 1857.] L. Plioc.–Pleist.; Eu. U. Plioc.–Pleist.; As.

†*Synconolophus* Osborn, 1929. U. Mioc.–M. Plioc.; As.

†*Stegomastodon* Pohlig, 1912 (=†*Rhabdobunus* Hay, 1914). [Subgenus: group without a valid name, called †*Cuvieronius* in Osborn, 1936, etc., but not †*Cuvieronius* Osborn, 1923.] U. Plioc.–Pleist.; N.A. Pleist.; S.A.

†Subfam. Cuvierioninae Cabrera, 1929, p. 76 (=†Notorostrinae Osborn, 1921b, p. 330). [Including †Notiomastodontinae Osborn, 1936, pp. 590, 730.] U. Plioc.–Pleist.; N.A. Pleist.; S.A.

†*Cuvieronius* Osborn, 1923 (=†*Cordillerion* Osborn, 1926; †*Teleobunomastodon* Revilliod, 1931). U. Plioc.–Pleist.; N.A. Pleist.; S.A.

†*Notiomastodon* Cabrera, 1929. Pleist.; S.A.

†Subfam. Rhynchotheriinae Hay, 1922, p. 101 (=†Rhynchorostrinae Osborn, 1918a, p. 136). U. Mioc.–U. Plioc.; N.A. M. Plioc.; As. Mioc.; Af.

†*Rhynchotherium* Falconer, 1868 (=†*Dibelodon* Cope, 1884). [Subgenera: †*Blickotherium* Frick, 1933; †*Aybelodon* Frick, 1933.] U. Mioc.–U. Plioc.; N.A. M. Plioc.; As. L. Mioc.; Af.

†Subfam. Platybelodontinae Borissiak, 1928, p. 119. [Including †Amebelodontinae Barbour, 1929, p. 138.] U. Mioc.; As. L.–M. Plioc.; N.A.

†*Platybelodon* Borissiak, 1928. [Subgenus: †*Torynobelodon* Barbour, 1929.] U. Mioc.; As. L.–M. Plioc.; N.A.

†*Amebelodon* Barbour, 1927. M. Plioc.; N.A.

†Fam. Mammutidae Cabrera, 1929, p. 74 (=†Mastodontidae Girard, 1852, p. 328; †Mastodonadae Gray, 1821, p. 306). L. Mioc.–U. Plioc.; Eu. M. Mioc.–Pleist.; N.A. L. Plioc.; As.

†*Mammut* Blumenbach, 1799 (=†*Mastodon* Cuvier, 1817). [Subgenera: †*Zygolophodon* Vacek, 1877=†*Turicius* Osborn, 1926; †*Miomastodon* Osborn, 1921; †*Pliomastodon* Osborn, 1926; and an unnamed subgenus called †*Zygolophodon* by Osborn but not †*Zygolophodon* Vacek, 1877.] L. Mioc.–U. Plioc.; Eu. M. Mioc.–Pleist.; N.A. L. Plioc.; As. L. Mioc.; Af. Mastodonts.

Fam. Elephantidae Gray, 1821, p. 305. [Including †Stegodontidae Hopwood, 1935, p. 71.] L. Plioc.–R.; As. Plioc.–Pleist.; Eu. Pleist.–R.; Af. Pleist.; N.A., ?S.A.

†Subfam. Stegodontinae Osborn, 1918a, p. 135. [Including †Stegolophodontinae Osborn, 1936, p. 700.] L. Plioc.–Pleist.; As. Plioc.; Eu.

†*Stegolophodon* Schlesinger, 1917. U. Mioc.–Pleist.; As. M. Plioc.; Eu.

†*Stegodon* Falconer, 1857. M. Plioc.–Pleist.; As.

Subfam. Elephantinae Gill, 1872, p. 13 (=Elephantina Bonaparte, 1838, p. 112). [Including Loxodontinae Osborn, 1918a, p. 135; †Mammontinae Osborn, 1921c, p. 234.] Pleist.; Eu., N.A., ?S.A. Pleist.–R.; As., Af.

Loxodonta Cuvier, 1827. [Subgenera: †*Palaeoloxodon* Matsumoto, 1924=†*Sivalikia* Osborn, 1924=†*Pilgrimia* Osborn, 1924; †*Hesperoloxodon* Osborn, 1931.] Pleist.; As., Eu. Pleist.–R.; Af. African elephant.

†*Mammuthus* Burnett, 1830 (=†"*Mammonteus* Camper, 1788," Osborn, 1924, not Linnaean in Camper, 1788). [Subgenera: †*Parelephas* Osborn, 1924, †*Archidiskodon* Pohlig, 1888, †*Metarchidiskodon* Osborn, 1934.] Pleist.; Eu., As., N.A., Af., ?S.A.[1] Mammoths.

Elephas Linnaeus, 1758. [Subgenera: †*Platelephas* Osborn, 1934, †*Hypselephas* Osborn, 1934.] Pleist.–R.; As. Asiatic elephant.

†Suborder DEINOTHERIOIDEA Osborn, 1921a, p. 2.[2]

†Fam. Deinotheriidae Bonaparte, 1845, p. 4[3] (=†Curtognathidae Osborn, 1936, pp. 81, 735; †Curtognati Kaup, 1833, p. 516). L. Mioc.–M. Plioc.; Eu. L. Mioc.–Pleist.; Af. M. Mioc.–M. Plioc.; As.

†*Deinotherium* Kaup, 1829. L. Mioc.–M. Plioc.; Eu., As. L. Mioc.–Pleist.; Af.

†Suborder BARYTHERIOIDEA, new name (=†Barytheria Andrews, 1904b, p. 482, *nec* Cope, 1898, p. 123).

†Fam. Barytheriidae Andrews, 1906b, p. 172. U. Eoc.; Af.

†*Barytherium* Andrews, 1901. U. Eoc.; Af. (Egypt).

†Order EMBRITHOPODA Andrews, 1906b, p. xiv[4] (=†Barypoda Andrews, 1904b, p. 482, *nec* Haeckel, 1866, p. clvii).

†Fam. Arsinoitheriidae Andrews, 1904a, p. 160. L. Olig.; Af.

†*Arsinoitherium* Beadnell, 1902. L. Olig.; Af. (Egypt).

Order HYRACOIDEA Huxley, 1869, p. 101. [Including †Myohyracoidea Stromer, 1926, p. 120.]

Fam. Procaviidae Thomas, 1892, p. 51 (=Hyracidae Gray, 1821, p. 306, invalid). [Including †Pliohyracidae Osborn, 1899, p. 172, in part=†Saghatheriidae Andrews, 1906b, p. 86.] L. Olig., L. Mioc., R.; Af. L. Plioc.; Eu. R.; W. As.

†*Pachyhyrax* Schlosser, 1910. L. Olig.; Af. (Egypt).

†*Saghatherium* Andrews and Beadnell, 1902. L. Olig.; Af. (Egypt).

†*Prohyrax* Stromer, 1926. L. Mioc.; Af.

†*Pliohyrax* Osborn, 1899 (=†*Leptodon* Gaudry, 1860, *nec* Sundevall, 1835). L. Plioc.; Eu. (Greece).

Dendrohyrax Gray, 1868. R.; Af. Tree hyrax.

Heterohyrax Gray, 1868. R.; Af. Rock hyrax.

Procavia Storr, 1780 (=*Hyrax* Hermann, 1783). R.; Af., W. As. Hyrax, "coney," dassie.

[1] A single fragment reputedly from French Guiana, requiring confirmation.

[2] Spelled †Dinotherioidea by Osborn in 1921; †Deinotherioidea in 1936, p. 81.

[3] Spelled †Deinotheridae in original publication; †Dinotheriidae in Bonaparte, 1850.

[4] Usually cited as 1905, but the exact date is Jan. 4, 1906. The name antedates Andrews' use of the prior, preoccupied name, †Barypoda, in his definitive memoir of 1906, but the latter was evidently in press or the sheets were printed before the change was decided upon.

†Fam. Geniohyidae Matsumoto, 1926, p. 259. [Including †Titanohyracidae Matsumoto, 1926, p. 259.] L. Olig.; Af. (Egypt).
†*Geniohyus* Andrews, 1904. L. Olig.; Af.
†*Bunohyrax* Schlosser, 1910. L. Olig.; Af.
†*Megalohyrax* Andrews, 1903. L. Olig.; Af.
†*Titanohyrax* Matsumoto, 1921. L. Olig.; Af.
†Fam. Myohyracidae Andrews, 1914, p. 171. L. Mioc.; Af.
†*Myohyrax* Andrews, 1914. L. Mioc.; Af.
†*Protypotheroides* Stromer, 1922. L. Mioc.; Af.

Order SIRENIA Illiger, 1811, p. 140.

Suborder TRICHECHIFORMES Hay, 1923, p. 109.

†Fam. Prorastomidae Cope, 1889c, p. 876. Eoc.; W. Indies.
†*Prorastomus* Owen, 1855. Eoc.; W. Indies (Jamaica).
†Fam. Protosirenidae Sickenberg, 1934, p. 193. M. Eoc.; N. Af., Eu.
†*Protosiren* Abel, 1904. M. Eoc.; Af. (Egypt), Eu. (France).
Fam. Dugongidae Gray, 1821, p. 309 (=Halicoridae Gray, 1825, p. 341). [Including Halitheriidae Gill, 1872, p. 13=Halitherida Carus, 1868, p. 168; Hydrodamalidae Palmer, 1895, p. 450=Rytinadae Gray, 1843, pp. xxiii, 107.] M.–U. Eoc.; Af. U. Eoc.–M. Plioc.; Eu. M. Mioc.–L. Plioc.; N.A.R.; Red Sea to N. Pacific.
†Subfam. Halitheriinae Abel, 1913a, p. 358 (=†Halitherida Carus, 1868, p. 168). M.–U. Eoc.; Af. U. Eoc.–M. Plioc.; Eu. M. Mioc.–L. Plioc.; N.A.
†*Eotheroides* Palmer, 1899 (=†*Eotherium* Owen, 1875, *nec* Leidy, 1853). [Including †*Eosiren* Andrews, 1902; †*Archaeosiren* Abel, 1913.] M.–U. Eoc.; Egypt.
†*Prototherium* Zigno, 1887. [Including †*Mesosiren* Abel, 1906; †*Paraliosiren* Abel, 1906.] U. Eoc.; Eu.
†*Halitherium* Kaup, 1838.[1] [Including †*Manatherium* Hartlaub, 1886.] L. Olig.–L. Mioc.; Eu.[2] Olig.; Madagascar.
†*Halianassa* Meyer, 1838. [Including †*Metaxytherium* Christol, 1840.[3]] L.–U. Mioc.; Eu. U. Mioc.; N.A.[2]
†*Thalattosiren* Sickenberg, 1928. M. Mioc.; Eu.
†*Hesperosiren* Simpson, 1932. M. Mioc.; N.A.
†*Felsinotherium* Capellini, 1865. L.–M. Plioc.; Eu. L. Plioc.; N.A.
†Subfam. Miosireninae Abel, 1919, p. 835. L. Plioc.; Eu.
†*Miosiren* Dollo, 1890. L. Plioc.; Eu.
†Subfam. Rytiodinae Abel, 1928, p. 503. U. Olig.; Eu.
†*Rytiodus*[4] Lartet, 1866. U. Olig.; Eu.
Subfam. Dugonginae Simpson, 1932, p. 424. R.; Red Sea, Indian Ocean, W. Pacific.
Dugong Lacépède, 1799 (=*Halicore* Illiger, 1811). R.; coasts of Red Sea, Indian Ocean, W. Pacific. Dugong, sea "cow."
†Subfam. Hydrodamalinae Simpson, 1932, p. 424. R.; N. Pacific Islands.

[1] "†*Halytherium*" in first citation, but this was probably a typographical error and was changed to †*Halitherium* by the same author in the same volume.

[2] Both †*Halitherium* and †*Halianassa* ("†*Metaxytherium*") have been reported in the American Atlantic mid-Tertiary on poor and inconclusive evidence. Possibly †*Dioplotherium* Cope, 1883, is a valid genus there, but it may equal †*Halianassa*. A relatively good specimen from the Upper Miocene of California is more surely referred to the European genus, but even this is not certain.

[3] All recent authors give †*Halianassa* as a synonym of †*Metaxytherium*, but apparently none has taken the necessary step of adopting the earlier, less familiar name.

[4] *Sic!* The usual spelling "*Rhytiodus*" is an invalid emendation.

†*Hydrodamalis* Retzius, 1794 (=*Rytina*[1] Illiger, 1811). R. (but now extinct); Bering Island and adjacent region in N. Pacific.

Fam. Trichechidae Gill, 1872, p. 14 (=Manatidae Gray, 1821, p. 309, *nec* Trichechidae Gray, 1825, p. 340). Pleist.–R.; N.A., S.A. R.; Af.

Trichechus Linnaeus, 1758, *nec* Linnaeus, 1766 (=*Manatus* Brünnich, 1772). Pleist.–R.; Atlantic N.A., S.A. R.; Atlantic Af. Manatee.

†Suborder DESMOSTYLIFORMES Hay, 1923, p. 109.

†Fam. Desmostylidae Osborn, 1905, p. 109. U. Olig.–Mioc.; N.A. Mioc.; Japan, Sakhalin.

†*Cornwallius* Hay, 1923. U. Olig.; Pacific N.A.

†*Desmostylus* Marsh, 1888. Mioc.; Pacific N.A., Japan, Sakhalin.

Superorder MESAXONIA Marsh, 1884, pp. 9, 127.

Order PERISSODACTYLA Owen, 1848, p. 131.

Suborder HIPPOMORPHA Wood, 1937, p. 106 (=in part, Solidungula Blumenbach, 1779, p. 109; Solipeda Meckel, 1809–1810, tab. 1).

Superfam. Equoidea Hay, 1902, p. 608 (=Hippoidea Osborn, 1898a, p. 79; essentially=Solidungula Blumenbach, 1779, p. 109, etc.).

†Fam. Palaeotheriidae Gill, 1872, p. 12 (=†Palaeotheridae Girard, 1852, p. 328; †Palaeotheriina Bonaparte, 1850). [Including †Paloplotheriinae Osborn, 1892, p. 93.] L. Eoc.–L. Olig.; Eu. Eoc.; As.

†*Propachynolophus* Lemoine, 1891. L. Eoc.; Eu.

†*Pachynolophus* Pomel, 1847. M.–U. Eoc.; Eu.

†*Propalaeotherium* Gervais, 1849. M.–U. Eoc.; Eu. L. or M. Eoc.; As.

†*Lophiotherium* Gervais, 1849. M.–U. Eoc.; Eu.

†*Anchilophus* Gervais, 1848–1852. M.–U. Eoc.; Eu.

†*Plagiolophus* Pomel, 1847. [Including †*Paloplotherium* Owen, 1848.] U. Eoc.–L. Olig.; Eu.

†*Palaeotherium* Cuvier, 1804. U. Eoc.–L. Olig.; Eu.

Fam. Equidae Gray, 1821, p. 307. L. Eoc.–Pleist.; N.A. L. Eoc.–R.; Eu. Mioc.–R.; As. Plioc.–R.; Af. Pleist.; S.A. R.; world wide in domestication.

†Subfam. Hyracotheriinae Cope, 1881c, p. 381. L.–U. Eoc.; N.A. L. Eoc.; Eu.

†*Hyracotherium* Owen, 1840. [Including †*Eohippus* Marsh, 1876.] L. Eoc.; N.A., Eu.

†*Orohippus* Marsh, 1872. M. Eoc.; N.A.

†*Epihippus* Marsh, 1877. [Including †*Duchesnehippus* Peterson, 1931.] U. Eoc.; N.A.

†Subfam. Anchitheriinae Osborn, 1910, p. 555 (=†Anchitheridae Leidy, 1869, pp. 362, 402). L. Olig.–M. Plioc.; N.A. Mioc.; Eu. Mioc.–L. Plioc. As.

†*Mesohippus* Marsh, 1875. [Including †*Pediohippus* Schlaikjer, 1935.] L.–M. Olig.; N.A.

†*Miohippus* Marsh, 1874. M. Olig.–L. Mioc.; N.A.

[1] *Sic!* The usual spelling "*Rhytina*" is an invalid emendation (and the name is invalid in any case).

†*Parahippus* Leidy, 1858. L.–U. Mioc.; N.A.
†*Archaeohippus* Gidley, 1906. L.–U. Mioc.; N.A.
†*Anchitherium* Meyer, 1844. [Including †*Kalobatippus* Osborn, 1915.] L.–M. Mioc.; N.A. M.–U. Mioc.; Eu. Mioc.; As.
†*Hypohippus* Leidy, 1858. [Including †*Megahippus* McGrew, 1937.] L. Mioc.–L. Plioc.; N.A. L. Plioc.; As.

Subfam. Equinae Steinmann and Döderlein, 1890, p. 769. [Including †Protohippinae Gidley, 1907, p. 868 = †Hippotheriinae Cope, 1881c, p. 400 = †Hippotheriina Bonaparte, 1850.] L. Mioc.–Pleist.; N.A. L. Plioc.–R.; Eu., As., Af. Pleist.; S.A. R.; world wide in domestication.
†*Merychippus* Leidy, 1857. [Including †*Protohippus* Leidy, 1858.] M.–U. Mioc.; N.A.
†*Hipparion* Christol, 1832 (= †*Hippotherium* Kaup, 1833). [Including †*Proboscidipparion* Sefve, 1927; †*Stylohipparion* van Hoepen, 1932; †*Notohipparion* Haughton, 1931; etc.] L.–U. Plioc.; N.A., Eu., As., Af.
†*Neohipparion* Gidley, 1903. L.–U. Plioc.; N.A.
†*Nannippus* Matthew, 1926. L.–U. Plioc.; N.A.
†*Calippus* Matthew and Stirton, 1930. L. Plioc.; N.A.
†*Pliohippus* Marsh, 1874. L.–M. Plioc.; N.A.
†*Hippidion* Owen, 1869 (= "†*Hippidium* Owen" of Burmeister, 1875, and almost all later writers). Pleist.; S.A.
†*Onohippidium* Moreno, 1891. Pleist.; S.A.
†*Parahipparion* C. Ameghino, 1904 (= †*Hyperhippidium* Sefve, 1910). Pleist.; S.A.
Equus Linnaeus, 1758. [Including, mainly as subgenera, †*Plesippus* Matthew, 1924; *Asinus* Frisch, 1775; *Hippotigris* H. Smith, 1841; *Dolichohippus* Heller, 1912; *Onager* Brisson, 1756; *Hemionus* F. Cuvier, 1823; †*Kraterohippus* van Hoepen, 1930; †*Kolpohippus* van Hoepen, 1930; †*Sterrohippus* van Hoepen, 1930; †*Neohippus* Abel, 1913; etc.] U. Plioc.–R.; Eu., As., Af. U. Plioc.–Pleist.; N.A. Pleist.; S.A. R.; world wide in domestication. Horses, asses or donkeys, onager or kiang, zebras.

†Superfam. Brontotherioidea Hay, 1902, p. 629 (= †Titanotherioidea Osborn, 1898a, p. 79).

†Fam. Brontotheriidae[1] Marsh, 1873b, p. 486 (= †Titanotheridae Flower, 1876, p. 109). [Including †Lambdotheriidae Cope, 1889a, p. 152; †Palaeosyopidae Osborn, 1910, p. 556.] L. Eoc.–L. Olig.; N.A. U. Eoc.–M. Olig.; As. U. Eoc., ?L. Olig.; Eu.

†Subfam. Lambdotheriinae Hay, 1902, p. 629 (= †Lambdotheriidae Cope, 1889a, p. 152). L. Eoc.; N.A.
†*Lambdotherium* Cope, 1880. L. Eoc.; N.A.

†Subfam. Palaeosyopinae Steinmann and Döderlein, 1890, p. 777. [Including †Eotitanopinae Osborn, 1914, p. 403.] L.–M. Eoc.; N.A.
†*Eotitanops* Osborn, 1907. L.–M. Eoc.; N.A.
†*Limnohyops* Marsh, 1890. M. Eoc.; N.A.
†*Palaeosyops* Leidy, 1870. M. Eoc.; N.A.

[1] Spelled †Brontotheridae by Marsh.

†Subfam. Dolichorhininae Osborn, 1929, p. 245 (= †Dolichorhinae Riggs, 1912, pp. 25, 40). [Including †Rhadinorhininae Osborn, 1929, p. 429.] M.–U. Eoc.; N.A.
- †*Eometarhinus* Osborn, 1919. M. Eoc.; N.A.
- †*Metarhinus* Osborn, 1908. [Including †*Heterotitanops* Peterson, 1914.] M.–U. Eoc.; N.A.
- †*Rhadinorhinus* Riggs, 1912. U. Eoc.; N.A.
- †*Mesatirhinus* Osborn, 1908. M.–U. Eoc.; N.A.
- †*Sphenocoelus* Osborn, 1895. U. Eoc.; N.A.
- †*Dolichorhinus* Hatcher, 1895. U. Eoc.; N.A.

†Subfam. Telmatheriinae Osborn, 1914, p. 403. [Including †Metatelmatheriinae Granger and Gregory, MS.[1]] M.–U. Eoc.; N.A. U. Eoc.–M. Olig.; As.
- †*Telmatherium* Marsh, 1872. M. Eoc.; N.A.
- †*Sthenodectes* Gregory, 1912. U. Eoc.; N.A.
- †*Sivatitanops* Pilgrim, 1925. U. Eoc.; As.
- †*Metatelmatherium* Granger and Gregory, 1938. U. Eoc.; As., N.A.
- †*Desmatotitan* Granger and Gregory, MS. U. Eoc.; As.
- †*Hyotitan* Granger and Gregory, MS. M. Olig.; As.

†Subfam. Brontopinae Osborn, 1914, p. 405. [Including †Manteoceratinae Osborn, 1914, p. 403; †Epimanteoceratinae Granger and Gregory, MS.] M. Eoc.–L. Olig.; N.A. U. Eoc.–M. Olig.; As. U. Eoc.; Eu.
- †*Manteoceras* Hatcher, 1895. M.–U. Eoc.; N.A.
- †*Epimanteoceras* Granger and Gregory, MS. U. Eoc.; As.
- †*Protitan* Granger and Gregory, MS. U. Eoc.; As.
- †*Microtitan* Granger and Gregory, MS. U. Eoc.; As.
- †*Dolichorhinoides* Granger and Gregory, MS. U. Eoc.; As.
- †*Gnathotitan* Granger and Gregory, MS. U. Eoc.; As.
- †*Rhinotitan* Granger and Gregory, MS. U. Eoc.; As.
- †*Pachytitan* Granger and Gregory, MS. U. Eoc.; As.
- †*Brachydiastematherium* Böckh and Maty, 1876. U. Eoc.; Eu.
- †*Protitanotherium* Hatcher, 1895. U. Eoc.; N.A.
- †*Teleodus* Marsh, 1890. U. Eoc.–L. Olig.; N.A.
- †*Protitanops* Stock, 1936. L. Olig.; N.A.
- †*Brontops* Marsh, 1887. [Including †*Diploclonus* Marsh, 1890.] L. Olig.; N.A., ?Eu.
- †*Parabrontops* Granger and Gregory, MS. L. Olig.; As.
- †*Metatitan* Granger and Gregory, MS. L.–M. Olig.; As.

†Subfam. Embolotheriinae Osborn, 1929, p. 942. U. Eoc.–M. Olig.; As.
- †*Titanodectes* Granger and Gregory, MS. U. Eoc.–L. Olig.; As.
- †*Embolotherium* Osborn, 1929. L.–M. Olig.; As.

†Subfam. Menodontinae Osborn, 1914, p. 405. [Including †Diplacodontinae Osborn, 1914, p. 403.] U. Eoc.–L. Olig.; N.A. L. Olig.; ?Eu.
- †*Notiotitanops* Gazin and Sullivan, 1942. U. Eoc.; N.A.
- †*Diplacodon* Marsh, 1875. U. Eoc.; N.A.
- †*Eotitanotherium* Peterson, 1914. U. Eoc.; N.A.

[1] Subfamilies and genera given as by "Granger and Gregory, MS." are in press in the Bulletin of the American Museum of Natural History and will be published before this classification.

†*Menodus* Pomel, 1849 (=†*Titanotherium* Leidy, 1852; †*Symborodon* Cope, 1873). [Including †*Allops* Marsh, 1887.[1]] L. Olig.; N.A., ?Eu.

†Subfam. Brontotheriinae Steinmann and Döderlein, 1890, p. 777. [Including †Megaceropinae Osborn, 1914, p. 405.] L. Olig.; N.A.

†*Megacerops* Leidy, 1870. L. Olig.; N.A.

†*Brontotherium* Marsh, 1873. L. Olig.; N.A.

†Superfam. Chalicotherioidea Gill, 1872, p. 76 (=†Order Ancylopoda Cope, 1889a, p. 153).

†Fam. Chalicotheriidae Gill, 1872, p. 8. [Including †Macrotheriidae Alston, 1878, p. 23; Moropodidae Marsh, 1877a, p. 249.] U. Eoc.–Pleist.; As. U. Eoc.–M. Mioc.; N.A. Eoc.–L. Plioc.; Eu.

†Subfam. Eomoropinae[2] Matthew, 1929b, p. 519. U. Eoc.; N.A. U. Eoc., ?L. Olig.; As.

†*Eomoropus* Osborn, 1913. U. Eoc.; N.A., As.

†*Grangeria* Zdansky, 1930. U. Eoc.–?L. Olig.; As.

†Subfam. Chalicotheriinae Matthew, 1929b, p. 518 (=†Macrotheriinae Holland and Peterson, 1913, pp. 202, 209). [Including †Schizotheriinae Holland and Peterson, 1913, pp. 202, 203, in part.] ?Eoc., Olig.–L. Plioc.; Eu. Olig.–Pleist.; As. L. Olig.–M. Mioc.; N.A.

†Tribe Chalicotherini Colbert, 1934, p. 354.[3] L. Olig.–M. Mioc.; N.A. Olig.–Pleist.; As. U. Mioc.–L. Plioc.; Eu.

†*Chalicotherium* Kaup, 1833. L. Plioc.; Eu.

†*Macrotherium* Lartet, 1837. M. Mioc.; N.A. U. Mioc.; Eu. Olig.–L. Plioc.; As.

†*Nestoritherium* Kaup, 1859 (=†*Circotherium* Holland and Peterson, 1914). ?Plioc., Pleist.; As.

†*Oreinotherium* Russell, 1934. L. Olig.; N.A.

†Tribe Schizotherini Colbert, 1934, p. 354. Olig.–L. Plioc.; Eu. Olig.–Pleist.; As. L.–M. Mioc.; N.A.

†*Schizotherium* Gervais, 1876. Olig.; Eu., As.

†*Metaschizotherium* von Koenigswald, 1932. U. Mioc.; Eu.

†*Moropus* Marsh, 1877. L.–M. Mioc.; N.A.

†*Phylotillon* Pilgrim, 1910. L. Mioc.; As.

†*Ancylotherium* Gaudry, 1863. L. Plioc.; Eu.

†*Postschizotherium* von Koenigswald, 1932. Pleist.; As.

†Chalicotheriidae *incertae sedis:*

†*Pernatherium* Gervais, 1876. Eoc.; Eu.

Suborder CERATOMORPHA Wood, 1937, p. 106 (=in part, Tridactyla Latreille, 1825, p. 61; Trichenae Gray, 1821, p. 306; Tapiromorpha Haeckel, 1873, p. 554).

Superfam. Tapiroidea Gill, 1872, p. 12. [Including †Lophiodontoidea Gill, 1872, p. 83.]

[1] In the literature previous to Osborn, 1929, the genus here called †*Menodus* was usually called †*Titanotherium*, the genus here called †*Megacerops* was usually called †*Symborodon*, and the genus here called †*Brontops* was usually called †*Megacerops*.

[2] †Eomoropodinae would be better etymologically, but Matthew's form is not invalid and is simpler.

[3] Winge, in 1906, p. 153, used the tribal name †Chalicotheriini, but in this case the recognition of a slight change in spelling as changing authorship is just, because Winge's concept was unlike Colbert's and was not really of tribal scope in comparison with other classifications of that day, and of this.

†Fam. Isectolophidae Peterson, 1919, p. 115. L.–M. Eoc.; N.A. U. Eoc.; As.
†*Homogalax* Hay, 1899.[1] L. Eoc.; N.A.
†*Parisectolophus* Peterson, 1919. M. Eoc.; N.A.
†*Isectolophus* Scott and Osborn, 1887. M.–U. Eoc.; N.A.
†*Indolophus* Pilgrim, 1925. U. Eoc.; As.
†Fam. Helaletidae Osborn, 1892, p. 127. L. Eoc.–M. Olig.; N.A. U. Eoc.–L. Olig.; As.
†Subfam. Helaletinae Wortman and Earle, 1893, p. 173. L.–U. Eoc.; N.A. U. Eoc.; As.
†*Heptodon* Cope, 1882. L. Eoc.; N.A.
†*Helaletes* Marsh, 1872. M. Eoc.; N.A.
†*Dilophodon* Scott, 1883. M. Eoc.; N.A.
†*Heteraletes* Peterson, 1931. U. Eoc.; N.A.
†*Diplolophodon* Zdansky, 1930. U. Eoc.; As.
†Subfam. Colodontinae Wortman and Earle, 1893, p. 173. M. Eoc.–M. Olig.; N.A. U. Eoc.–L. Olig.; As.
†*Desmatotherium* Scott, 1883. M. Eoc.; N.A. U. Eoc.; As.
†*Colodon* Marsh, 1890. L.–M. Olig.; N.A. L. Olig.; As.
†*Paracolodon* Matthew and Granger, 1925. L. Olig.; As.
†*Deperetella* Matthew and Granger, 1925. U. Eoc.; As.
†*Teleolophus* Matthew and Granger, 1925. U. Eoc.; As.
?†Helaletidae *incertae sedis:*
†*Cristidentinus* Zdansky, 1930. U. Eoc.; As.
†*Chasmotheroides* Wood, 1934. M. Eoc.; N.A.
†Fam. Lophiodontidae Gill, 1872, p. 12. L.–U. Eoc.; Eu. M.–U. Eoc.; ?As.
†*Lophiodochoerus* Lemoine, 1880. L. Eoc.; Eu.
†*Lophiodon* Cuvier, 1822. M.–U. Eoc.; Eu.
†*Lophiaspis* Depéret, 1910. L.–M. Eoc.; Eu.
†*Chasmotherium* Rütimeyer, 1862. M. Eoc.; Eu.
†*Atalonodon* Dal Piaz, 1929. Eoc.; Eu.
?†Lophiodontidae or †Helaletidae, *incertae sedis:*
†*Schlosseria* Matthew and Granger, 1926. M. Eoc.; As.
†*Lophialetes* Matthew and Granger, 1925. U. Eoc.; As.
Fam. Tapiridae Burnett, 1830a, p. 352 (=Taperidae Gray, 1821, p. 306). L. Eoc.–Pleist.; N.A. L. Olig.–Pleist.; Eu. Pleist.–R.; S.A. Mioc.–R.; As.
†*Protapirus* Filhol, 1877. [Including †*Tanyops* Marsh, 1894.] L. Olig.; Eu. M. Olig.–L. Mioc.; N.A.
†*Miotapirus* Schlaikjer, 1937. L. Mioc.; N.A.
†*Palaeotapirus* Filhol, 1888. [Including †*Paratapirus* Depéret, 1902.] L. Mioc.; Eu. Mioc.; ?As.
†*Tapiravus* Marsh, 1877. M. or U. Mioc.; N.A.[2]
†*Megatapirus* Matthew and Granger, 1923. Pleist.; As.
Tapirus Brisson, 1762. [Including *Tapirella* Palmer, 1903 =*Elasmognathus* Gill, 1865, *nec* Fieber, 1844; *Acrocodia* Goldman, 1913.] ?U. Mioc., Plioc.–Pleist.; Eu. Pleist.; N.A. L. Plioc.–R.; As. Pleist.–R.; S.A. Tapirs.

[1] In the older literature this genus is called †*Systemodon* Cope, 1881, but the type of †*Systemodon* belongs to †*Hyracotherium*.

[2] This "genus" is practically undefined but does show the presence of tapirs in North America between the Lower Miocene and the Pleistocene and is listed for that purpose.

Superfam. Rhinocerotoidea Gill, 1872, p. 12.
†Fam. Hyrachyidae Wood, 1927, pp. 166, 168 (= †Hyrachyinae Osborn, 1892, p. 93). L.–U. Eoc.; N.A. Eoc.; ?As.
†*Hyrachyus* Leidy, 1871. L.–U. Eoc.; N.A. Eoc.; ?As.
†*Colonoceras* Marsh, 1873. M. Eoc.; N.A.
†*Metahyrachyus* Troxell, 1922. M. Eoc.; N.A.
†*Ephyrachyus* Wood, 1934. M. Eoc.; N.A.
†Fam. Hyracodontidae Cope, 1879b, p. 228. M. Eoc.–U. Olig.; N.A. M.–U. Eoc.; ?As.
†Subfam. Triplopodinae Osborn, 1892, p. 93 (= †Triplopodidae Cope, 1881b, p. 340). M.–U. Eoc.; N.A.
†*Triplopus* Cope, 1880. M.–U. Eoc.; N.A.
†*Epitriplopus* Wood, 1927. U. Eoc.; N.A.
?†Triplopodinae *incertae sedis:*
†*Teilhardia* Matthew and Granger, 1926. M. Eoc.; As.
†*Ardynia* Matthew and Granger, 1925. U. Eoc.; As.
†*Caenolophus* Matthew and Granger, 1925. U. Eoc.; As.
†Subfam. Hyracodontinae Steinman and Döderlein, 1890, pp. 768, 772. U. Eoc.–L. Olig.; N.A.
†*Prothyracodon* Scott and Osborn, 1887. U. Eoc.; N.A.
†*Hyracodon* Leidy, 1856. L.–M. Olig.; N.A.
†Fam. Amynodontidae Scott and Osborn, 1883, pp. 4, 12. U. Eoc.–M. Olig.; N.A. U. Eoc.–L. Mioc.; As. M. Olig.; Eu.
†*Amynodon* Marsh, 1877. U. Eoc.; N.A., As.
†*Amynodontopsis* Stock, 1933. U. Eoc.; N.A.
†*Mesamynodon* Peterson, 1931. U. Eoc.; N.A.
†*Paramynodon* Matthew, 1929. U. Eoc.; As.
†*Metamynodon* Scott and Osborn, 1887. L.–M. Olig.; N.A. Olig.; As.
†*Cadurcotherium* Gervais, 1873. M. Olig.; Eu. ?L. Olig., ?L. Mioc.; As.
Fam. Rhinocerotidae Owen, 1845, p. 587 (= Rhynocerotidae Gray, 1821, p. 306). [Including †Caenopidae Cope, 1887d, p. 926; †Elasmotheriidae Gill, 1872, p. 12; etc.] M. Eoc.–Pleist.; Eu. U. Eoc.–L. Plioc.; N.A. U. Eoc.–R.; As. Mioc.–R.; Af.
†Subfam. Aceratheriinae Dollo, 1885, p. 295.[1] M. Olig.–L. Plioc.; Eu. L. Mioc.–U. Plioc.; As.
†*Protaceratherium* Abel, 1910. M.–U. Olig.; Eu.
†*Aceratherium* Kaup, 1832. M. Olig.–L. Plioc.; Eu. L. Mioc.–L. Plioc.; As.
†*Plesiaceratherium* Young, 1937. U. Mioc.; As.
†*Chilotherium* Ringström, 1924. L. Mioc.–U. Plioc.; As. U. Mioc.–L. Plioc.; Eu.
†Subfam. Caenopinae Breuning, 1923, p. 119 (= †Caenopidae Cope, 1887c, p. 992). [Including †Diceratheriinae Dollo, 1885, p. 295.] M. Eoc.–L. Plioc.; Eu. U. Eoc.–L. Plioc.; N.A. L. Mioc.–L. Plioc.; As.
†*Prohyracodon* Koch, 1897. M. Eoc.; Eu.
†*Eotrigonias* Wood, 1927. U. Eoc.; N.A.
†*Epiaceratherium* Abel, 1910. L.–U. Olig.; Eu.
†*Trigonias* Lucas, 1900. L. Olig.; N.A.

[1] "†Acerotheriinae," presumably a *lapsus.*

†*Caenopus* Cope, 1880. L.–U. Olig.; N.A.
†*Amphicaenopus* Wood, 1927. L.–U. Olig.; N.A.
†*Subhyracodon* Brandt, 1878. [Including †*Leptaceratherium* Osborn, 1898.] L.–M. Olig.; N.A.
†*Diceratherium* Marsh, 1875. [Including †*Metacaenopus* Cook, 1909; †*Menoceras* Troxell, 1921; etc.] U. Olig.–L. Mioc.; N.A.
†*Ronzotherium* Aymard, 1856. [Including †*Paracaenopus* Breuning, 1923.] L.–U. Olig.; Eu.
†*Meninatherium* Abel, 1910. U. Olig.; Eu.
†*Eggysodon*[1] Roman, 1911. M.–U. Olig.; Eu.
†*Pleuroceros* Roger, 1898.[2] U. Olig.–?L. Plioc.; Eu. L. Mioc.–?L. Plioc.; As.
†*Aphelops* Cope, 1873. M. Mioc.–L. Plioc.; N.A.
†*Peraceras* Cope, 1880. U. Mioc.–L. Plioc.; N.A.

†Subfam. Alloceropinae Wood, 1932, p. 170. L.–M. Olig.; Eu.
†*Allocerops* Wood, 1932. L.–M. Olig.; Eu.

†Subfam. Paraceratheriinae Osborn, 1923, p. 13 (=†Indricotheriinae Borissiak, 1923, p. 123[3]; †Baluchitheriinae Osborn, 1923, p. 13). ?U. Eoc.; U. Olig.–L. Mioc.; As.
†*Forstercooperia* Wood, 1939 (=†*Cooperia* Wood, 1938, *nec* Ransom, 1907). U. Eoc.; As.
†*Paraceratherium* Forster Cooper, 1911. U. Olig.; As.
†*Baluchitherium* Forster Cooper, 1913 (=†*Thaumastotherium* Forster Cooper, 1913, *nec* Kirkaldy, 1908). U. Olig.–L. Mioc.; As. (Includes the largest known land mammals.)
†*Indricotherium* Borissiak, 1915. U. Olig.; As.

†Subfam. Teleoceratinae Hay, 1902, p. 646. U. Olig.–L. Plioc.; Eu. U. Mioc.–L. Plioc.; N.A.
†*Brachypotherium* Roger, 1904. U. Olig.–L. Plioc.; Eu.
†*Teleoceras* Hatcher, 1894. U. Mioc.–L. Plioc.; N.A.

Subfam. Rhinocerotinae Dollo, 1885, p. 295. L. Plioc.–R.; As.
†*Gaindatherium* Colbert, 1934. L.–M. Plioc.; As.
Rhinoceros Linnaeus, 1758. U. Plioc.–R.; As. Indian and Javanese rhinoceroses.

Subfam. Dicerorhininae, new form (=Dicerorhinae Ringström, 1924, p. 5; Ceratorhinae Osborn, 1898a, p. 121). [Including Dicerinae (*sic*) Ringström, 1924, p. 97.] U. Olig.–R.; As. U. Olig.–Pleist.; Eu. Pleist.–R.; Af.
Dicerorhinus Gloger, 1841 (="*Didermocerus* Brookes, 1928"; *Ceratorhinus* Gray, 1867).[4] U. Olig.–Pleist.; Eu. U. Olig.–R.; As. Sumatran rhinoceros.
†*Coelodonta* Bronn, 1831 (=†*Tichorhinus* Brandt, 1849). Pleist.; Eu., As.

[1] Depéret's emendation to *Engyodon* is correct classicism but incorrect zoology.
[2] As Wood has noted, this name is not preoccupied by *Pleuroceras* Hyatt, 1868. The later Tertiary species referred to this genus probably do not belong to it.
[3] With priority over †Baluchitheriinae and †Paraceratheriinae.
[4] The first name applied to the genus was *Didermocerus*, but this is never used and can reasonably be left in desuetude on the convenient, if somewhat sophistic, grounds that its appearance in a sales catalogue was not publication. The nomenclature of the fossil forms is in a chaotic condition, but it seems certain that the line leading to this genus, if not the genus itself *sensu lato*, is known from the late Oligocene.

Ceratotherium Gray, 1867. Pleist.–R.; Af. White (African) rhinoceros.
Diceros Gray, 1821. Pleist.–R.; Af.[1] Black (African) rhinoceros.
†Subfam. Elasmotheriinae Dollo, 1885, p. 295 (= †Elasmotherina Bonaparte, 1845, p. 4). L. Plioc.–Pleist.; As. Pleist.; Eu.
†*Iranotherium* Ringström, 1924. L. Plioc.; As.
†*Sinotherium* Ringström, 1922. [Including †*Parelasmotherium* Killgus, 1923.] L. Plioc.; As.
†*Elasmotherium* Fischer, 1808. Pleist.; Eu., As.
Superorder PARAXONIA Marsh, 1884, p. 177.
Order ARTIODACTYLA Owen, 1848, p. 131.
Suborder SUIFORMES Jaeckel, 1911, p. 233 (essentially = non-ruminantia of various authors).
†Infraorder PALAEODONTA Matthew, 1929á, p. 406 (with Hyodonta essentially = Bunodonta Kovalevskiĭ, 1873b, p. 152). [Including †Hypoconifera Stehlin, 1910, p. 1135.]
†Superfam. Dichobunoidea Weber, 1904, pp. 644, 688.
†Fam. Dichobunidae Gill, 1872, p. 10 (= †Dichobunina Turner, 1849, p. 158). L.–U. Eoc.; N.A. L. Eoc.–M. Olig.; Eu.
†Subfam. Dichobuninae Zittel, 1893, p. 374. L. Eoc.; N.A. L. Eoc.–M. Olig.; Eu.
†*Diacodexis* Cope, 1882. [Including †*Trigonolestes* Cope, 1894.] L. Eoc.; N.A.
†*Bunophorus* Sinclair, 1914. L. Eoc.; N.A.
†*Wasatchia* Sinclair, 1914. L. Eoc.; N.A.
†*Protodichobune* Lemoine, 1891. L. Eoc.; Eu.
†*Dichobune* Cuvier, 1822. M. Eoc.–L. Olig.; Eu.
†*Hyperdichobune* Stehlin, 1910. L. Olig.; Eu.
†*Mouillacitherium* Filhol, 1882. M. Eoc.–L. Olig.; Eu.
†*Metriotherium* Filhol, 1882. M. Olig.; Eu.
†*Meniscodon* Rütimeyer, 1888. M. Eoc.; Eu.
†Subfam. Homacodontinae Peterson, 1919, p. 66. M.–U. Eoc.; N.A.[2]
†*Homacodon* Marsh, 1872. [Including †*Nanomeryx* Marsh, 1894.] M. Eoc.; N.A.
†*Bunomeryx* Wortman, 1898. U. Eoc.; N.A.
†*Hylomeryx* Peterson, 1919. U. Eoc.; N.A.
†*Sphenomeryx* Peterson, 1919. U. Eoc.; N.A.
†*Mesomeryx* Peterson, 1919. U. Eoc.; N.A.
†*Pentacemylus* Peterson, 1931. U. Eoc. (or L. Olig.); N.A.
?†Dichobunidae *incertae sedis:*
†*Sarcolemur* Cope, 1875. L. Eoc.; N.A.
†*Antiacodon* Marsh, 1872. M. Eoc.; N.A.
†*Microsus* Leidy, 1870. M. Eoc.; N.A.
†Fam. Choeropotamidae Owen, 1845, p. 559 (= †Choeropotamina Bonaparte, 1845, p. 4). [Including †Helohyidae Marsh, 1877b, p. 364.] L.–U. Eoc.; N.A. U. Eoc.–M. Olig.; Eu. M.–U. Eoc.; As.
†*Parahyus* Marsh, 1876. L. Eoc.; N.A.

[1] Rhinocerotids are known from the Miocene and Pliocene in Africa, but the Tertiary forms have not been accurately classified.

[2] Hay lists the lower Oligocene genera †*Limnenetes* and †*Oreonetes* as if they belonged in this group, but this must have been an involuntary lapse as no reason for it is given and these genera are well known to be quite characteristic oreodonts.

†*Helohyus* Marsh, 1872. M. Eoc.; N.A.
†*Lophiohyus* Sinclair, 1914. M. Eoc.; N.A.
†*Khirtharia* Pilgrim, 1940. M. Eoc.; As.
†*Brachyhyops* Colbert, 1937. U. Eoc.; N.A.
†*Gobiohyus* Matthew and Granger, 1925. U. Eoc.; As.
†*Choeropotamus* Cuvier, 1821.[1] U. Eoc.–M. Olig.; Eu.

†Fam. Cebochoeridae Lydekker, 1883, p. 146. [Including †Mixtotheriidae Pearson, 1927, p. 431; †Acrotherulidae Lydekker, 1883, p. 146.] M. Eoc.–L. Olig.; Eu.

†Subfam. Cebochoerinae, new form (= †Cebochoeridae of previous authors). M. Eoc.–L. Olig.; Eu.

†*Cebochoerus* Gervais, 1848–1852. [Including †*Acotherulum* Gervais, 1850; †*Leptacotherulum* Filhol, 1877.] M. Eoc.–L. Olig.; Eu.

†*Choeromorus* Gervais, 1848–1852. M.–U. Eoc.; Eu.

†Subfam. Mixtotheriinae, new form (= †Mixtotheriidae Pearson, 1927, p. 431; †Mixtotheriodontidae Lydekker, 1883, p. 146).[2] M.–U. Eoc.; Eu.

†*Mixtotherium* Filhol, 1880. M.–U. Eoc.; Eu.

†Fam. Leptochoeridae Marsh, 1894b, p. 273. L.–U. Olig.; N.A.

†*Stibarus* Cope, 1878. L.–M. Olig.; N.A.
†*Leptochoerus* Leidy, 1856. M.–U. Olig.; N.A.

†Superfam. Entelodontoidea Colbert, 1938a, p. 105.

†Fam. Entelodontidae Lydekker, 1883, p. 146 (= †Elotheriidae Alston, 1878, p. 18). [Including †Achaenodontidae Matthew, 1899, p. 34.] U. Eoc.–L. Mioc.; N.A. L. Olig.; Eu. ?U. Eoc., Olig.; As.

†Subfam. Achaenodontinae Zittel, 1893, p. 334. U. Eoc.; N.A., ?As.

†*Achaenodon* Cope, 1873. [Including †*Protelotherium* Osborn, 1895.] U. Eoc.; N.A.

†Subfam. Entelodontinae Osborn, 1909, p. 61 (= †Elotheriinae Cope, 1888, p. 1089). L. Olig.–L. Mioc.; N.A. L. Olig.; Eu. Olig.; As.

†*Entelodon* Aymard, 1847 (?) (= †*Elotherium* Pomel, 1847).[3] L. Olig.; Eu., ?N.A.[4]

†*Archaeotherium* Leidy, 1850. [Including, as subgenera, †*Pelonax* Cope, 1874; with †*Megachoerus* Troxell, 1920; †*Choerodon* Troxell, 1920; †*Scaptohyus* Sinclair, 1921.] L.–U. Olig.; N.A.

†*Daeodon* Cope, 1879. [Including, probably as a subgenus, †*Dinohyus* Peterson, 1905, and perhaps the very doubtful "genera" †*Boochoerus* Cope, 1879, and †*Ammodon* Marsh, 1893.] L. Mioc.; N.A.

[1] I consider the original spelling †*Chaeropotamus* to be a *lapsus* and, therefore, subject to valid correction. Cuvier himself later spelled it †*Choeropotamus*, as have most authors since then.

[2] Based on †*Mixtotherium* despite the erroneous form.

[3] The name †*Elotherium* probably has priority and is often used (necessitating changes of subfamily, family, and superfamily names as well), but recently †*Entelodon* is more common in the literature. As Peterson has shown, it is not certain that †*Elotherium* is prior, and the type specimen was inadequate, poorly described, unfigured, and is lost. No one but Pomel ever saw it, and it is fair to say that his genus was not recognizably established. †*Entelodon* was firmly established, and the name can legitimately continue in use.

[4] Even following the consensus in giving †*Archaeotherium* generic rank, one or more of the Lower Oligocene species referred to it may well be closer to †*Entelodon*.

Infraorder SUINA Gray, 1868a, p. 20 (=Hyodonta Matthew, 1929a, in part, p. 406.

Superfam. Suoidea Cope, 1887b, p. 381.

Fam. Suidae Gray, 1821, p. 306. [Including Phacochœridae Gray, 1868a, p. 47; †Listriodontidae Lydekker, 1884, p. 100; †Tetraconodontidae Lydekker, 1876, p. 60.] L. Olig.–R.; Eu. L. Mioc.–R.; Af. U. Mioc.–R.; As. R.; world wide in domestication.

†Subfam. Hyotheriinae Cope, 1888, p. 1087 (=†Palaeochoerinae Matthew, 1924, p. 176). L. Olig.–U. Mioc.; Eu. U. Mioc.–M. Plioc.; As. L. Mioc.; Af.

†*Propalaeochoerus* Stehlin, 1929. L.–U. Olig.; Eu.

†*Palaeochoerus* Pomel, 1847.[1] L.–M. Mioc.; Eu. U. Mioc.–M. Plioc.; As.

†*Hyotherium* Meyer, 1834. M.–U. Mioc.; Eu.

†*Chleuastochoerus* Pearson, 1928. L. Plioc.; As.

†Subfam. Listriodontinae, new form (=†Listriodontidae Lydekker, 1884, p. 100). M.–U. Mioc.; Eu. U. Mioc.–U. Plioc.; As.

†*Listriodon* Meyer, 1846. L.–U. Mioc.; Eu. U. Mioc.–M. Plioc.; As.

†Subfam. Tetraconodontinae, new form (=†Tetraconodontidae Lydekker, 1876, p. 60). U. Mioc.–Pleist.; As.

†*Conohyus* Pilgrim, 1926. U. Mioc.–M. Plioc.; As.

†*Tetraconodon* Falconer, 1868. L. Plioc.–Pleist.; As.

†*Sivachoerus* Pilgrim, 1926. M. Plioc.–Pleist.; As.

†Subfam. Sanitheriinae, new. L. Plioc.; As.

†*Sanitherium* Meyer, 1866. L. Plioc.; As.

Subfam. Suinae Zittel, 1893, p. 343. [Including Potamochoerina Gray, 1873b, p. 434; Babirussina Gray, 1868a, p. 21; Phacochoerinae van Hoepen and van Hoepen, 1932, p. 61.] L. Plioc.–R.; Eu., As. Pleist.–R.; Af.

†*Propotamochoerus* Pilgrim, 1926. L.–M. Plioc.; As.

Potamochoerus Gray, 1854 (=*Choiropotamus* Gray, 1843, *nec Chaeropotamus* Cuvier, 1821=*Choeropotamus* Cuvier, 1822).[2] Pleist.; As. R.; Af. (African) water hog.

†*Hyosus* Pilgrim, 1926. M. Plioc.; As.

†*Sivahyus* Pilgrim, 1926. M. Plioc.; As.

†*Hippohyus* Falconer and Cautley, 1840–1845. L. Plioc.–Pleist.; As.

†*Dicoryphochoerus* Pilgrim, 1926. L. Plioc.–Pleist.; As.

Sus Linnaeus, 1758. [Including *Porcula* Hodgson, 1847; †*Microstonyx* Pilgrim, 1926; etc.] L. Plioc.–R.; Eu., As. R.; world wide in domestication. Pigs.

Phacochoerus Cuvier, 1817. [Including †*Notochoerus* Broom, 1925; †*Metridiochoerus* Hopwood, 1926; †*Kolpochoerus* van Hoepen and van Hoepen, 1932; †*Tapinochoerus* van Hoepen

[1] I take the first spelling "*Paleocherus*" to be a *lapsus* legally corrigible, since it is manifestly contrary to Pomel's own and contemporary etymological usage and was at once corrected by Pomel.

[2] Under the informal rule that one different letter always makes a different name, the name for this pig would be *Choiropotamus*. I follow this rule when it helps to preserve a widely used name and to prevent confusion. I do not follow it here, where it would cashier the universally used name and promote confusion. The formal Rules do not explicitly condemn or enforce either practice.

and van Hoepen, 1932; †*Synaptochoerus* van Hoepen and van Hoepen, 1932; †*Stylochoerus* van Hoepen and van Hoepen, 1932.[1]] Pleist.–R.; Af. Wart hog.

Hylochoerus Thomas, 1904. Pleist.–R.; Af. (African) forest hog.

Babirussa Frisch, 1775. R.; E. Indies. Babirussa.

Suidae *incertae sedis:*

†*Diamantohyus* Stromer, 1922. L. Mioc.; Af.

†*Xenochoerus* Zdansky, 1909. U. Mioc.; Eu.

†*Lophochoerus* Pilgrim, 1926. L. Plioc.; As.

Fam. Tayassuidae Palmer, 1897, p. 174 (= Dicotylidae Gray, 1868a, p. 21; Dicotylina Turner, 1849, p. 157). L. Olig.–R.; N.A. Pleist.–R.; S.A. L. Olig., U. Mioc.; Eu. L. Plioc.; As.

†Subfam. Doliochoerinae, new. L. Olig., U. Mioc.; Eu. L. Plioc.; As.

†*Doliochoerus* Filhol, 1882. L. Olig.; Eu.

†*Taucanamo*, new name[2] (= †*Choerotherium* Lartet, 1851 [or 1838, or 1847?], *nec* †*Choerotherium* Cautley and Falconer, 1835). U. Mioc.; Eu.

†*Pecarichoerus* Colbert, 1933. L. Plioc.; As.

Subfam. Tayassuinae Hay, 1902, p. 658 (= Dicotylinae Leidy, 1853, p. 323; Dicotylina Turner, 1849, p. 157). L. Olig.–R.; N.A. Pleist.–R.; S.A.

†*Perchoerus* Leidy, 1869. [Including †*Thinohyus* Marsh, 1875 = †*Bothrolabis* Cope, 1888 = †*Chaenohyus* Cope, 1879.] L. Olig.–L. Mioc.; N.A.

†*Hesperhys* Douglass, 1903. [Including †*Desmathyus* Matthew, 1907; †*Pediohyus* Loomis, 1910.[3]] L.–M. Mioc.; N.A.

†*Dyseohyus* Stock, 1937. U. Mioc.; N.A.

†*Prosthennops* Gidley, 1904. U. Mioc.–M. Plioc.; N.A.

†*Mylohyus* Cope, 1889. Pleist.; N.A.

†*Platygonus* Le Conte, 1848.[4] [Including †*Antaodon* Ameghino, 1908; †*Parachoerus* Rusconi, 1930; †*Brasiliochoerus* Rusconi, 1930; and others.] U. Plioc.–Pleist.; N.A. Pleist.; S.A.

†*Catagonus* Ameghino, 1904. [Including †*Interchoerus* Rusconi, 1930.] Pleist.; S.A.

Tayassu Fischer, 1814 (= *Dicotyles* Cuvier, 1817). [Including *Pecari* Reichenbach, 1835.] Pleist.–R.; N.A., S.A. Peccaries.

Infraorder ANCODONTA Matthew, 1929a, p. 406.

[1] Aside from my strong opinion that these last four names apply to groups of subgeneric rank at very most, it would be legitimate to consider them as unpublished, since no description or diagnoses have appeared in any language but Afrikaans. It is no depreciation of the cultural worth of this excellent language to insist that literature in it has not been published to the scientific world and that non-Boer scientists are under no obligation to learn or read it.

[2] The various students of the Suidae do not seem to have noticed that the name †*Choerotherium* for this peculiar genus is preoccupied. It is so important that a valid name for it is essential here, and I supply one. The type is †*Choerotherium sansaniense* Lartet, 1851. †*Choeromorus pygmaeum* Depéret, 1893, is referred. †*Choerotherium* Cautley and Falconer possibly antedates some other generic name for Siwalik suids, but neither Pilgrim nor Colbert appears to have discussed this possibility.

[3] It is strange that Peterson, Matthew, Loomis, and others have repeatedly published on animals of this stage, Matthew and Loomis each giving a new generic name, without noting that Douglass had already well described, figured, and named a good specimen evidently of this generic group. †*Desmathyus* is now always used in the literature. It is probably a good subgenus of †*Hesperhys*.

[4] The first spelling was actually "*Platigonus*," but there is sufficient indication that this was a misprint. The name is differently misprinted "*Platydonus*" in another paper by Le Conte, published almost simultaneously. "*Platygonus*" is now universally used and may be retained.

Superfam. Anthracotherioidea Gill, 1872, p. 11.

†Fam. Anoplotheriidae Bonaparte, 1850 (= †Anoplotheriadae Gray, 1821, p. 306). [Including †Tapirulidae Cope, 1879b, p. 228.] M. Eoc.–M. Olig.; Eu.

†*Catodontherium* Depéret, 1908 (= †*Catodus* Depéret, 1905).[1] M.–U. Eoc.; Eu.

†*Dacrytherium* Filhol, 1876. M.–U. Eoc.; Eu.

†*Leptotheridium* Stehlin, 1910. U. Eoc.; Eu.

†*Tapirulus* Gervais, 1850. U. Eoc.; Eu.

†*Hyracodontherium* Filhol, 1877. L. Olig.; Eu.

†*Anoplotherium* Cuvier, 1804. L. Olig.; Eu.

†*Diplobune* Rütimeyer, 1862. L.–M. Olig.; Eu.

†Fam. Anthracotheriidae Gill, 1872, p. 11 (= †Anthracotheridae Leidy, 1869, p. 202). [Including †Merycopotamidae Gill, 1872, p. 10; †Hyopotamidae Kōvalevskii, 1873a, p. 147 = †Hyopotaminae Gill, 1872, p. 11 = †Ancodontidae Marsh, 1894a, p. 178.] M. Eoc.–L. Mioc.; Eu. U. Eoc.–Pleist.; As. L. Olig.–L. Mioc.; Af., N.A.

†*Haplobunodon* Depéret, 1908. M.–U. Eoc.; Eu.

†*Lophiobunodon* Depéret, 1908. M. Eoc.; Eu.

†*Thaumastognathus*[2] Filhol, 1890. U. Eoc.; Eu.

†*Rhagatherium* Pictet and Humbert, 1855–1857. [Including †*Amphirhagatherium* Depéret, 1908.] M. Eoc.–L. Olig.; Eu. L. Olig.; Af. (Fayûm). L. Plioc.; As. (this genus?).

†*Anthracobune* Pilgrim, 1940. M. Eoc.; As.

†*Anthracohyus* Pilgrim and Cotter, 1916. U. Eoc.; As.

†*Anthracokeryx* Pilgrim and Cotter, 1916. U. Eoc.; As.

†*Anthracothema* Pilgrim, 1928. U. Eoc.; As.

†*Anthracosenex* Zdansky, 1930. U. Eoc.; As.

†*Anthracotherium* Cuvier, 1822. L.–U. Olig.; Eu. L. Mioc., ?L. Plioc.; As.

†*Bothriodon* Aymard, 1846[3] (= †*Ancodon* Pomel, 1847; †*Ancodus* Pomel, 1848; †*Hyopotamus* Owen, 1848). [Including †*Aepinacodon* Troxell, 1921.] L. Olig.; Eu. L.–M. Olig.; N.A.

†*Elomeryx* Marsh, 1894. U. Olig.; N.A.

†*Heptacodon* Marsh, 1894. L.–U. Olig.; N.A.

†*Octacodon* Marsh, 1894. U. Olig.; N.A.

†*Arretotherium* Douglass, 1901. L. Mioc.; N.A.

†*Brachyodus* Depéret, 1895. L. Olig.–L. Mioc.; Eu. L. Olig.; Af. (Fayûm). U. Olig.; As.

†*Microbunodon* Depéret, 1908. [Including †*Microselenodon* Depéret, 1908.] M. Olig.; Eu.

†*Hemimeryx* Lydekker, 1883. L. Mioc.–L. Plioc.; As.

†*Hyoboops* Trouessart, 1904. [Including †*Merycops* Pilgrim, 1910.] L. Mioc.–L. Plioc.; As. L. Mioc.; Af.

†*Telmatodon* Pilgrim, 1907. [Including †*Gonotelma* Pilgrim, 1908.] L. Mioc.–L. Plioc.; As.

[1] Proposed on the grounds that †*Catodus* is preoccupied by *Catodon* Linnaeus, 1761. This is not preoccupation, but †*Catodus* was a *nomen nudum* in its earlier publication (1905) so that †*Catodontherium* may be retained.

[2] Spelled "*Taumastognathus*" and "*Taumastognatus*" in the original publication, but the fact that one must be a misprint suggests that both are and that the now universal emended spelling is permissible.

[3] This date has been doubted, and consequently †*Ancodon* (usually misspelled "*Ancodus*") has generally been used in the literature, but there is little doubt that †*Bothriodon* is the older, and hence the valid, name.

†*Parabrachyodus* Forster Cooper, 1915. L. Mioc.; As.
†*Choeromeryx* Pomel, 1848. L.–M. Plioc.; As.
†*Merycopotamus* Falconer and Cautley, 1847. M. Plioc.–Pleist.; As.

Fam. Hippopotamidae Gray, 1821, p. 306. M. Plioc.–Pleist.; As. M. Plioc.–R.; Af. Pleist.; Eu.
†*Hexaprotodon* Falconer and Cautley, 1836. M. Plioc.–Pleist.; As.
Hippopotamus Linnaeus, 1758. M. Plioc.–R.; Af. Pleist.; Eu., As. Hippopotamus.
Choeropsis Leidy, 1853 (= *Choerodes* Leidy, 1852, *nec* White, 1846; *Diprotodon* Duvernoy, 1849, *nec* Owen, 1838). Pleist.; Madagascar, Mediterranean.[1] R.; Af. Pygmy hippopotamus.

†Superfam. Cainotherioidea Camp and VanderHoof, 1940, p. 339.
†Fam. Cainotheriidae Camp and VanderHoof, 1940, p. 339 (= †Caenotheriidae Cope, 1881c, p. 378; †Cainotherida Rütimeyer, 1891, p. 87). U. Eoc.–L. Mioc.; Eu.
†*Oxacron* Filhol, 1884. U. Eoc.–L. Olig.; Eu.
†*Paroxacron* Hürzeler, 1936. U. Eoc.–L. Olig.; Eu.
†*Plesiomeryx* Gervais, 1873.[2] L.–M. Olig.; Eu.
†*Caenomeryx* Hürzeler, 1936. L. Olig.; Eu.
†*Procaenotherium* Hürzeler, 1936. L. Olig.; Eu.
†*Cainotherium*[3] Bravard, 1828 (= †*Caenotherium* Agassiz, 1846). M. Olig.–L. Mioc.; Eu.

†Infraorder OREODONTA Osborn, 1910, p. 549. U. Eoc.–M. Plioc. N.A.
†Superfam. Merycoidodontoidea Thorpe, 1937, p. 23.
†Fam. Agriochoeridae Leidy, 1869, p. 131.[4] U. Eoc.–L. Mioc.; N.A.
†*Protagriochoerus* Scott, 1899. U. Eoc.; N.A.
†*Agriochoerus* Leidy, 1850–1851. L. Olig.–L. Mioc.; N.A.
†*Mesagriochoerus* Peterson, 1934. U. Eoc. (or L. Olig.); N.A.
†*Diplobunops* Peterson, 1919. U. Eoc.; N.A.
†Fam. Merycoidodontidae Thorpe, 1923, p. 239 (= †Oreodontidae Leidy, 1869, pp. 71, 379). [Including †Protoreodontidae Scott, 1890b, p. 503.] U. Eoc.–M. Plioc.; N.A.
†Subfam. Protoreodontinae Scott, 1890a, pp. 320, 361. U. Eoc.; N.A.
†*Protoreodon* Scott and Osborn, 1887. [Including †*Eomeryx* Marsh, 1894.[5]] U. Eoc.; N.A.
†*Hyomeryx* Marsh, 1894. U. Eoc.; N.A.
†Subfam. Merycoidodontinae Hay, 1902, p. 665 (= †Oreodontinae Gill, 1872, p. 81). L. Olig.–M. Plioc.; N.A.
†*Oreonetes* Loomis, 1924. L. Olig.; N.A.

[1] It may be doubted whether in all cases the generic reference indicates real affinity and not merely convergently small size.
[2] The original spelling "*Plesiomaeryx*" seems an obvious misprint and was corrected by Gervais himself.
[3] This spelling was unquestionably intentional and cannot well be changed, although almost everyone now uses "†*Caenotherium*."
[4] Spelled Agriochaeridae in 1869, Agriochoeridae by Leidy in 1871, but since Leidy used the generic spelling *Agriochoerus* the former must be a misprint.
[5] Thorpe credits †*Eomeryx* to Marsh in 1875, and on this showing he should have used this name instead of †*Protoreodon*. The fact, however, appears to be that Marsh did not publish †*Eomeryx* until 1877 and that it remained essentially a *nomen nudum* until 1894, so that it is antedated by †*Protoreodon*.

†*Merycoidodon* Leidy, 1848 (= †*Oreodon*[1] Leidy, 1851). L.–M. Olig.; N.A.
†*Eporeodon* Marsh, 1875.[2] M. Olig.–L. Mioc.
†*Mesoreodon* Scott, 1893. L. Mioc.; N.A.
†*Paroreodon* Thorpe, 1921. L. Mioc. (or U. Olig.); N.A.
†*Merycoides* Douglass, 1907. L.–M. Mioc.; N.A.
†*Phenacocoelus* Peterson, 1906. L. Mioc.; N.A.
†*Poatrephes* Douglass, 1903. U. Mioc.; N.A.
†*Metoreodon* Matthew and Cook, 1909. U. Mioc.–M. Plioc. N.A.

†Subfam. Ticholeptinae Schultz and Falkenbach, 1940, p. 215. M. Mioc.–M. Plioc.; N.A.
†*Ticholeptus* Cope, 1878. M.–U. Mioc.; N.A.
†*Mediochoerus* Schultz and Falkenbach, 1941. M.–U. Mioc.; N.A.
†*Ustatochoerus* Schultz and Falkenbach, 1941. L.–M. Plioc.; N.A.

†Subfam. Merycochoerinae Schultz and Falkenbach, 1940, p. 216. U. Olig.–U. Mioc.; N.A.
†*Promerycochoerus* Douglass, 1901. [Including †*Paracotylops* Matthew, 1901; †*Desmatochoerus* Thorpe, 1921; †*Hypselochoerus* Loomis, 1924.] U. Olig.–L. Mioc.; N.A.
†*Merycochoerus* Leidy, 1858. L.–U. Mioc.; N.A.
†*Brachycrus* Matthew, 1901 (= †*Pronomotherium* Douglass, 1907). M.–U. Mioc.; N.A.

†Subfam. Merychyinae, new. L. Mioc.–L. Plioc.; N.A.
†*Oreodontoides* Thorpe, 1921. L. Mioc.; N.A.
†*Merychyus* Leidy, 1858. L. Mioc.–L. Plioc.; N.A.

†Subfam. Leptaucheniinae Schultz and Falkenbach, 1940, p. 215. L. Olig.–U. Mioc.; N.A.
†*Limnenetes* Douglass, 1901. L. Olig.; N.A.
†*Leptauchenia* Leidy, 1856. U. Olig.–L. Mioc.; N.A.
†*Cyclopidius* Cope, 1878. [Including †*Sespia* Stock, 1930; †*Chelonocephalus* Thorpe, 1921.] L.–U. Mioc.; N.A.

†Merycoidodontidae *incertae sedis:*
†*Trigenicus* Douglass, 1903. L. Olig.; N.A.
†*Bathygenys* Douglass, 1901. L. Olig.; N.A.

Suborder TYLOPODA Illiger, 1811, p. 102.

†Fam. Xiphodontidae Flower, 1884, pp. xxviii, 335. M. Eoc.–L. Olig.; Eu.
†*Dichodon* Owen, 1848. [Including †*Tetraselenodon* Schlosser, 1886.] M. Eoc.–L. Olig.; Eu.
†*Xiphodon* Cuvier, 1822. U. Eoc.–L. Olig.; Eu.
†*Haplomeryx* Schlosser, 1886. U. Eoc.; Eu.

Fam. Camelidae Gray, 1821, p. 307. U. Eoc.–Pleist.; N.A. Pleist.–R.; S.A., As. Pleist.; Eu., N. Af.

[1] †*Oreodon* has been incorrectly considered to be preoccupied. There is no question that it is antedated and invalid for that reason. It is, however, very widely used in the literature.

[2] As reviewed by Thorpe, there is some evidence that this genus is synonymous with †*Eucrotaphus* Leidy, 1850, and hence should bear the latter name. Leidy's genus is, however, practically indeterminate and his name can well be considered a *nomen vanum*, as it has in practice. The very widespread and important genus is always called †*Eporeodon*, and it would be contrary to common sense and is not unequivocally necessary under the Rules to start calling it †*Eucrotaphus* at this time.

†Subfam. Poëbrotheriinae[1] Zittel, 1893, p. 361 (=†Poebrotheriidae Cope, 1874, p. 26). U. Eoc.–M. Olig.; N.A.
†*Protylopus* Wortman, 1898. U. Eoc.; N.A.
†*Camelodon* Granger, 1910. U. Eoc.; N.A.
†*Poabromylus* Peterson, 1931. U. Eoc. (or L. Olig.); N.A.
†*Eotylopus* Matthew, 1910. L. Olig.; N.A.
†*Poëbrotherium* Leidy, 1847. M. Olig.; N.A.
Subfam. Camelinae Zittel, 1893, p. 364. [Including †Protolabinae Zittel, 1893, p. 363=†Protolabidae Cope, 1884c, p. 16.] U. Olig.–Pleist.; N.A. Pleist.–R.; S.A., As. Pleist.; Eu., N. Af.
†*Dyseotylopus* Stock, 1935. U. Olig.; N.A.
†*Protomeryx* Leidy, 1856. U. Olig.–L. Mioc.; N.A.
†*Protolabis* Cope, 1876. M. Mioc.–L. Plioc.; N.A.
†*Procamelus* Leidy, 1858. U. Mioc.–L. Plioc.; N.A.
†*Pliauchenia* Cope, 1875. L.–U. Plioc.; N.A.
†*Megatylopus* Matthew and Cook, 1909. L. Plioc.; N.A.
†*Megacamelus* Frick, 1929.[2] U. Plioc.; N.A.
†*Gigantocamelus* Barbour and Schultz, 1939. U. Plioc.–Pleist.; N.A.
†*Titanotylopus* Barbour and Schultz, 1934. Pleist.; N.A.
†*Camelops* Leidy, 1854. Pleist.; N.A.
†*Tanupolama* Stock, 1928.[3] Pleist.; N.A.
†*Palaeolama* Gervais, 1867. Pleist.; S.A.
Lama Frisch, 1775 (=*Auchenia* Illiger, 1811, *nec* Thunberg, 1789).[4] Pleist.–R.; S.A. Llama, alpaca, vicuña, and guanaco.
Camelus Linnaeus, 1758. Pleist.; Eu., N. Af. (also R. in domestication). Pleist.–R.; As. Camel, dromedary.
†Subfam. Pseudolabidinae, new. U. Olig.; N.A.
†*Pseudolabis* Matthew, 1904. U. Olig.; N.A.
†Subfam. Alticamelinae, new. [Including †Miolabinae Hay, 1902, p. 676.[5]] M. Olig.–L. Plioc.; N.A.
†*Paratylopus* Matthew, 1904. M. Olig.–L. Mioc.; N.A.
†*Oxydactylus* Peterson, 1904. L. Mioc.; N.A.
†*Miolabis* Hay, 1899. M. Mioc.; N.A.
†*Alticamelus* Matthew, 1901.[6] M. Mioc.–L. Plioc.; N.A.
†Subfam. Stenomylinae Frick, 1937, p. 656. L. Mioc.–L. Plioc.; N.A.
†*Stenomylus* Peterson, 1906. L. Mioc.; N.A.
†*Rakomylus* Frick, 1937. L. Plioc.; N.A.
?Camelidae *incertae sedis* (=†Pseudoceratini, †Pseudoceratinae Frick, 1937, p. 649):
†*Pseudoceras* Frick, 1937. ?Plioc.; N.A.

[1] †Poebrotherinae in the original reference.
[2] It is doubtful whether this genus has been published and defined under the Rules.
[3] Perhaps including †*Prochenia* Frick, 1929, a *nomen nudum* at present.
[4] *Auchenia*, in this sense, is thus both antedated and preoccupied, but it is still occasionally used by careless authors.
[5] The older name is not used because †*Miolabis*, far from being typical of the subfamily, is only doubtfully referred to it. Hay's subfamily was essentially synonymous with †Protolabinae Zittel, 1893=†Protolabidae Cope, 1884, and very different from the present †Alticamelinae.
[6] †*Altomeryx* Frick, 1929 (L. Plioc.; N.A.), probably belongs in this subfamily and may be separable from †*Alticamelus*, but it is a *nomen nudum* at present.

Suborder RUMINANTIA Scopoli, 1777, pp. 493–496.
Infraorder TRAGULINA Flower, 1883, p. 184.
†Superfam. Amphimerycoidea Colbert, 1941a, p. 21.
†Fam. Amphimerycidae Stehlin, 1910, p. 1143. U. Eoc.–L. Olig.; Eu.
†*Pseudamphimeryx* Stehlin, 1910. U. Eoc.–L. Olig.; Eu.
†*Amphimeryx*[1] Pomel, 1849. L. Olig.; Eu.
†Superfam. Hypertraguloidea Scott, 1940, p. 507.
†Fam. Hypertragulidae Cope, 1879a, p. 66 (= †Leptomerycidae Scott, 1899, p. 15). U. Eoc.–L. Mioc.; N.A. U. Eoc.; As.
†Subfam. Hypertragulinae Matthew, 1908, p. 561. [Including proposed subfamilies here made tribes, as listed below.] U. Eoc.–L. Mioc.; N.A.
†Subfam. Archaeomerycinae, new. U. Eoc.; As.
†*Archaeomeryx* Matthew and Granger, 1925. U. Eoc.; As.
†Tribe Leptotragulini, new rank (= †Leptotragulinae Zittel, 1893, p. 361). U. Eoc.; N.A.
†*Leptotragulus* Scott and Osborn, 1887. [Including or = †*Parameryx* Marsh, 1894.[2]] U. Eoc.; N.A.
†*Leptoreodon* Wortman, Apr. 9, 1898 (= †*Camelomeryx* Scott, Apr. 15, 1898). U. Eoc.; N.A.
†*Oromeryx* Marsh, 1894. U. Eoc.; N.A.
†Tribe Hypertragulini Frick, 1937, p. 618[3] (= †Hypertragulinae Matthew, 1908, p. 561). U. Eoc.–L. Mioc.; N.A.
†*Simimeryx* Stock, 1934. U. Eoc.; N.A.
†*Hypertragulus* Cope, 1873. [Including †*Allomeryx* Sinclair, 1905.] M. Olig.–L. Mioc.; N.A.
†*Nanotragulus* Lull, 1922. L. Mioc.; N.A.
†Tribe Leptomerycini Frick, 1937, p. 618 (= †Leptomerycinae Zittel, 1893, p. 389). L.–U. Olig.; N.A.
†*Heteromeryx* Matthew, 1905. L. Olig.; N.A.
†*Leptomeryx* Leidy, 1853. L.–U. Olig.; N.A.
†Tribe Hypisodontini Frick, 1937, p. 618 (= †Hypisodontinae Cope, 1887b, p. 389). M. Olig.; N.A.
†*Hypisodus* Cope, 1873. M. Olig.; N.A.
†Hypertragulidae *incertae sedis:*
†*Floridatragulus* White, 1940. L. Mioc.; N.A.
†Fam. Protoceratidae Marsh, 1891, p. 82. L. Olig.–L. Plioc.; N.A.
†*Protoceras* Marsh, 1891. [Including †*Calops* Marsh, 1894; †*Pseudoprotoceras* Cook, 1934.] L.–U. Olig.; N.A.
†*Paratoceras* Frick, 1937. "Late Tertiary"; N.A.
†*Syndyoceras* Barbour, 1905. L. Mioc.; N.A.
†*Synthetoceras* Stirton, 1932. [Including †*Prosynthetoceras* Frick, 1937.[4]] L. Plioc.; N.A.
Superfam. Traguloidea Gill, 1872, pp. 9, 73, 88.

[1] Always now so spelled, but "*Amphimerix*" in the original publication, possibly as a correctable *lapsus*.

[2] A *nomen nudum* for a *genus coelebs* in 1877, based on scraps of several genera, and really a *nomen vanum* that should be discarded entirely.

[3] As explained elsewhere, Frick's names ending in "-ini" are not meant to be tribes but groups of about subfamily rank, larger than, and including, subfamilies in Frick's sense, unlike that of other authors. But the spelling and the contents are the same, so that Frick is definitely the author of this name regardless of the rank given it.

[4] Frick described †*Prosynthetoceras* as a subgenus, with which I agree, but Scott lists it as a genus. It may extend the range of the genus, but its age has not been determined.

†Fam. Gelocidae Schlosser, 1886a, p. 41. U. Eoc.–L. Olig.; Eu., As.
†*Indomeryx* Pilgrim, 1928. U. Eoc.; As.
†*Miomeryx* Matthew and Granger, 1925. L. Olig.; As.
†*Phaneromeryx* Schlosser, 1886. U. Eoc.; Eu.
†*Lophiomeryx* Pomel, 1854. U. Eoc.–L. Olig.; Eu. L. Olig.; As.
†*Cryptomeryx* Schlosser, 1886. U. Eoc.; Eu.
†*Gelocus* Aymard, 1855. L. Olig.; Eu.
†*Paragelocus* Schlosser, 1902. L. Olig.; Eu.
†*Pseudogelocus* Schlosser, 1893. L. Olig.; Eu.
†*Bachitherium* Filhol, 1882. L. Olig.; Eu.
†*Prodremotherium* Filhol, 1877. L. Olig.; Eu.
Fam. Tragulidae Milne Edwards, 1864, p. 157. [Including Hyemoschidae Gray, 1872a, pp. 5, 99.] U. Mioc.–R.; As. U. Mioc.–L. Plioc.; Eu. Pleist.–R.; Af.
†*Dorcatherium* Kaup, 1833. U. Mioc.–L. Plioc.; Eu. U. Mioc.–U. Plioc.; As.
†*Dorcabune* Pilgrim, 1910. L.–M. Plioc.; As.
Hyemoschus Gray, 1845.[1] Pleist.–R.; Af. Water chevrotain.
Tragulus Brisson, 1762. [Including *Moschiola* Hodgson, 1843.] ?M. Plioc., Pleist.–R.; As. Chevrotain.
Infraorder PECORA Linnaeus, 1758, p. 65.
Superfam. Cervoidea Simpson, 1931a, p. 284 (=Cervoidae Hay, 1930, p. 815).
Fam. Cervidae Gray, 1821, p. 307 (=Cervina Goldfuss, 1820, pp. xx, 374). [Including †Palaeomerycidae Lydekker, 1883, p. 173; Moschidae Gray, 1821, p. 307; etc.[2]] L. Olig.–R.; As. U. Olig.–R.; Eu. L. Mioc.–R.; N.A. Pleist.–R.; S.A.
†Subfam. Palaeomerycinae Matthew, 1904, p. 102 (=†Palaeomerycidae Lydekker, 1883, p. 174). [Including †Longirostromerycinae Frick, 1937, p. 217; †Parablastomerycinae Frick, 1937, p. 217; †Pseudoblastomerycinae Frick, 1937, p. 253.] L. Olig., L. Mioc.; As. U. Olig.–U. Mioc.; Eu. L. Mioc.–M. Plioc.; N.A.
†Tribe Blastomerycini Frick, 1937, p. 215. L. Olig.; As. L. Mioc.–M. Plioc.; N.A.
†*Eumeryx* Matthew and Granger, 1923. L. Olig.; As.
†*Blastomeryx* Cope, 1877. [Including (subgenera as defined) †*Parablastomeryx* Frick, 1937; †*Pseudoparablastomeryx* Frick, 1937; †*Problastomeryx* Frick, 1937; †*Pseudoblastomeryx* Frick, 1937.] L. Mioc.–M. Plioc.; N.A.
†*Machaeromeryx* Matthew, 1926. L. Mioc.; N.A.
†*Longirostromeryx* Frick, 1937. M. Mioc.–L. Plioc.; N.A.
†Tribe Palaeomerycini, new. U. Olig.–U. Mioc.; Eu. L. Mioc.; As.
†*Amphitragulus* Pomel, 1846. U. Olig.–L. Mioc.; Eu. L. Mioc.; As.
†*Dremotherium* Geoffroy, 1833. L. Mioc.; Eu.
†*Palaeomeryx* Meyer, 1834. M.–U. Mioc.; Eu.

[1] Commonly but erroneously written "*Hyaemoschus*." This genus also often goes by the name of the extinct †*Dorcatherium* from which it is, however, distinct.

[2] Almost every genus of living cervids has been taken as type of a supposedly distinct family, even such manifestly close allies as *Cervus* (*Cervus*) and *Cervus* (*Rusa*) having at times been placed in different "families."

Subfam. Moschinae Zittel, 1893, p. 395 (=Moschidae Gray, 1821, p. 307). ?Plioc., Pleist.–R.; As.

Moschus Linnaeus, 1758. ?L. Plioc., Pleist.–R.; As. Musk deer.

†Subfam. Dromomerycinae Frick, 1937, p. 99. [Including †Cranioceratinae Frick, 1937, p. 75; †Barbouromerycinae Frick, 1937, p. 127; †Drepanomerycinae Frick, 1937, p. 137; †Yumaceratinae Frick, 1937, p. 142; †Aletomerycinae Frick, 1937, p. 147.] L. Mioc.–U. Plioc.; N.A.

†Tribe Dromomerycini Frick, 1937, p. 75. L. Mioc.–U. Plioc.; N.A.

†*Barbouromeryx* Frick, 1937. [Including (subgenera as defined) †*Probarbouromeryx* Frick, 1937; †*Protobarbouromeryx* Frick, 1937; †*Bouromeryx* Frick, 1937.] L.–M. Mioc.; N.A.

†*Drepanomeryx* Sinclair, 1915. [Including (subgenus as defined) †*Matthomeryx* Frick, 1937.] M. Mioc.; N.A.

†*Dromomeryx* Douglass, 1909. [Including (subgenus as defined) †*Subdromomeryx* Frick, 1937.] M. Mioc.; N.A.

†*Rakomeryx* Frick, 1937. M.–U. Mioc.; N.A.

†*Cranioceras* Matthew, 1918. [Including (subgenus as defined) †*Procranioceras* Frick, 1937.] M. Mioc.–U. Plioc.; N.A.

†Tribe Aletomerycini Frick, 1937, p. 142. L. Mioc.–U. Plioc.; N.A.

†*Aletomeryx* Lull, 1920. [Including †*Dyseomeryx* Matthew, 1924.] L. Mioc.; N.A.

†*Sinclairomeryx* Frick, 1937. M. Mioc.; N.A.

†*Yumaceras* Frick, 1937. M.–U. Plioc.; N.A.

Subfam. Muntiacinae Pocock, 1923a, p. 207 (=Cervulinae Sclater, 1870, p. 115). L. Mioc.–U. Plioc.; Eu. U. Mioc.–R.; As.

†Tribe Dicrocerini, new. L. Mioc.–L. Plioc.; Eu. U. Mioc.–L. Plioc., ?M. Plioc.; As.

†*Dicrocerus* Lartet, 1837. [Including †*Heteroprox* Stehlin, 1928; †*Euprox* Stehlin, 1928.] L. Mioc.–L. Plioc.; Eu. U. Mioc.–L. Plioc.; As.

†*Stephanocemas* Colbert, 1936. M.–U. Mioc.; Eu. U. Mioc.; As.

†*Platycemas* Teilhard de Chardin and Trassaert, 1937. ?M. Plioc.; As.

†*Palaeoplatycerus* Pacheco, 1915. M. Mioc.–L. Plioc.; Eu.

†*Micromeryx* Lartet, 1851. M.–U. Mioc.; Eu.

Tribe Muntiacini Weber, 1928, p. 572. L. Plioc.–R.; As. U. Plioc.; Eu.

†*Eostylocerus* Zdansky, 1925. L. Plioc.; As.

†*Metacervulus* Teilhard de Chardin and Trassaert, 1937. [Including †*Paracervulus* Teilhard de Chardin and Trassaert, 1937.] M. Plioc.–Pleist.; As. U. Plioc.; Eu.

Muntiacus Rafinesque, 1815 (=*Cervulus* De Blainville, 1816; *Prox* Ogilby, 1837). [Including *Procops* Pocock, 1923.] Pleist.–R.; As. Muntjak.

Elaphodus Milne Edwards, 1871. R.; As. Tufted deer, Tibetan muntjak.

Subfam. Cervinae Baird, 1857, p. 630. [Including †Pliocervinae Khomenko, 1913, pp. 107, 108.] L. Plioc.–R.; Eu., As. ?U. Plioc., Pleist.–R.; N.A.

†*Cervocerus* Khomenko, 1913. [Including †*Damacerus* Khomenko, 1913.] L. Plioc.; Eu., As.

†*Cervavitus* Khomenko, 1913. L. Plioc.; Eu. ?Pleist.; ?As.

†*Procerus* Alexejev, 1914. L. Plioc.; Eu.

†*Pliocervus* Hilzheimer, 1922. L.–U. Plioc.; Eu.

†*Eucladocerus* Falconer, 1868 (=†*Polycladus* Pomel, 1854, *nec* Blanchard, 1847). M. Plioc.–Pleist.; Eu. Pleist.; As.

†*Megaloceros* Brookes, 1828 (=†*Megaceros* Owen, 1844). U. Plioc.–Pleist.; Eu.

Dama Frisch, 1775. Pleist.–R.; Eu., As. Fallow deer.

Axis H. Smith, 1827. [Including *Hyelaphus* Sundevall, 1846.] L. Plioc.–R.; As. Axis deer.

Cervus Linnaeus, 1758 (=*Elaphus* H. Smith, 1827). [Including †*Epirusa* Zdansky, 1925; *Rusa* H. Smith, 1827; *Sika* Sclater, 1870=*Pseudaxis* Gray, 1872; *Rucervus* Hodgson, 1838.] M. Plioc.–R.; As. U. Plioc.–R.; Eu.[1] Pleist.–R.; N.A.[2] Red deer, stag, wapiti (=American elk), maral, barasinga, sambar, sika, etc.

Elaphurus Milne Edwards, 1866. R.; As.[3] Mi-lu, Père David's deer.

Subfam. Odocoileinae Pocock, 1923a, p. 206.[4] [Including Capreolidae Brookes, 1828, p. 62, *fide* Palmer, 1904, p. 731; Alcinae Jerdon, 1874, p. 253; Rangiferinae Pocock, 1923a, p. 206 =Rangerinae Gray, 1852, p. 188=Rangiferinidae Brookes, 1828, p. 61, *fide* Palmer, 1904, p. 767; Hydropotinae Trouessart, 1898, p. 865.] L. Plioc.–R.; Eu., As. Pleist.–R.; N.A., S.A.

Tribe Odocoileini, new rank (=Odocoileinae Pocock, 1923a, p. 206; Mazamadae Brookes, 1828, p. 62, *fide* Palmer, 1904, p. 752). Pleist.–R.; N.A., S.A.

†*Antifer* Ameghino, 1889.[5] [Including †*Paraceros* Ameghino, 1889.] Pleist.; S.A.

†*Epieuryceros* Ameghino, 1889. Pleist.; S.A.

[1] Many older fossil deer have been referred to *Cervus*, but it is doubtful whether any before the Middle or Upper Pliocene belong to it in a strict sense.

[2] *Procoileus* Frick, 1937 (U. Plioc.; N.A.), is defined as a subgenus, but it is not clear in what genus it was intended to be placed. Frick considers it a true cervine, and this extends the American distribution of the subfamily, and perhaps of the genus *Cervus*, into the Tertiary.

[3] Surviving only in domestication.

[4] But, as frequently in the classification and not usually noted, the present subfamily is far more extensive than Gray's, or than Brookes' "family."

[5] The nomenclature of the fossil and, to less extent, the recent South American deer is bitterly disputed. My use of generic names is based on these decisions: (a) Carette may, as Castellanos and Kraglievich insist, have used poor judgment in selecting †*P. ensenadensis* as type of †*Paraceros*, but this has nothing to do with the case; he did legally select it and this is irrevocable; the subsequent selection of †*P. fragilis* by Castellanos is illegal and void; (b) Kraglievich has shown that †*P. ensenadensis* is congeneric with the type of †*Antifer*, of which †*Paraceros* is thus either a synonym or a subgenus; (c) †*Antifer* and †*Paraceros* were published simultaneously; it would create confusion and would be absurd to prefer †*Paraceros* because of page or line priority; (d) on the showing made by the several reviewers, †*Paraceros* (*nec* †*Antifer*) *fragilis*, †*Morenelaphus*, †*Pampaeocervus*, and †*Habromeryx* are closely related and may best be distributed among two or, at most, three subgenera of one genus.

The generic nomenclature of the two living deer usually called *Blastocerus campestris* (=*bezoarticus*) and *B. paludosus* (=*dichotomus*) is equally troublesome. These very distinct species probably represent different genera, certainly different subgenera. Cabrera confines *Blastocerus* to the latter and uses *Ozotoceras* for the former, on grounds that appear to me open to serious question or at least insufficiently established. The problem is too complex to discuss here, and I follow Cabrera with much misgiving. It is at least possible that *Blastocerus* should be confined to *bezoarticus*, not *dichotomus*, and that the latter should either be called *Dorcelaphus* Gloger, 1841, or be given a new name.

†*Morenelaphus* Carette, 1922. [Including †*Pampaeocervus* Carette, 1922; †*Habromeryx* Cabrera, 1929 = †"*Paraceros* Ameghino" Castellanos, 1924, *et* Kraglievich, 1932, *nec* Ameghino, 1889, *emend.* Carette, 1922.] Pleist.; S.A.

Odocoileus Rafinesque, 1832. [Including †*Palaeodocoileus* Spillmann, 1931; *Otelaphus* Fitzinger, 1874 = *Macrotis* Wagner, 1855, *nec* Dejean, 1833.] Pleist.–R.; N.A., S.A. American deer, white-tailed deer, black-tailed deer, mule deer, waiking, etc.

Mazama Rafinesque, 1817. [Including †*Protomazama* Spillmann, 1931.] Pleist.–R.; S.A. (R. into Cent. A.). Brocket, cariacu, guazubira.

Hippocamelus Leuckart, 1816. Pleist.–R.; S.A. Huemul, Andean deer.

Blastocerus Wagner, 1844. (Or perhaps should be called *Dorcelaphus* Gloger, 1841, or receive a new name.) Pleist.–R.; S.A. Swamp deer, suasupucu. (Or perhaps should apply to the pampas deer.)

Ozotoceras Ameghino, 1891 (perhaps = *Blastocerus* Wagner, 1844, which perhaps is the proper name of this genus and not of the last). Pleist.–R.; S.A. Pampas deer, guazuy, suasutinga.

Pudu Gray, 1852. [Including *Pudella* Thomas, 1913.] Pleist.–R.; S.A. Pudu.

Tribe Alcini, new rank (= Alcinae Jerdon, 1874, p. 253; Alcedae Brookes, 1828, p. 61, *fide* Palmer, 1904, p. 726). Pleist.–R.; N.A., Eu., As.

†*Cervalces* Scott, 1885. Pleist.; N.A.

Alce Frisch, 1775 (= *Alces* Gray, 1821). Pleist.–R.; N.A., Eu., As. Elk,[1] moose.

Tribe Rangiferini, new rank (= Rangiferinidae Brookes, 1828, p. 61, *fide* Palmer, 1904, p. 767). Pleist.–R.; N.A., Eu., As.

Rangifer Frisch, 1775. Pleist.–R.; N.A., Eu., As. Caribou, reindeer.

Tribe Hydropotini, new rank (= Hydropotinae Trouessart, 1898, p. 865). R.; As.

Hydropotes Swinhoe, 1870. R.; As. (Chinese) water deer.

Tribe Capreolini, new rank (= Capreolidae Brookes, 1828, p. 62, *fide* Palmer, 1904, p. 731). L. Plioc.–R.; Eu., As.

†*Procapreolus* Schlosser, 1924. L. Plioc.; Eu., As.

Capreolus Frisch, 1775. M. Plioc.–R.; Eu. Pleist.–R.; As. Roe deer, roebuck.

Cervidae *incertae sedis:*

†*Pronodens* Koerner, 1940. L. Mioc.; N.A.

Superfam. Giraffoidea Simpson, 1931a, p. 284.

†Fam. Lagomerycidae Pilgrim, 1941a, p. 176.[2] L.–U. Mioc.; Eu. M. Mioc.; Af. U. Mioc.; As.

†*Procervulus* Gaudry, 1878. L.–U. Mioc.; Eu.

†*Lagomeryx* Roger, 1904. [Including †*Heterocemas* Young, 1937.] L.–U. Mioc.; Eu. U. Mioc.; As.

[1] As is well known, the American elk is a *Cervus*, while the European elk is an *Alce*.

[2] The family was proposed by Teilhard de Chardin in 1939, but he neglected to apply any name to it.

†*Climacoceras* MacInnes, 1936. M. Mioc.; Af.

Fam. Giraffidae Gray, 1821, p. 307 (=Camelopardalidae Bonaparte, 1831, p. 24). [Including †Helladotheridae Dawkins, 1868, p. 4; †Sivatheriidae Gill, 1872, p. 9=†Sivatheriina Bonaparte, 1850.] L. Mioc.–Pleist.; As. L. Plioc.; E. Eu. Plioc.–R.; Af.

Subfam. Palaeotraginae Pilgrim, 1911, p. 29. ?L. Mioc., U. Mioc.–L. Plioc.; As. L. Plioc.; E. Eu. R.; Af.

†*Palaeotragus* Gaudry, 1861. [Including †*Achtiara* Borissiak, 1914.] U. Mioc.–L. Plioc.; E. Eu., As.

†*Giraffokeryx* Pilgrim, 1910. L. Plioc.; As.

Okapia Lankester, 1901. R.; Af. Okapi.

†*Samotherium* Forsyth Major, 1888. [Including †*Alcicephalus* Rodler and Weithofer, 1890; †*Shanshitherium* Killgus, 1922; †*Chersonotherium* Alexejev, 1916.] L. Plioc.; E. Eu., As.

?Palaeotraginae *incertae sedis:*

†*Propalaeomeryx* Lydekker, 1883. L. Plioc.; As.

†*Progiraffa* Pilgrim, 1908. L. Mioc.; As.

Subfam. Giraffinae Zittel, 1893, p. 407. L. Plioc.–Pleist.; As. Pleist.–R.; Af.

Giraffa Brisson, 1756 (=*Camelopardalis* Schreber, 1784). L. Plioc.–Pleist.; As. Pleist.–R.; Af.[1] Giraffe.

†*Bohlinia* Matthew, 1929[2] (=*Orasius* of authors, not of Oken, 1816). L. Plioc.; E. Eu.

†*Honanotherium* Bohlin, 1927. Plioc.; As.

†Subfam. Sivatheriinae Zittel, 1893, p. 409 (=†Sivatheriina Bonaparte, 1850). L. Plioc.; E. Eu. L. Plioc.–Pleist.; As. Pleist.; Af.

†*Sivatherium* Falconer and Cautley, 1835. Pleist.; As.

†*Indratherium* Pilgrim, 1910. Pleist.; As.

†*Bramatherium* Falconer, 1845. M. Plioc.; As.

†*Hydaspitherium* Lydekker, 1878. M. Plioc.; As.

†*Vishnutherium* Lydekker, 1876. M. Plioc.; As.

†*Helladotherium* Gaudry, 1860. L. Plioc.; E. Eu., W. As.

†*Griquatherium* Haughton, 1922. Pleist.; Af.

Giraffidae *incertae sedis:*

†*Libytherium* Pomel, 1893. Plioc.; N. Af.

Superfam. Bovoidea Simpson, 1931a, pp. 264, 284 (=Booidea Gill, 1872, pp. 8, 9; Cavicornia Carus, 1875, p. 148).

Fam. Antilocapridae Gray, 1866c, p. 326. [Including †Merycodontidae Matthew, 1904, pp. 102, 103.] M. Mioc.–R.; N.A.

†Subfam. Merycodontinae Matthew, 1909b, pp. 114, 115 (=†Cosorycinae Cope, 1887b, p. 396). [Including †Ramocerotinae Frick, 1937, p. 271.] M. Mioc.–M. Plioc.; N.A.

[1] The record of supposed occurrence in the Pleistocene of North America is not worthy of credence without decidedly stronger confirmation.

[2] Called †*Orasius* Wagner, 1861, in most of the literature, but Matthew has pointed out (as Palmer had much earlier, without notice being taken of the fact) that *Orasius* is of Oken, 1816, not Wagner, and that it is a strict synonym of *Giraffa*, not an extinct or distinct genus. Matthew, although calling the genus "*Orasius*" (with quotation marks) said that "one might call it *Bohlinia*" if †*Propalaeomeryx* Lydekker, 1883, proved to be different. †*Propalaeomeryx* is virtually a *nomen vanum*, and the chance that it is *Orasius* Wagner, *nec* Oken, is slight in any case. The genus needs a name, and I follow Matthew's suggestion. Colbert continues to use *Orasius* "in a provisional way"—this is my only difference from him in the classification of this family.

†*Merycodus* Leidy, 1854 (=or including †*Cosoryx* Leidy, 1869). [Including (subgenera as defined) †*Subcosoryx* Frick, 1937; †*Paracosoryx* Frick, 1937; †*Subparacosoryx* Frick, 1937.] M. Mioc.–M. Plioc.; N.A.

†*Meryceros* Frick, 1937. [Including (subgenus as defined) †*Submeryceros* Frick, 1937.] ?L. Plioc.; N.A.

†*Ramoceros* Frick, 1937. [Including (subgenera as defined) †*Paramoceros* Frick, 1937; †*Merriamoceros* Frick, 1937.] U. Mioc.–L. Plioc.; N.A.

Subfam. Antilocaprinae Brooke, 1876, p. 223. [Including †Ilingoceratinae Frick, 1937, pp. 469, 481; †Pliocerotinae Frick, 1937, pp. 469, 482; †Stockocerotinae Frick, 1937, pp. 469, 482.] L. Plioc.–R.; N.A.

†*Osbornoceros* Frick, 1937. ?M. Plioc.; N.A.

†*Ilingoceros* Merriam, 1909. M. Plioc.; N.A.

†*Proantilocapra* Barbour and Schultz, 1934. L. Plioc.; N.A.

†*Sphenophalos* Merriam, 1909 (=or including †*Plioceros* Frick, 1937). L.–U. Plioc.; N.A.

†*Texoceros* Frick, 1937. M.–U. Plioc.; N.A.

†*Capromeryx* Matthew, 1902. Pleist.; N.A.

†*Hexobelomeryx* Furlong, 1941. [Including †*Hexameryx* White, 1941.[1]] L. Plioc.; N.A.

†*Ceratomeryx* Gazin, 1935. U. Plioc.; N.A.

†*Tetrameryx* Lull, 1921. [Including (subgenera as defined) †*Hayoceros* Frick, 1937; †*Stockoceros* Frick, 1937.] Pleist.; N.A.

Antilocapra Ord, 1818 (=†*Neomeryx* Parks, 1925). Pleist.–R.; N.A. Pronghorn, prong buck, American "antelope."

Fam. Bovidae Gray, 1821, p. 308. [Including many supposed families.[2]] L. Mioc.–R.; Eu. L. Plioc.–R.; As., Af. Pleist.–R.; N.A. R.; world wide in domestication.

Subfam. Bovinae Gill, 1872, p. 8. L. Mioc.–R.; Eu. L. Plioc.–R.; As., Af. Pleist.–R.; N.A. R.; world wide in domestication.

Tribe Strepsicerotini, new rank (=Strepsicerotidae Gray, 1872a, pp. vi, 4, 46; "Tragelaphinae Blyth" Jerdon, 1874, p. 271). U. Mioc.–L. Plioc.; Eu. L. Plioc.–Pleist.; As. L. Plioc.; N. Af. Pleist.–R.; Af.[3]

†*Palaeoreas* Gaudry, 1861. U. Mioc.–L. Plioc.; Eu. L. Plioc.; As., N. Af.

†*Prostrepsiceros* Major, 1891. L. Plioc.; E. Eu., W. As.

†*Hemistrepsiceros* Pilgrim and Hopwood, 1928. L. Plioc.; E. Eu.

†*Sivoreas* Pilgrim, 1939. L. Plioc.; As.

†*Lyrocerus* Teilhard de Chardin and Trassaert, 1938. M. Plioc., ?U. Plioc.; As.

†*Sinoreas* Teilhard de Chardin and Trassaert, 1938. M. Plioc.; As.

[1] †*Hexobelomeryx* and †*Hexameryx* were described almost simultaneously from Mexico and Florida, respectively. The species are different. The genera may be, but this is not demonstrated by the published data.

[2] Virtually all the tribes listed below, and some other groups, have been granted family rank by some authors. It would serve no useful purpose to list these 15 or 20 names here. Recent students are almost unanimous in placing the whole group in one family, Bovidae.

[3] The several reported American occurrences of this group have all been proved erroneous.

Strepsiceros Frisch, 1775.[1] [Including *Tragelaphus* De Blainville, 1816; *Limnotragus* Sclater and Thomas, 1900.] ?L. Plioc.; ?E. Eu. Pleist.–R.; Af. Kudu, sitatunga, harnessed antelope, bushbuck, nyala, etc.

Taurotragus Wagner, 1855 (=*Oreas* Desmarest, 1822, *nec* Hübner, 1806). [Including *Boocercus* Thomas, 1902=*Eurycerus* Gray, 1850, *nec Eurycerus* Illiger, 1807.] Pleist.–R.; Af. Eland, bongo.

Tribe Boselaphini, new rank (=Boselaphinae Knottnerus-Meyer, 1907, pp. 38, 98, 116). L. Mioc.–L. Plioc.; Eu. L. Plioc.–R.; As.

†*Protragocerus* Depéret, 1887. L.–U. Mioc.; Eu.

†*Strogulognathus* Filhol, 1890. U. Mioc.; Eu. ?L. Mioc.; ?Af.

†*Eotragus* Pilgrim, 1939 (=†*Eocerus* Schlosser, 1911, *nec* Sharp, 1907). U. Mioc.; Eu.

†*Miotragocerus* Stromer, 1928. U. Mioc.; Eu.

†*Tragocerus* Gaudry, 1861. [Including †*Graecoryx* Pilgrim and Hopwood, 1928.] L. Plioc.; Eu. L.–M. Plioc.; As.

†*Pachyportax* Pilgrim, 1937. L.–U. Plioc.; As.

†*Selenoportax* Pilgrim, 1937. L.–M. Plioc.; As.

†*Strepsiportax* Pilgrim, 1937. L. Plioc.; As.

†*Helicoportax* Pilgrim, 1937. L. Plioc.; As.

†*Sivaceros* Pilgrim, 1937. L.–M. Plioc.; As.

†*Tragoportax* Pilgrim, 1937. M. Plioc.; As.

†*Perimia* Pilgrim, 1939. M. Plioc.; As.

†*Ruticeros* Pilgrim, 1939. M. Plioc.; As.

†*Sivaportax* Pilgrim, 1939. U. Plioc.; As.

†*Duboisia* Stremme, 1911. Pleist.; As.

†*Proboselaphus* Matsumoto, 1915. Pleist.; As.

Bosèlaphus De Blainville, 1816. Pleist.–R.; As. Nilgai.

Tetracerus Leach, 1825. Pleist.–R.; As. Four-horned antelope =doda, bekra, bhokra, etc.

Tribe Bovini, new rank (=Bovinae *sensu stricto* of most authors). M. Plioc.–R.; As. U. Plioc.–R.; Eu. Pleist.–R.; Af., N.A. R.; world wide in domestication.

†*Proamphibos* Pilgrim, 1939. M.–U. Plioc.; As.

†*Proleptobos* Pilgrim, 1939.[2] M. Plioc.; As.

†*Leptobos* Rütimeyer, 1877. U. Plioc.; Eu. Pleist.; As.

†*Hemibos* Falconer, 1865. Pleist.; As.

†*Bucapra* Rütimeyer, 1877. Pleist.; As.

Bubalus Frisch, 1775, or H. Smith, 1827.[3] Pleist.–R.; As. (True) buffalo, Asiatic buffalo.

Anoa H. Smith, 1827 (=†*Probubalus* Rütimeyer, 1865). Pleist.–R.; As. Anoa, pygmy buffalo, tamarao.

†*Platybos* Pilgrim, 1939. Pleist.; As.

Bos Linnaeus, 1758. [Including *Poëphagus* Gray, 1843.] Pleist.–

[1] This name is subject to some question, but even if Frisch's date be refused, it was correctly used by Rafinesque in 1815 and in either case antedates *Tragelaphus* and appears to be the correct name of the genus if, as I believe, *Tragelaphus* and *Limnotragus* are best considered as subgenera.

[2] A *nomen nudum* since 1913, but defined in 1939.

[3] Frisch's two names *Bubalis* and *Bubalus*, published simultaneously, refer to two very different animals, the hartebeest and the Asiatic buffalo. Their similarity has given rise to endless confusion. They can probably be discarded as not binomial, but *Bubalus*, in any case, is validated by its correct use by H. Smith.

R.; Eu., As. Pleist.; Alaska.[1] R.; world wide in domestication. Urus, yak, domestic cattle.

†*Parabos* Barbour and Schultz, 1941. Pleist.; N.A.

Bibos Hodgson, 1837. Pleist.–R.; As. Gaur, gayal, banteng.

†*Bularchus* Hopwood, 1936. Pleist.; Af.

Syncerus Hodgson, 1847. R.; Af. African or Cape buffalo.

Bison H. Smith, 1827. [Including †*Simobison* Hay and Cook, 1930; †*Superbison* Frick, 1930; †*Stelabison* Figgins, 1933; etc.] Pleist.–R.; N.A., Eu. Pleist.; As. Bison, wisent, (American) "buffalo."

Subfam. Cephalophinae Brooke, 1876, p. 224 (=Cephalophidae Gray, 1872a, pp. v, 3, 21; Cephalophoridae Gray, 1871, p. 588). Pleist.–R.; Af. Duikers (vernacular name of all three genera, the species adjectivally designated).

Tribe Cephalophini, new. Pleist.–R.; Af.

Cephalophus H. Smith, 1827. [Including *Cephalophula* C. H. Smith, 1907.] R.; Af. Yellow-backed duiker, etc.

Philantomba Blyth, 1840. Pleist.–R.; Af. Maxwell's duiker, "fulintongue," etc.

Sylvicapra Ogilby, 1837. Pleist.–R.; Af. Common duiker, duiker bok, etc.

Subfam. Hippotraginae Brooke, 1876, p. 223 (="Hippotragina Sundevall" Retzius and Loven, 1845, p. 445). L. Plioc.; Eu. L. Plioc.–Pleist.; As. R.; S.W. As. Pleist.–R.; Af.

Tribe Reduncini, new rank (=Reduncinae Lydekker and Blain, 1914, p. 197; "Adenotinae Blyth" Jerdon, 1874, p. 271; Cervicapridae Rochebrune, 1883, pp. 126, 156). ?L. Plioc., M. Plioc.–Pleist.; As. Pleist.–R.; Af.

†*Kobikeryx* Pilgrim, 1939. L. or M. Plioc.; As.

†*Cambayella* Pilgrim, 1939. M. Plioc.; As.

†*Hydaspicobus* Pilgrim, 1939. U. Plioc.; As.

†*Vishnucobus* Pilgrim, 1939. Pleist.; As.

†*Indoredunca* Pilgrim, 1939. Pleist.; As.

†*Gangicobus* Pilgrim, 1939. Pleist.; As.

†*Sivadenota* Pilgrim, 1939. Pleist.; As.

†*Sivacobus* Pilgrim, 1939. Pleist.; As.

Kobus A. Smith, 1840 (=*Cobus* Buckley, 1876). R.; Af. Waterbuck.

Adenota Gray, 1847. Pleist.–R.; Af. Kob, puku.

Onotragus Gray, 1872. R.; Af. Lechwe.

Redunca H. Smith, 1827 (=*Cervicapra* De Blainville, 1816, *nec* Sparrman, 1780). R.; Af. Reedbuck=reitbok, bohor, nagor.

Pelea Gray, 1841. R.; Af. Vaal, rhebok.

Tribe Hippotragini, new rank (=Hippotraginae *sensu stricto* of authors). L. Plioc.; Eu. L. Plioc.–Pleist.; As. R.; S.W. As. Pleist.–R.; Af.

†*Pachytragus* Schlosser, 1904. L. Plioc.; E. Eu.

†*Protoryx* Major, 1891. L. Plioc.; E. Eu., As.

†*Leptotragus* Bohlin, 1936. L. Plioc.; E. Eu.

[1] *Bos* (*Poëphagus*), a yak, recently reported by Frick.

†*Paraprotoryx* Bohlin, 1935. L. Plioc.; As.
†*Prosinotragus* Bohlin, 1935. L. Plioc.; As.
†*Sinotragus* Bohlin, 1935. L. Plioc.; As.
†*Sinoryx* Teilhard de Chardin and Trassaert, 1938. L. Plioc.; As.
†*Palaeoryx* Gaudry, 1861. L. Plioc.; E. Eu., As.
†*Pseudotragus* Schlosser, 1904. L. Plioc.; E. Eu.
†*Microtragus* Andree, 1926. L. Plioc.; E. Eu.
†*Olonbulukia* Bohlin, 1937. L. Plioc.; As.
†*Tragoreas* Schlosser, 1904. L. Plioc.; E. Eu., As.
†*Sivatragus* Pilgrim, 1939. U. Plioc.–Pleist.; As.
†*Sivoryx* Pilgrim, 1939. Pleist.; As.
Hippotragus Sundevall, 1846.[1] Plioc.; Eu., As. Pleist.–R.; Af. Bluebuck, roan antelope, sable antelope.
Oryx De Blainville, 1816. [Including *Aegoryx* Pocock, 1918.] Pleist.–R.; Af. R.; Arabia. Oryx, gemsbok, beisa.
Addax Rafinesque, 1815. R.; N. Af., S.W. As. Addax.

Tribe Alcelaphini, new rank (=Alcelaphidae Rochebrune, 1883, pp. 132, 156; Bubalinae Trouessart, 1898, p. 904).[2] L. Plioc.; E. Eu. Pleist.; As. Pleist.–R.; Af.

†*Prodamaliscus* Schlosser, 1904. L. Plioc.; E. Eu.
†*Damalops* Pilgrim, 1939. Pleist.; As.
Damaliscus Sclater and Thomas, 1894 (=*Damalis* Gray, 1846, *nec* H. Smith, 1827). Pleist.–R.; Af. Korrigum, tiang, topi, bontebok, blesbok, sassaby.
†*Parmularius* Hopwood, 1934. Pleist.; Af.
Alcelaphus De Blainville, 1816 (="*Bubalis* Frisch, 1775").[3] Pleist.–R.; Af. Hartebeest, bubal, tora.
Beatragus Heller, 1912. Pleist.–R.; Af. Hunter's antelope, herola.
Connochaetes Lichtenstein, 1814. Pleist.–R.; Af. Gnu.
Gorgon Gray, 1850. Pleist.–R.; Af. Brindled gnu.

Subfam. Antilopinae Baird, 1857, p. 664 (=Antilopidae Gray, 1821, p. 307; Gazellinae Coues, 1889, p. 2474).[4] L. Plioc.; Eu. L. Plioc.–R.; As. Pleist.–R.; Af.

Tribe Neotragini, new rank (=Neotraginae Sclater and Thomas, 1894, p. 2). Pleist.–R.; Af.

†*Palaeotragiscus* Broom, 1934. Pleist.; Af.
Oreotragus A. Smith, 1834. R.; Af. Klipspringer.
Ourebia Laurillard, 1841. R.; Af. Oribi.
Raphicerus H. Smith, 1827. R.; Af. Grysbok, steinbok.
Nesotragus Düben, 1847. Pleist.–R.; Af. Zanzibar and Livingston's "antelopes," suni.
Neotragus H. Smith, 1827. [Including *Hylarnus* Thomas, 1906.] R.; Af. Royal "antelope."[5]

[1] *Egocerus* Desmarest, 1822, *nec Aegoceros* Pallas, 1811. The Rules have been officially suspended in favor of *Hippotragus*.

[2] Based on "*Bubalis*," not *Bubalus*, Bubalidinae of many authors.

[3] "*Bubalis*" may conveniently be dropped and much confusion avoided by following Lyon's suggestion that it was not a binomial and not available in nomenclature as of Frisch, 1775, giving *Alcelaphus* priority.

[4] This group (in the stricter sense of my Antilopini) is now usually called Gazellinae, but the name Antilopinae is older and is valid.

[5] *Nesotragus* and *Neotragus* appear to have no good vernacular names. "Royal antelope" is ridiculous for these tiny creatures, the smallest living artiodactyls and not antelopes in the strictest sense.

Madoqua Ogilby, 1837. R.; Af. Dik-dik.
Rhynchotragus Neumann, 1905. R.; Af. Damara dik-dik.
Dorcatragus Noack, 1894. R.; Af. Beira.

Tribe Antilopini, new rank (=Antilopinae or Gazellinae, *sensu stricto*, of most authors). L. Plioc.; Eu. L. Plioc.–R.; As. Pleist.–R.; Af.

†*Helicotragus* Palmer, 1903 (=†*Helicoceras* Weithofer, 1888, *nec* D'Orbigny, 1842; †*Helicophora* Weithofer, 1889, *nec* Gray, 1842). L. Plioc.; E. Eu.
†*Protragelaphus* Dames, 1883. L. Plioc.; E. Eu., As.
†*Gazellospira* Pilgrim and Schaub, 1939. U. Plioc.; Eu.
†*Antilospira* Teilhard de Chardin and Young, 1932. L.–M. Plioc., ?U. Plioc.; As.
†*Spirocerus* Boule and Teilhard de Chardin, 1929. U. Plioc.–Pleist.; As.
†*Dorcadoryx* Teilhard de Chardin and Trassaert, 1938. U. Plioc.; As.
Antilope Pallas, 1766. U. Plioc.–R.; As. Blackbuck, (true)[1] antelope.
†*Dorcadoxa* Pilgrim, 1939. M. Plioc.; As.
Aepyceros Sundevall, 1847. R.; Af. Pallah, pala, impala.
Ammodorcas Thomas, 1891. R.; Af. Dibatag.
Litocranius Kohl, 1886 (=*Lithocranius* Thomas, 1891). R.; Af. Gerenuk.
Gazella De Blainville, 1816.[2] L. Plioc.; Eu. L. Plioc.–R.; As. Pleist.–R.; Af. Gazelles, mhorr, aoul, etc. (many different species with various local names).
†*Phenacotragus* Schwarz, 1937. Pleist.; Af.
Antidorcas Sundevall, 1847. L. Plioc.; Eu., As. R.; Af. Springbuck.
Procapra Hodgson, 1846. Pleist.–R.; As. Black-tailed gazelle, khara-sultei.

Subfam. Caprinae Gill, 1872, p. 9 (=Capridae Gray, 1821, p. 307; Ovinae Baird, 1857, pp. xxxi, 664; Ovicaprina Noack, 1887, p. 202; Ovicaprinae Schlosser, 1911, p. 591).[3] L. Plioc.–R.; Eu., As. Pleist.–R.; Af., N.A. R.; world wide in domestication.

Tribe Saigini, new rank (=Saigadae Gray, 1872a, pp. vi, 3, 32). Pleist.–R.; As., Eu. Pleist.; Alaska.

Pantholops Hodgson, 1834. Pleist.–R.; As. Chiru.
Saiga Gray, 1843. Pleist.–R.; As., Eu. Pleist.; Alaska. Saiga.

Tribe Rupicaprini, new rank (=Rupicapradae Brookes, 1828, p. 63, *fide* Palmer, 1904, p. 768; Rupicaprinae Trouessart, 1905, p. 734). L. Plioc.–R.; As. Pleist.–R.; Eu., N.A.

†*Pachygazella* Teilhard de Chardin and Young, 1932. L. Plioc.; As.

[1] "True" by the scientific accident that *Antilope* has become confined to this animal. There is no etymological reason or historic precedent for considering the English word "antelope" as applying exclusively, particularly (or, indeed, at all) to the blackbuck.

[2] *Gazella* was previously used by Pallas, 1769, and by Lichtenstein, 1814, in conflicting senses. By suspension of the Rules, the International Commission has authorized its use for the present genus as of De Blainville, 1816.

[3] Use of Ovicaprinae seems to be increasing recently, but it is indefensible since the name is based on both *Ovis* and *Capra*, not on a single generic name as is required.

Naemorhedus H. Smith, 1827. R.; As.[1] Goral.
Capricornis Ogilby, 1837. R.; As. Serow.
†*Neotragocerus* Matthew and Cook, 1909. Pleist.; N.A.
Oreamnos Rafinesque, 1817 (=*Aplocerus* H. Smith, 1827). Pleist.–R.; N.A. Rocky Mountain "goat."
†*Myotragus* Bate, 1909. Pleist.; Mediterranean.
Rupicapra Frisch, 1775 (or De Blainville, 1816). Pleist.–R.; Eu. R.; S.W. As. Chamois.

Tribe Ovibovini, new rank (=Ovibovinae Gill, 1872, p. 72). L. Plioc., Pleist.–R.; Eu., As. Pleist.–R.; N.A.
†*Criotherium* Major, 1891. L. Plioc.; E. Eu., W. As.
†*Urmiatherium* Rodler, 1888. L. Plioc.; As.
†*Tsaidamotherium* Bohlin, 1935. L. Plioc.; As.
†*Parurmiatherium* Sickenberg, 1935. L. Plioc.; As.
†*Plesiaddax* Schlosser, 1903. L. Plioc.; As.
†*Boopsis* Teilhard de Chardin, 1936. Pleist.; As.
Budorcas Hodgson, 1850. Pleist.–R.; As. Takin.
†*Bootherium* Leidy, 1852. Pleist.; N.A.
†*Symbos* Osgood, 1905. Pleist.; N.A.
†*Euceratherium* Furlong and Sinclair, 1904. [Including †*Preptoceras* Furlong, 1905; †*Aftonius* Hay, 1913.] Pleist.; N.A.
Ovibos De Blainville, 1816. Pleist.–R.; Eu., As., N.A. Musk ox.

Tribe Caprini, new rank (=Caprinae *sensu stricto* of authors). L. Plioc., R.; Eu. L. Plioc.–R.; As. Pleist.–R.; Af., N.A. R.; world wide in domestication.
†*Oioceros* Gaillard, 1902. L. Plioc.; Eu., As.
†*Tossunnoria* Bohlin, 1937. L. Plioc.; As.
†*Sivacapra* Pilgrim, 1939. Pleist.; As.
Hemitragus Hodgson, 1841. R.; As. Tahr.
Capra Linnaeus, 1758. [Including *Aegoceros* Pallas, 1811; *Orthaegoceros* Trouessart, 1905; etc.] Pleist.–R.; As. R.; Eu., N. Af., and world wide in domestication. Markhor, ibex, goat, tur, etc.
Pseudois Hodgson, 1846. R.; As. Nahur, burrhel.
†*Pultiphagonides* Hopwood, 1934. Pleist.; Af.
†*Pelorovis* Reck, 1928. Pleist.; Af.
Ammotragus Blyth, 1840. Pleist.–R.; Af. Audad, arui, "maned sheep."
Ovis Linnaeus, 1758. U. Plioc.–R.; As. Pleist.–R.; N.A. R.; S. Eu., N. Af., and world wide in domestication. Moufflon, argali, mountain sheep, sheep, etc.

Bovidae (?) *incertae sedis:*
†*Propalaeoryx* Stromer, 1926. L. Mioc.; Af.
†*Thaleroceros* Reck, 1935. Pleist.; Af.
†*Qurliqnoria* Bohlin, 1937. L. Plioc.; As.
†*Vishnumeryx* Pilgrim, 1939. Pleist.; As.
†*Procobus* Khomenko, 1913. L. Plioc.; E. Eu.

[1] A North American record appears to be incorrect.

PART 3. REVIEW OF MAMMALIAN CLASSIFICATION

INTRODUCTION

THE FOLLOWING PAGES may be viewed either as an elaborate footnote to the formal classification, explaining how that classification was reached, or as a separate contribution reviewing the broader features of mammalian history and affinities. For each order and many lesser groups, there is given a brief outline of the history and present status of knowledge and the major steps by which the modern sort of classification was reached. The probable affinities and phylogeny of the various important lines of evolution are discussed, as are the relationships between these theories and the particular classification here based on them. Some of the more important dissenting theories, deviant classifications, and disputed points are mentioned, and attention is also drawn to some of the many gaps in present knowledge, especially those presenting research problems that could most profitably be attacked in the near future. Some of the broader or more complicated questions regarding nomenclature are discussed, although lesser details, for instance, the selection of particular generic names, are either implicit in the formal classification or mentioned in footnotes to it.

It is obviously impossible to document every decision involved in so complex a synthesis, but authority is cited for the most important or most disputed points. Each section ends with a few citations (referring to the bibliography) which cannot, in any case, be exhaustive or anything like it but which are intended to assist the first steps in finding the special literature of the group in question. Sound and relatively modern general reviews of the group are cited, if any are available, and in most cases also a few recent papers that have modified knowledge of the group but the data of which have not yet been incorporated in the more general studies.

MAMMALIA

RECOGNITION OF THE CLASS AND ITS BASIC SUBDIVISION

The recognition of the viviparous quadrupeds as constituting a natural group, in some sense, is extremely ancient and doubtless existed vaguely in the mind of prehistoric man. Certainly it was evident to the more learned ancients, but it cannot fairly be claimed that even Aristotle had an idea of this class much more sophisticated than this obvious delimitation. The scholars of the Middle Ages made real but slow progress in taxonomy and had the idea of making a hierarchic system, so vaguely adumbrated by classical authors that they can hardly be credited with it. A good landmark for the scientific discovery of the Class Mammalia, as opposed to its intuitive perception, is the reference to this group of the bats, rather than placing them with birds, and, especially, of the whales, rather than placing them with fishes. This was earlier foreshadowed, as such discoveries commonly are, but it can best be dated from John Ray's great work of 1693, a remarkable production that was in some respects as progressive as any of the taxonomy of the following century. Ray had a division of animals with blood, breathing by lungs, with two ventricles in the heart, and viviparous, which is a thoroughly scientific and exact definition of mammals, including bats and whales and excluding all other quadrupeds and all other viviparous animals.[1] This is a far better definition than that of Linnaeus in earlier editions of his "Systema naturae," where he defined the mammals (not under that name) as animals with hairy bodies, four feet, with viviparous and milk-giving females (sixth edition), a definition that is exclusive (includes no non-mammals) but not inclusive (excludes many mammals). Finally in his tenth edition, Linnaeus returned to the concept and essentially to the definition of Ray and coined the word "Mammalia." Thus in 1758, the date now taken as the zero point of zoologic nomenclature, the name and contents of this class were established just as we have them now except, of course, for the forms discovered since then.

Ray subdivided the mammals into aquatic or cetacean and terrestrial or quadruped, in-

[1] Of course it is no detraction that oviparous mammals do exist, since these were undiscovered in Ray's day.

cluding the sea cows with the latter. Linnaeus initiated a more complex superordinal arrangement in his twelfth edition (1766) by dividing mammals into Unguiculata, Ungulata, and Mutica, the latter group with the one order Cete (=Cetacea). The same or closely analogous groupings run through many subsequent classifications down to our own day (within the Placentalia). Lacépède (1799) is an instructive example, with the following superordinal divisions (here translated from the French vernacular):

- Mammals
  - True quadrupeds
    - Four-handed animals (primates)
    - "Pedimanes" (marsupials and the aye-aye)
    - Plantigrades (plantigrade carnivores and insectivores)
    - Digitigrades (other carnivores, rodents, edentates, and monotremes)
    - Pachyderms (elephant, rhinoceros, and non-ruminant artiodactyls)
    - Two-hoofed mammals ("bisulcates") or ruminants (ruminants)
    - One-hoofed mammals ("solipedes") (horse)
  - Winged mammals (Bats and colugos)
  - Marine mammals (Seals, walrus, sea-cows, and cetaceans)

These early workers were unaware of the great gulf between the reproductive and other systems of the monotremes (discovered about 1790), the marsupials (opossums discovered in the sixteenth century and the Australasian forms about 1760), and the placentals (the only mammals really well-known until the nineteenth century), and thus the basis for primary subdivision of the Mammalia was unlike that now universally accepted. It was De Blainville (in 1816) who first made subclasses on this basis, the monodelphs, our Placentalia, and the didelphs, our Marsupialia and Monotremata. Later (1834) De Blainville made three subclasses, restricting the designation "didelphs" to the marsupials and calling the monotremes "ornithodelphs" (i.e., "Les ornithodelphes" in French vernacular).

The propriety of these divisions has not since been seriously questioned, but their relative ranks have. Thus Gill, in his epochal work of 1872, made a division, Prototheria, for the Ornithodelphia, and another, Eutheria, for the Placentalia or Monodelphia and the Didelphia, a dual primary subdivision like that of De Blainville in 1816 but with the marsupials associated with the placentals rather than with the monotremes. Huxley later (1880) supplemented this terminology by adding "Hypotheria" and "Metatheria." Many subsequent students have overlooked the fact that Huxley's words in "-theria" were not really taxonomic names but merely theoretical terms designating stages of evolution. Thus "Hypotheria" designated an unknown, hypothetical, first stage of mammalian evolution, and the later stages were designated successively "Prototheria," "Metatheria," and "Eutheria." According to Huxley the primates of today, for example, are eutherian but were derived from metatherian primates (not from marsupials), these in turn from prototherian primates (not from monotremes), and these, finally, from hypotherian primates. The marsupials happen to be still metatherian, but there is no monophyletic subclass Metatheria, and the monotremes are prototherian, but there is no monophyletic subclass Prototheria.

Despite Huxley's decidedly different usage, his terms were confused with Gill's, and the names Eutheria, Metatheria, and Prototheria are now almost invariably used for taxonomic, phyletic divisions to include the Placentalia (not also Marsupialia as in Gill's original usage), Marsupialia, and Monotremata, respectively. Although these terms have poor authority in the light of original definitions, they are so widely accepted and so generally understood in these senses that it would be puristic to reject them or to attempt to maintain their forgotten original significations. They are used in the present classification in the way usual in other recent work.

Later research on living and fossil mammals seems to me to support Gill's view that the marsupials are more closely related to the placentals than to the monotremes. If this is true, the Prototheria, comprising the mono-

tremes, are, indeed, a quite separate major division of the Mammalia, while the Metatheria and Eutheria of recent work (i.e., the Eutheria of Gill) form another. Since revival of Eutheria in this sense rather than for the placentals alone would give rise to endless confusion (besides demanding another similar name for the Eutheria in the stricter sense), another name is necessary for this group, and Theria is available, appropriate, and clear.

It has been commonly supposed that the Eutheria were derived from the Metatheria not in Huxley's sense, explained above, but in a true phyletic sense, that is, that the placentals were derived from marsupials naturally allied to those now living. This view has become untenable in the light of recent research and is being abandoned.

It is true that the marsupials retain certain primitive characters lost in most or all placentals, and they are also, as a group, less progressive, potent, or varied than the placentals and have never achieved the extremes of divergence and of specialization seen in the latter. It is, however, also true that the less progressive placentals retain other primitive characters lost in marsupials and that the characters by which the marsupials are recognized and defined, those that make them marsupials from a taxonomic point of view, are in greater part specializations within that group and not characters that occurred in the common marsupial-placental ancestry and were later lost in placentals.

Although they are too poorly known for certainty, there is good evidence that some of the very primitive and ancient Jurassic mammals, the †Pantotheria, are an offshoot of, and nearly represent, the common placental-marsupial ancestry before it had split up into the Metatheria and Eutheria properly definable as such (Simpson, 1928a, 1929a). If this is true, these mammals were also Theria but were not Metatheria or Eutheria.

These are the conceptions formalized by recognizing a Subclass Theria with three secondary divisions, †Pantotheria, Metatheria, and Eutheria.

There is one great division of fossil mammals that will not enter into either the Prototheria or the Eutheria, although these animals, the †multituberculates, have been referred to both on evidence now unacceptable. Everything now points to their having been distinct from all other mammals since the very beginnings of the Mammalia, and if this is true they can hardly be classified except as another subclass, a conclusion that I have supported and documented in detail elsewhere (see references under †Multituberculata). The name †Allotheria is available for this subclass.

The underlying considerations and concrete evidence have been presented here only in the barest possible outline, but they seem to support the following as the most convenient and most natural primary arrangement of the mammals:

Class Mammalia
- Subclass Prototheria (monotremes)
- †Subclass Allotheria (†multituberculates)
- Subclass Theria
  - †Infraclass Pantotheria (†pantotheres and †symmetrodonts)
  - Infraclass Metatheria (marsupials)
  - Infraclass Eutheria (placentals, many orders)

As far as present knowledge shows, the three subclasses have been separate since the beginning of the Class Mammalia, and there is no clear evidence of special relationship between any two of these subclasses exclusive of the third. The †pantotherian differentiation of the Theria occurred very early, in the Jurassic. The subsequent bifurcation of this general stock into Metatheria and Eutheria was less ancient, but also very early with respect to the more familiar Tertiary mammals. It was definitely established well before the end of the Cretaceous.

Literature on Mammals

Some of the books and papers of importance for particular groups of mammals are cited in the following discussions of orders and lesser groups. Here some mention will be made of books that cover all or a considerable variety of mammals. Citation of these will not be constantly repeated in dealing with the separate groups of mammals, and it will be taken as understood that in each case the student should refer first to such of these general works as are of appropriate scope to include the group in question.

HISTORY: Gregory, 1910, has given an invaluable summary of the development of the classification of mammals from Aristotle to Weber. This book should be closely studied by every taxonomist. It has been constantly used in preparing the brief historical comments included in the following pages, and I am greatly indebted to it, although most of the early publications that it discusses have also been directly consulted. The following very summary list includes works that have particularly influenced the development of the modern systems of mammalian classification as a whole. Reading them in sequence gives a fairly adequate conception of the history of this part of taxonomy. These works are, of course, "out of date" now, but it must be emphasized that they are not simply quaint relics for the delectation of bibliophiles. Many of them have enduring value and can be read with real profit and instruction by mammalogists today. Linnaeus, 1758; Brisson, 1762; Blumenbach, 1779; Vicq d'Azyr, 1792; Cuvier, 1798; Lacépède, 1799; Cuvier, 1800; Illiger, 1811; De Blainville, 1816; Gray, 1825; Bonaparte, 1831; De Blainville, 1834; Bonaparte, 1838; Giebel, 1855; Milne Edwards, 1868–1874; Owen, 1868; Huxley, 1869; Gill, 1872; Huxley, 1880; Flower, 1883; Cope, 1889c; Flower and Lydekker, 1891; Haeckel, 1895; Weber, 1904.

MODERN WORKS ON MAMMALS IN GENERAL: Although now entirely inadequate for fossil mammals and outmoded in details of classification, Flower and Lydekker, 1891, and Beddard, 1902, remain probably the best semi-popular discussions in English of living mammals. A briefer but sound and up-to-date discussion of similar character is included in Parker, Haswell, and Forster Cooper, 1940. More popular discussions, like that included in Hegner, 1935, are less useful to the student serious enough to use the present classification. The four volumes of the "big Brehm," Brehm, Heck, and Hilzheimer, 1912–1916, are perhaps the best single source of information on habits, pictures of living animals, etc. Among more strictly technical works, Weber, 1927–1928, stands supreme and is indispensable for any serious mammalogist, despite the fact that the style is occasionally difficult for non-German-speaking students and that the treatment of fossils is somewhat erratic. An excellent little book in Spanish, which has been undeservedly neglected, is Cabrera, 1922. Winge, 1923–1924, has had the odd fate of becoming rather a famous work, although only a handful of students outside Denmark have ever read it. It is an eccentric production and much of it dates from about 30 years before the book's publication, but it is provocative and stimulating and it has had considerable indirect influence on mammalian taxonomy. An English translation has recently been completed, but only the first part has been printed and this is not yet generally available. Besides the historical summary, Gregory, 1910, gives an excellent discussion of mammalian ordinal relationships.

Romer, 1933, has a short, competent résumé of fossil mammals, and these are treated in greater detail, but with antiquated taxonomy, in Schlosser, 1923. There is a revised English translation of an earlier edition of this work, Zittel, Eastman, and Woodward, 1932. Osborn, 1910, gave a classification of mammals, recent and fossil, that was the best that had then ever appeared and is still usable, and this book also includes an account of mammalian evolution and migration in the Northern Hemisphere. Matthew, 1928, summarizes much of mammalian phylogeny. Although confined to the Western Hemisphere, Scott, 1937a, is one of the best and most interesting treatments of fossil mammals ever written.

REGIONAL FAUNAS: There are innumerable check lists and descriptions of the living mammals of particular regions, and only a few of those of broadest scope can be cited here. For North America the standard check list is Miller, 1924, and the best systematic discussion and illustration is Anthony, 1928. Good popular treatments are, for instance, those of Anthony, 1917b, and Seton, 1925–1928 (game animals, but the term is interpreted as broadly as possible). A fine summary of the very extensive ecological, physiological, and economic literature, not otherwise mentioned in the present taxonomic paper, is given by Hamilton, 1939.

For South American living mammals there is now the handsome, competent, and inclusive volume by Cabrera and Yepes, 1940.

The standard treatment of European mammals (outside Russia) is the technical catalogue by Miller, 1912. No subsequent general revision, as distinct from local lists and popular discussions, seems to be available.

There are excellent works in Russian on the mammals of European Russia and of northern and central Asia, but it would serve no useful purpose to cite these here; Russian students know them, and others cannot read them. I do not know of any work on the mammals of Asia as a whole. Allen, 1938, 1940, fully covers the Chinese and Mongolian faunas, and all the mammals of India, Ceylon, and Burma are included in Blanford, 1888, 1891, Osman Hill, 1939, and Pocock, 1939, 1941.

Allen, 1939a, has provided a check list of African mammals. There seems to be no descriptive work on the mammals of the whole continent, but it is well covered by more local treatments, for instance, Monard, 1935, and Hill and Carter, 1941, for Angola; Bigourdan and Prunier, 1937, for West Africa; Shortridge, 1934, for South West Africa; etc.

The basic check list for Australia is that of Iredale and Troughton, 1934. There have been many summaries and descriptions of all or parts of the peculiar Australian mammalian fauna. Gould's great classic, 1863, can never lose its value, and among successive contributions (of varying quality) may be mentioned Ogilby, 1892; Lydekker, 1894a; Lucas and Le Souef, 1909; Wood Jones, 1923–1926; Le Souef, Burrell, and Troughton, 1926.

Faunal lists, emendations and additions, and references to other current literature appear regularly in the pages of the special mammalogical journals, among which the Journal of Mammalogy is outstanding.

Revisions of the fossil faunas of particular ages and regions are also numerous, for instance, Matthew, 1937, on the Paleocene of New Mexico, Stehlin, 1903–1906, on the Eocene of Europe, Scott, Jepsen, and Wood, 1936–1941, on the Oligocene of South Dakota, and Colbert, 1935c, on the later Tertiary and Pleistocene of northern India. Other such revisions are cited in connection with the orders for which they are particularly important.

BIBLIOGRAPHIES, CATALOGUES, AND NOMENCLATORS: Trouessart, 1897–1905, produced a nearly complete catalogue of all mammals, living and fossil, known at that time. Since then the number of known forms has increased so enormously that no one has attempted, and it is unlikely that anyone will again attempt, to compile so all-embracing a catalogue. A nomenclator of all animal genera and species down to 1850 has been completed, Sherborn, 1902–1933. For genera and subgenera, a nomenclator is now available for all names published through 1935, Neave, 1939–1940, which supersedes various earlier works of the same kind.[1] Current nomenclature is listed and indexed (yearly and in periodic cumulative indexes) in the "Zoological record," the long sequence of which also provides an absolutely indispensable systematic bibliography of all important literature on mammals. Biological Abstracts gives excellent summaries of much of the current literature.

North American fossil vertebrates known before about 1900 were catalogued, and the literature on them was listed, by Hay, 1902, and this was brought down to about 1928 in a later compilation, Hay, 1929–1930. There has been no such bibliography and catalogue for fossil mammals outside North America since Trouessart, but one covering the period 1928–1933, by Camp and VanderHoof, 1940, and one covering the period 1934–1938, by Camp, Taylor, and Welles, 1942, have been published, and it is planned to continue it indefinitely under Camp. This work includes all the fossil vertebrates of the world. A similar work for those outside North America prior to 1928, complementing Hay, is now being compiled under the direction of A. S. Romer. These various projects will provide a complete bibliography and index of all known fossil mammals.

Finally Palmer's "Index," 1904, has long been the inseparable companion of mammalian taxonomists. It lists all proposed genera of mammals, fossil and recent, with references to places of publication, designa-

[1] And also the similar German nomenclator by Schulze, Kükenthal, Heider, and Kuhlgatz (usually cited as Heider), 1926–1935, which is, as far as I know, incomplete, having taken the alphabetic sequence only through P.

tions of type species and localities, derivations of names, and other information. A new edition or supplement to this wonderful work, bringing it down to date, is in press at the United States National Museum, but had not yet appeared when the present classification went to press.

MONOTREMATA

The classification of the monotremes is that now almost universal and requires little special comment. Their combination of extreme specialization in habitus characters with the retention of some very primitive and even reptilian heritage characters makes the monotremes entirely isolated among recent mammals. The known fossils are of Pleistocene age and do not differ essentially from the recent forms. Reports of older fossil monotremes outside of Australia have all proved to be incorrect. There now appear to be only two reasonable theories of monotreme relationships: that they have evolved independently and in isolation from a very early period of mammalian history, perhaps even from the reptilian ancestry, and that they were derived from very early marsupials and owe their peculiar nature to divergent specialization, retention of ancient marsupial characters, some degeneration, and perhaps also reversion. There is much to be said for the latter view, but the former seems more probable, is more commonly held, and is reflected in this and in almost all other classifications of mammals.

The ordinal name Monotremata is preferred to the prior Ornithodelphia because it is in much more common use, both in this form and as the vernacular "monotremes," and also because the terms Didelphia and Monodelphia, coordinate with Ornithodelphia, have also fallen into disuse.

The literature on the monotremes is enormous, and few mammals have been so carefully investigated. Most of these studies, however, have little bearing on the relationships of the monotremes beyond the now rather obvious facts that they are mammals, are a natural unit, and are greatly different from all other mammals. Discussions of mooted relationships to the †Multituberculata and to †*Desmostylus* are cited elsewhere. Watson, 1915, and Simpson, 1929c, discuss two of the most important lines of evidence on monotreme affinities, skull and teeth. Many of the works cited under Marsupialia also include the Monotremata.

†MULTITUBERCULATA

The †multituberculates are among the oldest known mammals and also cover a larger span than is known for any other order. This great span is, however, one in which mammalian fossils are scanty and this great order is not well known. The skeleton as a whole is not known in any †multituberculate, although a few limb elements of two or three genera have been identified. Considerable parts of the skull are known only in †*Djadochtatherium*, †*Taeniolabis*, †*Ptilodus*, and one other genus (material undescribed when this was written).

The †multituberculates were long considered ancestral monotremes or marsupials, but reweighing of the evidence strongly opposes either view. The †multituberculate structure was so radically distinctive throughout their history that it seems hardly possible that they are related to other mammals except by a common origin at, or even before, the appearance of the class as such, a conclusion that necessitates placing them in a separate subclass as well as order.

The †Multituberculata were formerly divided into two subclasses, the †Tritylodontoidea, best known by †*Tritylodon* and †*Bienotherium*, and the †Plagiaulacoidea, including all the †multituberculates of the present classification. After this manuscript was complete, the paper inserted in the bibliography as Watson, 1942, was received. In this study Watson reviews †*Bienotherium* on the basis of Young's preliminary paper (Young, 1940) and concludes that it and, therefore, also the manifestly closely related †*Tritylodon* are reptiles. The question is not so basic as it may seem, because at this point there is an almost perfect transition from reptiles to mammals, and whether †*Bienotherium* should be considered the most mammalian known among reptiles or the most reptilian known among mammals is to some extent arbitrary.

The possibilities stressed by Watson give further emphasis to two conclusions previ-

ously reached (e.g., Simpson, 1928a) and as yet somewhat imperfectly represented in the classification: first, that the †Tritylodontoidea and †Plagiaulacoidea may really have very little or virtually nothing to do with each other, and, second, that the †Multituberculata of earlier taxonomy probably represent one or more lines derived from the Reptilia independently of other known mammals, but nevertheless derived from the same limited reptilian stock. Although definite confirmation of Watson's views is still lacking, the omission of the †Tritylodontoidea from the Mammalia is tentatively accepted.

In this order convenience and common sense have dictated rejection of priority in some family names. The †Plagiaulacidae and †Ptilodontidae are based on lower jaws, primarily, and both families were early given other names based on upper jaws of the same or closely allied forms, †Bolodontidae and †Chirogidae, respectively, before this relationship was discovered. The name †Ptilodontidae is antedated by numerous family names based on genera now placed in the same family, but in every case the genera used as types for the older names are either invalid or of very doubtful structure and relationships.

Virtually everything that is known about these ancient and strange mammals is summarized in the following studies: Granger and Simpson, 1929; Jepsen, 1940; Simpson, 1928a, 1929a, 1935c, 1937a, c; Young, 1940.

†MICROCLEPTIDAE

This family, known only from a few, tiny, isolated teeth found in England and Germany, has usually been referred to the †Multituberculata. There is not the slightest valid evidence for such allocation, which is merely a guess rather opposed than favored by the probabilities. The †microcleptids may have been mammals, since their teeth do have divided roots, but in reality their closer affinities are wholly unknown and are beyond reasonable conjecture at present. In fact the only definite resemblance that their teeth show is to certain specialized living bats, and it is completely incredible that this is an indication of relationship. Most of the known specimens are described in Simpson, 1928a, e.

†TRICONODONTA

Knowledge of these small Jurassic mammals (with one dubious Triassic possible ally) is almost confined to teeth and jaws. Something is known of the skull and brain, but these show only that †triconodonts are exceedingly primitive mammals, as would be expected, and do not show special affinities. Some resemblances have been noted to the †Multituberculata on one hand and the †Symmetrodonta, on the other, but these resemblances are very superficial, differences are radical, and supposed intermediate types do not, in fact, occur. The †triconodonts have a dental pattern that was already clearly developed among mammal-like reptiles, and at present I suspect that they are simply an offshoot of such reptiles, acquiring mammalian diagnostic features by parallel evolution and not really related to other mammals except through the pre-mammalian ancestry. If this is true, they should perhaps be placed as a separate subclass of mammals, but they are much too poorly known and too unimportant for mammalian history as a whole to warrant taking such a step at present.

The known †triconodonts are all described, and the previous literature is cited in Simpson, 1928a, 1929a. The one important later discovery is that of a possible †triconodont, †*Eozostrodon*, in the Triassic, Parrington, 1941.

†PANTOTHERIA

These are the only Jurassic mammals that show real and unmistakable signs of affinity with the later marsupials and placentals. They were formerly believed to be marsupials, but this was an *a priori* judgment based on the ill-founded belief that marsupials must of necessity have preceded placentals. In fact †pantothere morphology does not warrant considering †pantotheres either marsupial or placental, and it is more likely that they are a group of more or less aberrant offshoots of the common ancestry of both marsupials and placentals before the latter groups arose or were definable as such. Mammals are almost completely unknown in the early and middle Cretaceous, and this enormous gap prevents any actual tracing of †pantotheres into later groups. Despite a general resemblance, the dental differences in

detail are great, and various attempts to homologize molar cusps or to specify closer affinities are so contradictory and hypothetical as to provide no worth while data for taxonomy.

†*Amphitherium* may be an almost completely generalized structural ancestor for all the Theria, but its upper teeth are unknown and these are most distinctive and difficult to homologize among other †pantotheres. †Paurodonts and †dryolestids represent two varied, slightly divergent groups. The †docodonts are more distinctive, to the point that some students think their dental patterns are not at all homologous with those of other †pantotheres and that they should be placed elsewhere. This is possible, but I believe that they are simply specialized †pantotheres and could have arisen from forms fairly similar to the †dryolestids.

The use of the same word, †Pantotheria, both for an infraclass and for an order is unfortunate, and such homonyms are avoided elsewhere in this classification, but in this case no other course seems acceptable at present. Marsh defined †Pantotheria as an order, and for this and other reasons (detailed in Simpson, 1928a) its use for this order is almost demanded. It is, however, proper in form and meaning for the larger group, here defined as an infraclass, containing that order. No other name for the infraclass could be so appropriate, and it would be unfortunate to propose a wholly new and necessarily less appropriate name for what is, after all, a strictly provisional and quite possibly temporary arrangement.

The only new †pantothere described since my memoirs reviewing them all, Simpson, 1928a, 1929a, is †*Araeodon*, see Simpson, 1937b.

†SYMMETRODONTA

These mammals were formerly confused with †triconodonts, on one hand, and †pantotheres, *sensu stricto*, on the other. As now known, they are certainly sharply distinguished from either in the morphology of jaws and teeth. They are very inadequately known. Their association with true †pantotheres in an infraclass †Pantotheria is rather hypothetical, but there is some evidence for it, and the arrangement is convenient in the absence of better indications. The known forms are all described in Simpson, 1928a, 1929a.

MARSUPIALIA

Linnaeus placed his one marsupial genus *Didelphis* in the extraordinarily heterogeneous Order Bestiae. Inevitably misled by the convergence of marsupials to different placentals, the eighteenth century naturalists did not recognize the unity of the Marsupialia, but that was noted by De Blainville who in 1816 united them as "didelphes normaux." There has since been no doubt as to the validity of the order or as to its contents among recent forms. The Australian fossils, of late date and manifestly allied to living groups, have given rise to no special taxonomic problems. The Mesozoic †triconodonts, †symmetrodonts, †pantotheres, and †multituberculates have been considered marsupials at various times, but it now seems to be generally agreed that they should be placed in distinct orders, at least. Curiously enough, the Mesozoic forms that really are marsupials, late Cretaceous didelphids, were long excluded from the Marsupialia. Better specimens and more detailed study leave no doubt that they are correctly placed here. The South American marsupial carnivores, †borhyaenids, were not generally accepted as truly marsupial until Sinclair's work on them (1901), but their ordinal affinities are now so completely established that no alternative need be discussed. Various fossils incorrectly supposed to be marsupials have been described from North America, Africa, etc., but these, too, require no discussion now as their placental affinities are well established at present.

There are, indeed, only two important genera of possible but dubious marsupial affinities. †*Necrolestes* from the Miocene of South America is generally believed to be an insectivore, and is so classified in the present arrangement, but may be marsupial. †*Argyrolagus* from the Pliocene of South America is an extraordinary, rather rodent-like animal so unlike all others known, and itself so imperfectly known, that its affinities are almost beyond conjecture. Conjectures have nevertheless been made, and Kraglievich and Rusconi both think it a "diprotodont" mar-

supial, which is conceivable but is not to be taken as fact or even as established theory.

Although the boundaries of the order are thus well established, the same cannot be said for its subdivision. As is generally recognized and as I have sufficiently pointed out elsewhere (e.g., Simpson, 1930), there are six marsupial groups, each of which is, beyond serious doubt, a natural unit. The groups are here called Didelphoidea, †Borhyaenoidea, Dasyuroidea, Perameloidea, Caenolestoidea, and Phalangeroidea. Many attempts have been made to unite these basic groups, under these or other names, into higher categories of about subordinal rank. The best known and most frequently adopted system is division into Polyprotodontia and Diprotodontia, following the characters of the incisor teeth, see, e.g., Gregory, 1910. An old alternative is to classify them according to whether the second and third toes of the hind foot are or are not united, giving such suborders as Didactyla and Syndactyla, see, e.g., Wood Jones, 1923–1925. The arrangements are as follows:

Incisors	
Polyprotodontia	Didelphoidea
	†Borhyaenoidea
	Dasyuroidea
	Perameloidea
Diprotodontia	Caenolestoidea
	Phalangeroidea

Toes	
Didactyla	Didelphoidea
	†Borhyaenoidea
	Dasyuroidea
	Caenolestoidea
Syndactyla	Perameloidea
	Phalangeroidea

As might be expected of classifications based essentially on single characters, these are contradictory and unsatisfactory. The Caenolestoidea and Perameloidea are anomalous in any arrangement of this kind, and if they are, in turn, elevated to separate subordinal rank the advantage of simplicity, the primary aim of this attempt to define suborders, is lost. Structurally it would be justifiable to combine the Didelphoidea, †Borhyaenoidea, and Dasyuroidea into one higher group, as these are nearly intergrading morphological complexes. The other three basic groups do not even remotely intergrade, and there really is no proper basis for uniting any two of them on the subordinal level.

The recorded history of marsupials is very defective because of the almost complete ignorance of Tertiary Australian forms. Nevertheless the rather good American documentation and comparative anatomical studies strongly suggest (a) that the Didelphoidea are the primitive marsupial stock, with several persisting lines, (b) that the five other groups arose from the earliest didelphoids, (c) that if any two of them had a common post-didelphoid ancestry this is now so remote and was so short-lived that all five appear to have arisen independently, and (d) that all five arose at about the same early time, probably late Cretaceous or earliest Tertiary at latest, and have since been entirely separate phylogenetically.

If this reconstruction of the phylogeny is correct, the best systematic expression of it is, I think, to retain the six coordinate groups, which I call superfamilies, and not to unite them further into suborders. This at least is more conservative than following any one disputed and ill-supported hypothesis.

Sinclair, 1901, and numerous others have claimed that the South American predaceous marsupials, †Borhyaenidae, belong in the otherwise Australian family Dasyuridae or Thylacinidae. Broader knowledge of the South American fossils, especially the earlier forms, has tended to oppose this idea which is being greatly modified or abandoned by those competent to judge. Wood, for instance, was formerly one of the strongest adherents to the union of the two geographic groups (Wood, 1924) but now opposes this view (pers. com.). I have recently reviewed the evidence and presented the case for making †Borhyaenoidea coordinate with Dasyuroidea (Simpson, 1941a).

A similar but admittedly more distant union of the Caenolestoidea with the Perameloidea, Phalangeroidea, or both has been claimed, see Osgood, 1921. This view, however, does not fully meet or explain earlier evidence, as in Dederer, 1909, Gregory, 1910, for "polyprotodont" affinities of the caenolestoids, and it leans rather heavily on supposed evidence now known to be decidedly incorrect, for instance, the supposed perame-

loid affinities of †*Myrmecoboides*, which turns out to be a placental with no bearing whatever on this problem. The whole question needs review in the light of increased knowledge of both fossil and living forms, but it seems fair to say that previous available evidence, frankly inconclusive, is at least as consistent with independent derivation of caenolestoids from didelphoids as with their special alliance with any Australian group.

In older classifications the †Polydolopidae were usually placed in the †Multituberculata, but in 1928c I argued that they were a specialized offshoot of the caenolestids, and later discoveries and studies, partly unpublished, have placed this beyond any possible doubt.

Most of the literature on fossil marsupials and much of that on the recent forms is listed in Simpson, 1930. The present arrangement of the order is nearly the same as in that publication, with a few later discoveries inserted, e.g., †*Thylacosmilus*. I no longer recognize Cabrera's subfamilies of †Borhyaenidae because closer study of the materials convinces me that they were based on somewhat erratic structural stages independent in numerous different lines and do not correspond with phylogenetic reality or practical convenience. Broom's subfamily †Burramyinae is now tentatively recognized. †Diprotodontidae is now preferred to †Nototheriidae because it is the older name, is equally familiar, and has as good a type.

Some important references on the classification of marsupials, or various questionable details of this, are Anderson, 1933; Bensley, 1903; Cabrera, 1919; Wood Jones, 1923–1925; Riggs, 1934; Simpson, 1939. Also the following, already cited in the previous discussion: Dederer, 1909; Gregory, 1910; Osgood, 1921; Simpson, 1928c, 1930, 1941a; Sinclair, 1901; Wood, 1924.

EUTHERIA

Cohort Groupings

Linnaeus (in his twelfth edition, 1766) divided the Mammalia into Unguiculata, Ungulata, and Mutica, which were essentially subdivisions of the placentals or Eutheria since the marsupials were then virtually, and the monotremes completely, unknown. Similar divisions, which may well be called cohorts (cf. "cohors" in Storr, Osborn's "Cohorts," etc.) are frequent in early classification. In addition to the three Linnaean cohorts, another for the bats (e.g., Pennant, 1781, Lacépède, 1799) and sometimes one for the pinnipeds (e.g., Storr, 1780), were used. Several rival systems were later proposed, for instance, that of C. L. Bonaparte, 1837, with "Educabilia" (primates, carnivores, sirenians, whales, ungulates) and "Ineducabilia" (edentates, bats, insectivores, and rodents). That of De Blainville had "Primates" (primates and doubtful sloths), "Secundates" (insectivores and carnivores), "Tertiates" (rodents), and "Quaternates" (ungulates and sirenians), all in a grand division of the "well-toothed" ("bien dentés"), opposed to the ill-toothed ("mal dentés"), i.e., the edentates. Owen, 1868, adopted Bonaparte's system, calling the "Educabilia" "Gyrencephala," the "Ineducabilia" "Lissencephala," and adding a new division "Archencephala" for man alone. Gill, 1872, also adopted Bonaparte's system without change.[1]

Cope (1898 and earlier) returned to the Linnaean triple division, with some adjustment of the contents of the cohorts. So, in our own century, did Osborn, 1910, except that he made the primates a cohort distinct from the unguiculates.

The Bonaparte-Owen system, based on superficial brain characters, had no phylogenetic validity and has long been abandoned by evolutionary taxonomists. Like so much that Linnaeus did, however, his arrangement in this respect has proved remarkably viable and adaptable to a theoretical basis quite different from his. There is still no serious question that his three cohorts are natural groups, as regards their typical or nuclear collocations, although there is much question as to the placing in them of a few orders and as to whether they are properly inclusive and should not be supplemented by one or two more. The early attempts at rearrangement were mostly retrogressive. Bats are close to insectivores, not meriting cohort

[1] He had previously (1870) used six "series," placing together the carnivores and whales; artiodactyls, perissodactyls, hyracoids, proboscideans, and sirenians; insectivores and bats; and leaving the Primates, Glires (Rodentia), and Bruta (Edentata) as isolated orders.

rank, and pinnipeds are still closer to carnivores, not even meriting ordinal rank. Osborn's much later emendation is hardly more acceptable, for it is now impossible to maintain by objective evidence that the primates are separable from the insectivores on this high level of taxonomy; the two orders intergrade almost completely in known forms, both recent and fossil, and certainly are of close common origin.

One other important later arrangement deserving consideration is that of Gregory, 1910, although it is (as he states) on a somewhat lower level, superordinal rather than cohort. His superorders are: Therictoidea (insectivores and carnivores), Archonta ("menotyphlans," dermopterans, bats, and primates), Rodentia, Edentata (queried; †taeniodonts, tubulidentates, pangolins, and xenarthrans), Paraxonia (artiodactyls), and Ungulata (ungulates in the broadest sense, except artiodactyls). In the light of later research (and of personal opinion) this classification, one of the most original and best grounded in the history of the subject, seems still to have certain flaws. Gregory's "Archonta" is almost surely an unnatural group. The "menotyphlans" are certainly near the primates, in fact the forms that he considered typical, the tupaiids, are here classed as primates. The Dermoptera are perhaps allied to the bats. But it is incredible to me, and to most recent students, that the primates are really more closely related to the bats than to the insectivores, and all recent research (including Gregory's own later work) opposes that opinion.

It is also now believed (by Gregory himself and almost all others) that his queried edentate group is an unnatural assemblage. There is much new strong evidence that the typical edentates, the xenarthrans, were derived from insectivores and can (as students previous to Gregory also thought) be associated with the latter, on the cohort level, at least. Thus as regards the Therictoidea, Archonta, and Edentata, this subdivision of the Linnaean unguiculate cohort is no longer acceptable. Gregory's separation of the Rodentia (Glires = Lagomorpha + Rodentia of this classification) is, however, in agreement with the latest consensus. The early rodents do not, like the Primates, for instance, definitely converge toward the early insectivores, and there is increasing reason to believe that the rodents (and less surely the lagomorphs with them) represent a very ancient and basic placental subdivision of cohort rank. This theory is accepted here, and a Cohort Glires is added to the three Linnaean cohorts.

Gregory's splitting of the classical ungulate cohort by removing the artiodactyls was based on his belief that the artiodactyls were derived from carnivores while the other ungulates came from unknown Cretaceous forms distinct from the carnivores and nearly like the early Tertiary †condylarths. Since 1910 the evidence on this point has been materially modified by far better knowledge of the †condylarths, including the discovery that certain forms then believed to be insectivores and recognized by Gregory and others as similar to the primitive artiodactyls, were really †condylarths. Indeed some of the early Tertiary †condylarths and artiodactyls are so like that only thorough knowledge of most of the skeletal structure suffices to distinguish them ordinally.

The evidence of an exclusive connection between the carnivores and the artiodactyls, alone among the ungulates, is not now so impressive as it was when Gregory first stated it. Nevertheless that view showed great insight into a relationship between the carnivores and the ungulates in general, only dimly glimpsed in 1910 but now fairly well established.

To students of recent mammals, the association of carnivores and ungulates in a single cohort must appear thoroughly unnatural. On the basis of living forms only, the recent carnivores more nearly resemble the recent insectivores than the recent ungulates, so that it has, as far as I know, never occurred to a neozoologist to group carnivores and ungulates together, with no others, and in contrast with all unguiculates. As far as this is possible, however, classification has as its principal basis not merely resemblances as such but natural affinities as far as these can be determined from resemblances. Students of early mammals have for some time been increasingly aware that the earliest carnivores and ungulates (*sensu lato*) are more closely similar to each other than either group is to the contemporaneous insectivores

and their special allies. Some early Tertiary forms, even among those fairly well known, could almost as well be called ungulates as carnivores. The earliest ungulates were primitively, not secondarily, clawed, literally unguiculate, and the early carnivores often had simple and blunt claws that lacked little of becoming primitive hoofs. The whole structure of the dentition and skeleton becomes closely similar in these two great groups as they are traced back nearer to their common origin. Both groups also converge toward the typical unguiculates, but not so closely as toward each other.

Matthew, particularly, has shown that the earliest Tertiary mammals (leaving aside the Glires and Mutica) seem to involve variations on two broad and basic types of structure, one typically represented by the Insectivora, ramifying into the Primates, Chiroptera, Edentata, etc., and the other common to the earliest †creodonts and †condylarths and ramifying into the Fissipeda, †Notoungulata, Proboscidea, Perissodactyla, Artiodactyla, etc. It is this dichotomy, made sufficiently probable by present evidence,[1] that I represent by the divisions Unguiculata and Ferungulata. It is extremely ancient and very broad, quickly overlain by myriad specializations. This sort of basic division is what is properly apprehended as of cohort grade.

From a phyletic point of view it is almost certainly erroneous to suppose the carnivores to be closer, say, to the primates than to the ungulates. The unguiculate aspect of the recent carnivores as compared to recent insectivores and ungulates can be wholly explained by the fact that the carnivores and the insectivores have on the whole been relatively less progressive in molars and in limbs than have the ungulates, and hence that their resemblances to each other are primitive eutherian characters and not those of a natural unguiculate cohort. The common stock of the Unguiculata and of the Ferungulata (doubtless also of the still more obscure early Glires and Mutica) lay far back, well into the Cretaceous at a time when the Eutheria must have been relatively unified and can hardly have shown any definitely incipient ordinal divisions.

[1] And generally recognized by the few students who have had special access to this evidence.

The four cohorts of this classification are thus the Linnaean Cohort Unguiculata minus the Ferae (Carnivora) and Glires (Lagomorpha and Rodentia), the Linnaean Glires raised to cohort rank, the Linnaean Cohort Mutica (Cetacea) unchanged, and the Linnaean Cohort Ungulata plus the Ferae. The names Unguiculata, Glires, and Mutica may be retained in these senses without ambiguity or confusion. The concept of the Ungulata is, however, so changed by the addition to it of the Ferae that a new name is imperative. It is recognized that some Ungulata, even in the strict sense, do have claws (e.g., †chalicotheres), and also that the etymology of a technical name has little bearing on its taxonomic use. Despite these facts, the words "Ungulata" and "ungulates" have always carried the clear significance of mammals normally hoofed and the taxonomic idea of a group not only excluding but also diametrically contrasting with the carnivores. It would be confusing and ridiculous to call the cohort as here constituted "Ungulata" and to speak, for instance, of dogs or of lions as "ungulates."

No other term has any serious claim to consideration,[2] and it is necessary to coin one. "Ferungulata" is formed by combination and syncope of the Linnaean terms "Ferae" and "Ungulata." The result is mellifluous and at once suggests the composition of the cohort.

UNGUICULATA

With rodents, lagomorphs, and carnivores excluded and primates included, eight generally recognized orders may be placed in this cohort. The most important and least dubious of these are Insectivora, Chiroptera, Primates, and Edentata. Remarkably diverse as they are, these orders have much in common, and even their living representatives retain numerous primitive characters that stamp them as among the most ancient and, in general, conservative of the eutherians. Modern insectivores are unusually specialized in diverse details that overlie this generally primi-

[2] The only authoritative names for a group including carnivores and ungulates but excluding insectivores are Educabilia Bonaparte, 1837, and Gyrencephala Owen, 1868, but in both cases it is essential to the concept designated by these names that the Primates and Cetacea also be included, collocations that are here absolutely rejected.

tive basis. It is probable that the common ancestry of the four orders would belong nominally or by definition to the first of them, the Insectivora. The other three have been distinct from one another certainly since the middle Paleocene and doubtless since the Cretaceous. Primates and edentates definitely converge toward insectivores if followed backward in time. Bats do not, on the basis of present evidence, but they are really insectivores now in all but the flight specialization, and the intermediate forms were almost surely rare and in a state of rapid change.

Indeed, with some over-simplification, each of these latter three orders can be thought of as representing insectivores that went off on particular trends of specialization while remaining primitive or insectivoran in other respects. The Chiroptera: flight. The Primates: cerebral complication, with associated features such as manual dexterity and posture. The Edentata: a triple trend, unevenly pursued by different edentates—digging and climbing (adaptively related activities), dietary restriction with tooth degeneration, defense by dermal armor.

The small order Dermoptera undoubtedly belongs in this cohort, as it has many and apparently significant resemblances to insectivores on one side and to bats on the other. The equally small order Pholidota is more dubious but may really be close to the edentates, with which it was formerly combined. The †Tillodontia and †Taeniodonta were short-lived groups, incompletely known, and their origin and affinities are largely conjectural, although I agree with Matthew in thinking that what little evidence there is suggests that they were early, rapidly evolving offshoots of the late Cretaceous Insectivora.

INSECTIVORA

Linnaeus and his contemporaries failed to recognize this group. Linnaeus himself confounded the insectivores, pigs, armadillos, and opossums in his "Bestiae," on the whole the least successful (from a modern point of view) of his collocations. Relying on equally misleading but more obvious resemblances, some other eighteenth century authors, like Brisson and Blumenbach, confused insectivores and rodents. The earlier work of Cuvier, followed in essentials by Illiger and De Blainville, placed the insectivores with the plantigrade carnivores, an arrangement that was anatomically defensible but is now known to be thoroughly unsound phylogenetically. Finally in 1817 Cuvier recognized the Insectivora under the vernacular name "insectivores" which they have ever since borne. He then considered them as related to the bats and the colugos (*"Galeopithecus"* = *Cynocephalus*), a relationship still believed to be correct on a superordinal level. The existence and the general contents of this order were thus early recognized and have not since been questioned.

The insectivores are a protean group difficult to classify logically and of extremely ancient origin and differentiation. The characters that unite them are in great part primitive for all placental mammals, and in this sense the common view that the insectivores are the most primitive of placentals and stand near the origin of all other groups is apparently true. It is, however, also true that each group of living insectivores and most known fossil forms are strongly specialized in some peculiar direction and that they are hence not generalized placentals despite their many primitive characters. It is probable that the most characteristic insectivores, such as the erinaceoids and the soricoids, do belong to an order of unified origin. Some other groups are placed here rather because they are primitive in many respects and cannot conveniently be placed elsewhere than because they have definite anatomical peculiarities diagnostic of the Insectivora. Particularly when the fossil families are considered, the order has thus come to be something of a scrap basket for small animals of generally primitive character that are not clearly referable to some more distinctive order.

Among recent insectivores, four fairly well-defined groups have long been recognized. Using the nomenclature of the present classification, these are (1) the Tenrecoidea, tenrecs (etc.), and Chrysochloroidea, golden "moles"; (2) the Erinaceoidea, hedgehogs and their allies; (3) the Soricoidea, true shrews and true moles; (4) the Macroscelidoidea and Tupaioidea, "elephant shrews" and tree "shrews." On this basis two conflicting subordinal divisions were proposed and have long been used, as follows:

Suborders of Haeckel, 1866, as Now Used	Present Superfamilies	Suborders of Gill, 1885, as Now Used
Lipotyphla	Tenrecoidea	Zalambdodonta
	Chrysochloroidea	
	Erinaceoidea	
	Soricoidea	
Menotyphla	Macroscelidoidea	Dilambdodonta
	Tupaioidea	

Although both arrangements are still current, both now seem to be unnatural. The obvious solution of the conflict by making three groups, "zalambdodont lipotyphlans," "dilambdodont lipotyphlans," and "menotyphlans," improves the situation somewhat, but not much.

In the first place, Broom, especially, has shown that the chrysochloroids are basically different from the other "zalambdodonts." He removed them from the Insectivora altogether and made a new order for them. This seems too radical, but the structural difference is so great that it cannot be affirmed that the chrysochloroids are phyletically closer to the tenrecoids than to the other insectivores, although the two share the single anatomical feature of being zalambdodont, that is, having a single outer V on the upper molars instead of two. A suborder Zalambdodonta or a division of zalambdodont lipotyphlans is thus unnatural because it combines two groups as distinct from each other as either is from the Dilambdodonta.

The supposed Suborder Menotyphla may be equally unnatural for a similar reason. In most recent work, "Menotyphla" is taken to mean the tupaioids and their allies. Since the tupaioids resemble the primates (indeed are primates as I now believe), it has also been customary to refer to the "Menotyphla" various fossil groups of uncertain position between the Insectivora and the Primates, even though they do not really resemble the tupaioids, a curious departure from objective taxonomic procedures.[1] In fact the group "Menotyphla" was not based on the tupaioids at all, but on the macroscelidoids and must properly remain with that group, including tupaioids only if the latter are considered nearer to the macroscelidoids than to any other mammals. This is a moot point. Carlsson (1909, 1922) sharply distinguished the Macroscelididae and Tupaiidae, considering the former as most closely allied to the Erinaceidae and the latter as near the lemuroids or Prosimiae. Le Gros Clark (1933 and elsewhere) followed this lead and definitely placed the Tupaiidae in the Lemuroidea. His evidence is detailed and cogent; I have elsewhere accepted his arrangement (e.g., Simpson, 1935d) and continue to do so in the present classification.

Since this manuscript was completed, however, Evans (1942) has published an excellent, detailed osteological review of the Macroscelididae, and he maintains that the Macroscelididae and Tupaiidae are really closely related and should not be separated subordinally (or, *a fortiori*, ordinally). In his opinion, then, both should be considered Lemuroidea, or both should be placed in the Insectivora, in which case the Suborder Menotyphla is valid and should be used to separate these families from all other insectivores, the Lipotyphla. All the resemblances and morphological relationships listed by Evans are real, and they emphasize the essential lack of a deep, natural division between Insectivora and Primates. He has also strengthened the case for common origin of the Macroscelididae and Tupaiidae from some one group of Insectivora (probably protoerinaceoid, although this point is not stated by Evans). Yet there remain grounds for differences of opinion as to the more exact phylogenetic relationship and, still more, as to the most convenient taxonomic arrangement consistent with these. In these respects Evans' well-documented conclusions appear to me quite dubious, and I am not at present disposed to accept his arrangement as a whole, while recognizing the possibility that it might eventually prove best. His evidence, weighed in the light of probable phylogeny rather than of simple morphological balance, does not seem to me to establish as close a union of macroscelidids and tupaiids as he maintains. For instance, I still believe that the fossil †*Anagale* is definitely tupaioid and could not, as Evans thinks, be a common ancestor of tupaiids and macroscelidids. Very

[1] Especially as it has been supported mainly by Matthew and students following him, despite the fact that he was in general strongly insistent on objective criteria in taxonomy.

tentatively, I have left this classification as it was before Evans' paper appeared, following Carlsson, Le Gros Clark, and my earlier work, rather than returning to the older arrangement now supported anew by Evans. Even if all his other conclusions were accepted, it would not be acceptable to consider the "Lipotyphyla" a unit and coordinate with "Menotyphla."

Many fossil insectivores are more or less clearly allied to recent groups even when they represent distinctive families; for instance, the †Leptictidae appear to be related to the Erinaceidae and the †Nesophontidae to the Soricidae and Talpidae. Other fossil groups are not so clearly allied to later forms, either because they are exceedingly ancient and mingle primitive characters of groups later very divergent, as the †Deltatheridiidae which seem to stand midway between "zalambdodonts" and "dilambdodonts," or because, like the †Pantolestidae and †Mixodectidae, they are early branches specialized in a way unlike any recent insectivores. These extinct families also tend to break down either of the two classic subordinal arrangements of the Insectivora.

Some other subordinal divisions have been proposed, but none has been generally adopted and none is satisfactory. For instance, Osborn (1910) made a suborder †Hyopsodonta for the †Hyopsodontidae, now believed to be †condylarths, not insectivores, and another, †Proglires, for the †Apatemyidae and †Mixodectidae, which are not especially related to each other and of which the first are probably primates, the second probably aberrant insectivores. Another system is simply to make each well-defined group, like my eight superfamilies, a suborder, but this solves no problem and it degrades the proper value of a suborder, as I see it and use it in this classification.

The fact is that in the Insectivora, as in some other orders, the point now reached in the progress of research is such that satisfactory basic subdivisions, such as suborders, are highly desirable but practically unattainable. We know enough to demonstrate errors in the subordinal groupings most widely accepted, but we do not know enough of the earliest history of the group really to demonstrate its ancient splitting up into primary subdivisions, the only evidence that would permit a stable and natural arrangement. It seems better, therefore, at present to omit suborders and to use superfamilies for the largest divisions that are now believed to be natural beyond much reasonable doubt.

Turning to some of the more questionable details, it is not certain that the †Didelphodontinae belong in the †Deltatheridiidae, but it is more probable than their previous reference to the †Leptictidae, and no other assignment is supported by the evidence. This question is discussed in Simpson, 1928d.

†*Apternodus* has been placed in a distinct family (e.g., in my previous classification, 1931a), but I now follow Schlaikjer (1933) in referring it to the Solenodontidae, in a separate subfamily. The far more primitive †*Palaeoryctes*, however, merits family distinction. The Chrysochloridae are still sometimes referred to the Tenrecoidea (under that or another name), but, as mentioned above, Broom (1916 and elsewhere) has shown that they are too distinct to permit such a collocation. The genera are given as in Forcart (1942), adding the scanty fossil records.

The peculiar †leptictids have been supposed to show relationships with the †creodonts and with the primates. The former resemblance is now shown to be surely misleading, as regards any ordinal affinity. The resemblance to the primates seems to be more real and deep-seated, but it is unlikely that it indicates anything more than that primitive insectivores of more or less erinaceoid stamp gave rise to the primates. That the †leptictids are most closely related to the erinaceids is now a well-supported theory. Several fossil genera might equally well be referred to either family on present knowledge, and the sorting of the varied genera referred with greater or less confidence to the †Leptictidae is not yet satisfactorily accomplished.

The unity of a family Erinaceidae is evident, even though some imperfectly known fossils seem to link this family with others. The subdivision of recent forms into two subfamilies is also well established, but the division of the various fossil genera between the two is dubious in the extreme, and the allocations of these genera in this classification, although not purely capricious, are not to be

taken too seriously. There were really more than two lines of descent, and the data do not yet show just how they should be grouped. This is particularly true of the American forms, which are themselves a complex group and which do not fall into a geographic unit. The fact that true erinaceids were present and varied almost throughout the Tertiary in North America is one of the more unexpected results of recent years of microfaunal studies. See, e.g., Patterson and McGrew, 1937.

The present placing of the Macroscelididae has been explained in discussing the proposed suborders. Among the soricoids, the †nyctitheriids are a primitive group known only from the teeth, which are shrew-like but without the more marked soricid specializations. †*Nyctitherium* has been tentatively called a bat, and such may be the real affinities of this family, or it may be an artificial group, but at present it is tentatively considered as a group of ancient soricoids. How difficult it is to classify such early, minute, and primitive animals from their teeth alone is shown by the fact that high authority may be found for placing some of them, like †*Domnina*, in three different orders, Marsupialia, Insectivora, and Chiroptera. The solution of the problem as regards that particular genus has been made possible by the discovery of more complete material and by recently developed methods of study, using fluorescence to discover enamel pigmentation and stereoscopic photography to reveal the microscopic cusp details (Patterson and McGrew). In most cases the material is still inadequate and such careful study has not yet been undertaken.

The subfamily arrangement of recent soricids still follows that of Milne Edwards (1868–1874). Several other subdivisions have been proposed, but none seems more satisfactory, and the fossils are as yet far too few to give any substantial aid. Recognition of a third subfamily for the rather lately discovered (1910) *Scutisorex* is very tentative. The animal appears to be only a typical African crocidurine shrew, close to *Sylvisorex*, which has developed an amazing specialization of the vertebral column. It is a matter of opinion whether this probably rapid and aberrant development warrants placing the genus in a separate subfamily rather than with the Crocidurinae, from which it was obviously derived.

True fossil moles are even rarer than fossil shrews, and the arrangement of the talpids is based on recent forms with the few extinct genera sandwiched in as best one can. The recognition of five subfamilies follows Thomas (1912) and Cabrera (1925) and is unsatisfactory because it involves undue splitting and because, even so, the two larger subfamilies are not clearly natural phyletic divisions, but no more satisfactory system has been devised. Certainly the more conservative and usual division into two subfamilies, Talpinae and Desmaninae, is more unbalanced and not more natural, and convenience demands some subfamily division of this rather large family.

The affinities of the †Pantolestoidea and †Mixodectoidea, or rather those of the genera here united in these groups but commonly widely scattered in the system, have been most dubious and disputed. I have discussed them in sufficient detail elsewhere (1937a). Although their relationship to the other or to the typical insectivores is not clearly established, it is now fairly certain that each of these is a natural group as here listed and that the †pantolestids were not artiodactyls or carnivores and the †mixodectids not primates or rodents, as was once believed and as is still occasionally stated.

The families appended to the Insectivora as *incertae sedis* have nothing in common except this doubtful status. Each family appears to be valid on morphological grounds, but none is sufficiently known to warrant any higher rank or more definite position. I have recently shown that †*Picrodus* and its synonym †*Megopterna*, formerly most capriciously assigned to various groups to which they can hardly belong, are really related to †*Zanycteris*. The latter was described as a possible phyllostomatid bat, and this may prove to be correct, but it rests on poor evidence. †*Necrolestes* is an important but annoying form, known from the whole skull, jaws, and part of the skeleton, but still of such peculiar character that authorities cannot agree even as to its correct infraclass. Scott, who knows the animal best, inclines to place it as an insectivore, perhaps a chrysochloroid, which involves baffling zoogeographic difficulties. Leche, Winge, and others have claimed that

it is a marsupial. I have studied the known material with care, but was unable to reach a conclusion.

The list of genera *incertae sedis* could be greatly extended, and I have mentioned only a few of the fairly well-defined genera, possibly insectivores, that should be remembered by a student of this order.

The best modern review of the whole order is probably that of Cabrera, 1925. Classic studies, taxonomic or anatomical, are Dobson, 1882–1890; Gill, 1875; Leche, 1902, 1907, 1921; Parker, 1885. On living erinaceids, see also Thomas, 1918; on soricids, Ärnbäck-Christie-Linde, 1907–1912; on chrysochlorids, Broom, 1916; on "menotyphlans," Carlsson, 1909; Le Gros Clark, 1933; Evans, 1942; and on talpids, Jackson, 1915. Among many more or less recent studies of fossil insectivores are Matthew, 1909a, 1929c; Meade, 1941; Patterson and McGrew, 1937; Schlaikjer, 1933; Scott and Jepsen, 1936; Simpson, 1928d, 1937a; Stehlin, 1940; Stirton, 1930; Viret, 1938. The palaeontological literature is widely scattered, and there are as yet no major monographs or revisions of all subdivisions or of any one broad subdivision of the fossil Insectivora.

DERMOPTERA

Although represented by a single living genus (with two subgenera, considered separate genera by some students), the colugos or so-called flying lemurs (which are not lemurs and cannot fly) are so distinctive that they are now almost always given ordinal rank. Recent students agree that the colugos are very aberrant derivatives of the Insectivora, of the insectivore ancestry of the Chiroptera, or of the earliest Chiroptera. In the latter case the colugos might with propriety be referred to the Chiroptera as they were, for instance, by Miller, 1906. The soaring adaptations of the colugos are, however, so unlike the flying adaptations of the bats that it is hard to see how the former could have any real relationship to the rise of the latter. Moreover, what appear to be well-differentiated colugos are known from the Paleocene, and entirely typical bats, with wings as specialized as now, from the Eocene, so that the two groups have probably been separate as long as most eutherian orders.

When Matthew first described the North American Eocene †Plagiomenidae (1918) he pointed out the resemblance of their teeth to those of recent colugos. I have not previously accepted this collocation because the evidence seemed insufficient for so remarkable an extension of dermopteran distribution, but additional material recently found by Jepsen (not yet published when this was written) seems to place these affinities beyond much doubt. The fossils do not, however, cast much light on the origin of the order except to show that the extraordinary teeth of the recent colugos did arise from the normal, primitive eutherian dentition, which few would have doubted in any case.

The living family has apparently always been called Galeopithecidae, but there is no doubt that the type genus must be called *Cynocephalus* and the family name changed accordingly. Although this would seem one of the most urgent and obvious cases for overruling priority in favor of common sense, the International Commission explicitly refused to validate the name *Galeopithecus* (Opinion 90). Such decisions cast discredit on the Commission and impede general adoption of the Rules, but it may be better to accept an occasional absurdity than to encourage anarchy.

There are few publications on the classification of this small order. Most of the pertinent data can be found in Leche, 1886; Matthew, 1918; Shufeldt, 1911.

CHIROPTERA

The resemblance of the bats to one another and their differences from all other animals are so obvious that the group has been intuitively recognized from the dawn of mankind. It is true that some very early students thought them a sort of bird, but they were obviously known as a different sort from the feathered birds. Linnaeus classed the bats as primates, part of the double confusion that made *Cynocephalus* a "flying lemur," and some of the other later eighteenth and early nineteenth century collocations seem similarly strange to us, but the essentially independent nature of the order has not been questioned for about a century. The evident and, beyond serious doubt, natural division of the bats into two great groups, suborders of this and most other classifications, was noticed by Gray as early as 1821,

although the names now generally adopted date only from Dobson, 1875. Dobson's classification was standard for a generation and is, indeed, the basis for all later work. In the Microchiroptera he recognized five families, which included 18 lesser units, subfamilies, and "groups." Winge, with his eye for broad outlines in taxonomy, in 1892 reduced the number of microchiropteran families to four by uniting Dobson's Rhinolophidae and Nycteridae.

Modern classifications of the Chiroptera are almost all based on Miller, 1907. Although Miller raised no serious question as to the reality and validity of the earlier four or five inclusive families of Microchiroptera aside from minor readjustment of contents, he split them up into 16 families. Miller's families are nearly equivalent in scope to Dobson's generic groups of less than subfamily rank.

The acuteness and practical value of Miller's family arrangement are abundantly demonstrated by the fact that it has hardly been challenged during the subsequent 35 years and is still in virtually universal use. The families are certainly of smaller scope than in many or most mammalian orders, but the number of forms to be classified is large, and so clear a weight of usage cannot be easily opposed. At the same time, it appears that this split classification unnecessarily obscures the synoptic view of relationships so desirable for general students of mammals.

For these reasons the present classification retains Miller's families but groups them into superfamilies which are the families of Winge. The broader outlines are thus retained without demoting the families so strongly sustained by most students. The genera of recent specialists also appear to me excessively split even in comparison with their families, and I have given many of the genera broader scope than is currently granted by specialists, but have not attempted exhaustive synonymy.

Comparative anatomy gives considerable evidence that this arrangement of the bats is generally consistent with the phylogeny of the order, but chiropteran history is almost unknown except in this indirect way. Although bats are among the most abundant and varied of mammals now, and probably have been through much of the Tertiary, they are among the rarest of fossils. It is unlikely that palaeontological materials will ever suffice to trace much of this history. Small size, fragile bones, and habits combine to make the discovery of identifiable fossil bat remains an unusual accident. It is, moreover, probable that crucial events in this history occurred where no terrestrial Tertiary strata are preserved.

The few fossil bats that are known show that the order was fully established by the middle Eocene, at latest, when the basic specialization was hardly less than it is today. The origin and differentiation of the order were certainly very ancient. The Paleocene †*Zanycteris* and †*Picrodus* may have been phyllostomatids and if so would indicate truly astonishing antiquity for a specialized modern family, but this is dubious and it seems less misleading for the present not to stress the possibility and to leave these forms as ?Insectivora *incertae sedis*.

Tertiary fossils surely referable to this order, almost exclusively European, warrant no important modification of the classification based on recent forms. Fossil and semifossil Pleistocene to Recent remains are fairly common in caves but as far as I know have added little of interest either to taxonomy or to distribution. No attempt has been made to list these casual and unimportant records exhaustively.

The classic studies of Dobson, 1875, Winge, 1892, and Miller, 1907, have been mentioned. Although it does not include a formal classification, the book by Allen, 1939b, gives the best recent review of the order and has an extensive bibliography. Most of the known fossils were discussed by Revilliod, 1917a–1922. More recent discoveries have been recorded by Gaillard, 1929, Heller, 1935b, and Stirton, 1931. (†*Mystipterus* Hall, 1930b, was described as a bat and is usually still listed as such, e.g., by Allen, 1939b, but it has been shown to be an insectivore, Patterson and McGrew, 1937). On the disputed †*Zanycteris* and its ally †*Picrodus*, see Simpson, 1935b, 1937a.

PRIMATES

The primates are inevitably the most interesting of mammals to an egocentric species that belongs to this order. No other mammals have been studied in such detail, yet from a taxonomic point of view this cannot be con-

sidered the best-known order, and there is perhaps less agreement as to its classification than for most other orders. A major reason for this confusion is that much of the work on primates has been done by students who had no experience in taxonomy and who were completely incompetent to enter this field, however competent they may have been in other respects, and yet once their work is in print it becomes necessary to take cognizance of it. For this reason, if for no other, it is not surprising that most primates have alternative names and that hardly any two students use the same nomenclature for them. The importance of distinctions within the group has also been so exaggerated that almost every color phase, aberrant individual, or scrap of fossil bone or tooth has been given a separate name, almost every really distinct species has been called a genus, and a large proportion of the genera have been called families. The peculiar fascination of the primates and their publicity value have almost taken the order out of the hands of sober and conservative mammalogists and have kept, and do keep, its taxonomy in a turmoil. Moreover, even mammalogists who might be entirely conservative in dealing, say, with rats are likely to lose a sense of perspective when they come to the primates, and many studies of this order are covertly or overtly emotional.

Because of all these factors, the preparation of this part of the classification has presented many special difficulties, and it will be discussed in rather more detail than the scope of the order would otherwise warrant, although it is impossible to follow each concept through the intricately tangled web of primate taxonomic history or to touch on every controversial point.

The basic division of the primates into two groups, the suborders of this classification, is old. The groups are, in fact, the Linnaean genera *Lemur* and *Simia*, grown almost beyond recognition. Linnaeus boldly included man in the Primates but as a third genus, hence coordinate with the modern suborders. Early nineteenth century writers, e.g., Cuvier, Illiger, Blumenach, usually either declined to classify man as a zoological specimen or made him the unique member of a separate order. The point requires no argument now. All zoologists agree that man is a primate, and there are few who do not admit *Homo* to the same large subdivision, suborder, as the apes. The only disagreement on this point comes from those who wish to derive man—or perhaps who wish that man had been derived—from a vaguely remote early Tertiary source independent of the origin of monkeys and apes. The consensus of zoologists so overwhelmingly opposes such a view that it need not be discussed further at this point.

Whatever many students of the classical nineteenth century did with man, they continued to divide other primates into two groups under many different names: "makis" and "singes" in Cuvier, De Blainville, and many other French authors, "Quadrumana" and "Prosimii" (essentially) in Illiger, "Lemuroidea" and "Anthropoidea" in Mivart and most later authors, etc. Illiger, however, excluded the tarsier and the aye-aye from the Prosimii and made each the type of a separate suborder, and many students divided the higher primates in distinct and coordinate groups, often called suborders, the Catarrhini and Platyrrhini of Ehrenberg (1820).

All these groupings, and others, still appear to be natural but may well be, and usually are, reduced below the subordinal level. It seems quite possible that New World and Old World monkeys arose independently from Eocene prosimians, but the transitional stages are not yet known in either case. They share characters not found in lemurs; their prosimian ancestors, if distinct, must have been closely allied; and there is no serious objection to continuing to unite them, along with apes and men, in a single suborder, as is done in almost all modern classifications.

There is less agreement regarding the lower primates. A few students (e.g., Abel, 1931a) place the aye-aye and its supposed allies in a separate suborder. This is largely based on belief that the aye-aye, "*Cheiromys*" in most discussions but properly *Daubentonia*, has had a distinct lineage since the Paleocene. I have studied this evidence and found some of it invalid and the rest equivocal, as will be remarked elsewhere. It now seems more probable that the peculiarities of *Daubentonia* are rather superficial and that it is a true lemur, perhaps even of rather late origin from the typical lemurs. At any rate its subordinal distinction is not warranted by present data.

As regards the tarsiers and their allies, perhaps a consensus favors giving them subordinal rank. At least one excellent anatomist, Sonntag, thinks them only moderately aberrant lemurs, but more, e.g., Wood Jones, Le Gros Clark, think they have, for all practical purposes, always been distinct from the lemurs. Without denying the obvious fact that later tarsioids, at least, form a well-defined and very distinctive group, I venture to go against the consensus to the extent of calling that group a secondary (infraorder) rather than primary (suborder) division of the Primates. The Paleocene and earlier Eocene members of the two groups are very much alike, indeed often indistinguishable on more than a generic level unless known by excellent materials. Synthetic and intermediate types occur. The indication is that a general, more lemur-like, prosimian stock was then splitting into many lines. Most of these divergent specializations led to early extinction, but the tarsioids happened to survive without, however, ever becoming varied enough or distinct enough to warrant (in my opinion) classing them as a group equal in rank to the whole of the ancestral stock plus all its less long-lived or less divergent descendants.

The classification of the Primates may thus still start with two suborders, for which I adopt the names Prosimii and Anthropoidea. The use of "Prosimii" rather than the antithetical and now more usual "Lemuroidea" depends on a somewhat complicated weighing of alternatives. Without going into these here, it may be noted that Prosimii is appropriate and prior and that Lemuroidea is needed as the name for a superfamily, a much less inclusive group.

As to the relationships of the two suborders, the Anthropoidea were almost surely derived from early members of the Prosimii. Given the variety of each group and the survival of both, this does not argue against considering their separation as the primary or most important (not necessarily the first) dichotomy of the Primates.

PROSIMII

Alternative subdivisions of these lower primates would be to contrast lemur-like and tarsier-like forms, to recognize these and a third group of loris-like prosimians, or to adopt a three-fold division into lemur-like, aye-aye-like, and tarsier-like. All three arrangements are current and all are defensible. In adopting the second, I nearly follow Gregory (1915 and elsewhere), and I also use his appropriate names for the groups, Lemuriformes, Lorisiformes, and Tarsiiformes. Reasons for suggesting that *Daubentonia* can properly be considered lemuriform are given elsewhere. The history of the Lorisiformes is obscure, but they are now a well-defined group. All three infraorders seem to be derived from a common prosimian ancestry from which the Lemuriformes have diverged the least (in their most conservative lines hardly at all), the Lorisiformes more, and the Tarsiiformes most.

The whole arrangement of the Prosimii here follows Gregory, 1915, in essential respects, aside from such points as including the tupaioids and †plesiadapids. Gregory's classification was not very widely adopted and was attacked especially by certain European students. I also formerly departed further from it than I do now, but reconsideration persuades me not only that it was the best arrangement ever made at its date, but also that the many discoveries of more than a quarter of a century since then have tended to support its main features and failed to support, or decidedly oppose, most of the alternative arrangements and criticisms.

LEMURIFORMES

Among recent forms, the tupaioids, lemuroids, and daubentonioids are clearly natural units, whatever opinion is held as to their association.

Until very recently, the tupaioids were always classified as Insectivora or, occasionally, as representing a separate order (Menotyphla) allied to the Insectivora. Their remarkably primitive character has long been recognized, and several students have even stressed their supposed possession of marsupial characters or affinities. (Regarding this point, the characters in question, listed by Gregory, 1910, are either primitive for both marsupials and placentals or are the result of quite superficial convergence in isolated details.) They are less specialized in their average or conjoint anatomy than are

any of the (other or true) living insectivores, and they share with the didelphids the distinction of being the most nearly generalized of surviving Theria. On the other hand, they also have unmistakable and significant resemblances to the primates.

This fact, too, has long been recognized, and all recent students agree that the tupaioids are either the most primate-like insectivores or the most insectivore-like primates. This recognition was involved in the conception of the Menotyphla as a sort of intermediate insectivore-primate group. For a time this supposed suborder or order was used as a dumping ground for forms resembling both insectivores and primates but not believed to be definitely assignable to either. Many of the fossils placed here showed no special resemblance to macroscelidids or tupaiids, and the arrangement was really indefensible on morphological grounds. It also overlooked the fact that the typical "menotyphlans" are the macroscelidids, not the tupaiids, and that the macroscelidids are more like (other) insectivores and less like primates than are the tupaiids.

The resemblance between macroscelidids and tupaiids is real, but it now appears to be less significant and less exclusive than was formerly supposed (see, e.g., Carlsson, 1922). In large part the resemblance is the same as that between tupaiids and insectivores in general: they share such primitive placental characters as are preserved in the various representatives of the two groups but share few specialized characters. Such residual and specific resemblance as exists suggests only that macroscelidids and tuapiids arose from the same very early, more or less proto-erinaceoid group of insectivores. (See also p. 176, and Evans, 1942, who opposes this view.)

The primates apparently arose from this same group, which is hypothetical but is nearly approached in structure by various known genera. It now appears that the tupaioids arose from the line leading definitely to the primates and after this line had become distinct and had acquired the most basic of primate characters. No other explanation seems adequate to account for the many definite and special lemuroid characters of the tupaiids, see, e.g., Le Gros Clark, 1934a. The most appropriate taxonomic expression of this phylogenetic inference is to place the tupaiids in the Primates.

Several early Tertiary genera in America and Europe have been placed in the Tupaiidae or Tupaioidea, but in every case better knowledge has shown, again, that the resemblance was confined to primitive or generalized characters and that the fossils in question are almost certainly true ("lipotyphlan") insectivores. The only known fossil that is definitely, unquestionably tupaioid is †*Anagale*, based on an isolated but beautifully preserved fossil from the early Oligocene of Mongolia (see Simpson, 1931b). In some respects this ancient tupaioid was even more lemur-like than are the living forms, and it strongly supports the inference that the tupaioids arose from primitive Lemuriformes and slightly diverged from the lemuroids proper while retaining most of their ancestral characters.

The †plesiadapids are a peculiar and interesting group that is only now becoming adequately known. The most important earlier opinions were (a) that these are ancestral daubentonioids ("cheiromyoids"), as maintained by Stehlin, 1912–1926, and most later European authors even to the present time, and (b) that they were "menotyphlan" insectivore-primates, as claimed by Matthew, e.g., 1937.[1] In a detailed account of much better material than has been studied by anyone else, however, I demonstrated (Simpson, 1935d) that the resemblances to tupaiids are only general lemuroid characters and those to *Daubentonia* likewise general lemuroid characters plus some demonstrable convergence. It now seems almost certain that the †plesiadapids were an offshoot from definitely lemuroid ancestors, closer to typical lemurs than are the tupaiids, roughly paralleling the probably later daubentoniids in the specialization of the incisors but not specially related to them.

The arrangement of the living Prosimii, other than Tupaiidae, follows Gregory, 1915, with a few modifications based on more recent work. Aside from the treatment of *Daubentonia* and *Tarsius* already sufficiently men-

[1] But note that this is a posthumous publication, and on this point it involves none of the new materials or new studies after about 1918.

tioned, this part of the classification is not particularly controversial and calls for no special comment.

Except for the two most recently named genera, †*Macrotarsius* and †*Paratetonius*, the relationships and classification of all the early Tertiary prosimian genera are discussed in Simpson, 1940a, and details need not be repeated here. Thanks to the work of Stehlin, 1912, and Gregory, 1920, the †Adapidae are much the best-known Eocene primates, and they are exceptionally important as nearly representing generalized lemuroid anatomy and structurally appropriate as ancestors for all the Anthropoidea, although it is improbable that the descent is nearly direct among the known forms. The extraordinarily varied †Anaptomorphidae will probably prove to be a partly unnatural group when some of the genera are better known, but in general these animals evidently represent an almost explosive early deployment of a division of Prosimii of which *Tarsius* is the sole survivor. The somewhat rodent-like †Apatemyidae were formerly confused with the really quite distinct †Plesiadapidae but were finally clearly separated by Jepsen, 1934. The †apatemyids appear to be less definitely lemur-like than the †plesiadapids. They are probably, but not surely, true primates. Supposed ancestry or other special relationship to *Daubentonia*, often claimed for the †apatemyids as well as the †plesiadapids, is not absolutely impossible but does not now appear to be supported by any good factual evidence. The highly distinctive †carpolestids were surely not ancestral to any known later forms and were of very dubious but possibly proto-tarsioid origin.

The Suborder †Ceciliolemuroidea and family †Ceciliolemuridae proposed by Weigelt, 1933, are omitted from this classification. They were defined principally on the absence of primate characters and it seems slightly ridiculous to insert in the Primates subdivisions based on their being unlike primates. †*Ceciliolemur* may eventually prove to be a primate, but its affinities are now too doubtful to warrant making a formal place for it in the classification. Although, or because, virtually no attention has been paid to it, mention may be made of †*Arrhinolemur* Ameghino, 1898, at first considered to be a lemur and later placed in a separate order †Arrhinolemuroidea. The one specimen in question is the crushed skull of a fish (personal observation).

ANTHROPOIDEA

The classic division of this group into Platyrrhini and Catarrhini, dating from Hemprich, 1820, is still widely current, but it is here abandoned. There are three, not two, well-marked subdivisions, the Ceboidea, Cercopithecoidea, and Hominoidea of this classification. As far as now known, they may be of about equal antiquity, and it is by no means well established or generally agreed that the later two form a single and exclusive unit, as implied by the classic arrangement. Incidentally, it has been shown by Pocock, 1925, that some "Platyrrhini" are descriptively catarrhine (have narrow noses). This does not in itself invalidate the systematic use of the names, but it may lessen regret at their abandonment.

CEBOIDEA

The history of the Ceboidea is virtually unknown. From their comparative anatomy and distribution, there is little doubt that all the ceboids represent the radiation of a single stock isolated in South America during Tertiary times, but known fossils are few and not very enlightening. Known Pleistocene forms are not very different from living ceboids of the same regions. The only known, or at least well-defined, Tertiary form is †*Homunculus* in the Miocene (or less probably late Oligocene to Miocene). Ameghino considered it as near the ancestry of man, and he erected a family †Homunculidae. The most recent student of the genus, Rusconi, 1935, insists on the retention of this family, but his excellent new materials, and all other considerations, seem rather to support the view of Bluntschli, 1931, and others that †*Homunculus* is a typical cebid, and probably not separable from the living subfamily Aotinae. Ameghino also named many other supposed fossil primates from South America, as did Roth, ranging in supposed age from Cretaceous to Pleistocene, but later study has shown that most of these are surely not primates and that none surely is a primate.

As far as the present record goes, ceboids thus appeared suddenly and in almost modern guise in the mid-Tertiary of South America. The most reasonable hypothesis is that ceboids arose from one of the Paleocene or Eocene prosimian stocks of North America and that their early deployment, or indeed almost all their history, occurred in the more tropical parts of South America, where Tertiary fossils are extremely rare. This is, however, only a hypothesis.

The living ceboids are a rather small group, including 14 genera in this classification (four or five others are occasionally separated), but their taxonomy is extremely confused. All the well-known genera have received two or more names each, and in several cases the names most widespread in the literature are invalid. For example, the familiar names *Nyctipithecus*, *Brachyurus*, *Mycetes*, *Chrysothrix*, *Hapale*, and *Midas* are all invalid as applied to members of this group, yet some or all of them are used in most books, even those of recent date. The arrangement has also been the subject of numerous changes and dispute, although not more so than in many other superfamilies.

The arrangement adopted here is an outgrowth of successive steps taken especially by Gray, Flower, Weber, Elliot, and Pocock. Aside from minor points of orthography and sequence it differs little from Elliot, 1913, and still less from Pocock, 1925. Pocock has also given a valuable review of classification, so that the only points requiring much notice here are those that differ from him.

Almost all authorities except Pocock have placed *Callicebus* in the Aotinae, but he makes a separate subfamily for it. (Elliot placed it in the Callithricidae, but, as Pocock remarks, this can only be explained as accidental.) I have preferred to follow the more usual arrangement. On the other hand, I have retained Atelinae for the rather unified group *Ateles-Brachyteles-Lagothrix*, an arrangement dating from Gray and supported by Pocock, although many recent authors unite them with the Cebinae.

The position of *Saimiri* (or *Chrysothrix*) has long been a moot point. Gray, Flower, and many others associated it with *Callicebus*, or the group Aotinae as here recognized, and Elliot transferred it to the Pithecinae, but Weber placed it near *Cebus*. Pocock strongly supported this, and I have followed their opinion.

Callimico is a curiously synthetic type, callithricid as to feet and cebid as to skull and teeth, so that it forms a rather well-defined subfamily. Pocock places it in the Callithricidae, Weber in the Cebidae, and I have followed the latter since the foot characters seem to be adaptive features that are suggested in some cebids and that could readily be merely convergent toward callithricids.

The tamarins (and their close allies) form a rather varied group and are commonly divided into three (Pocock) or four (Elliot) genera. I have followed Weber in considering these groups as subgeneric, a course also somewhat less confusing from a nomenclatural point of view. *Cercopithecus* is the oldest name applied to the tamarins, but this usage has been eliminated by official suspension of the Rules. The next oldest name, *Midas*, is common in the literature but is clearly preoccupied, so that *Leontocebus* becomes the correct name of the (collective) genus. Weber is wrong in adopting *Mystax* with the same inclusiveness, for *Leontocebus* has 31 years of priority.

Miller has recently (1924) given a partial classification which is extremely "split," with families Alouattidae, Aotidae, and Saimiridae. It is difficult to see much merit in a classification that gives family rank to distinctions, as between *Cebus* and *Saimiri*, that no one else considers as more than subfamilial and that some of the most competent recent authorities do not consider supergeneric, and I am not aware that Miller has adduced sufficient evidence for his radical views.

Perhaps mention should be made of sensational reports of the discovery of non-ceboid primates, presumably anthropoid apes, in South America. Without giving more publicity to this notorious case, the fact remains that no trace of primates other than Ceboidea has ever been found in South America.

CERCOPITHECOIDEA

With closer approach to man in the zoological system, the confusion bequeathed us by swarms of students, of all degrees of competence and shades of judgment, becomes in-

creasingly greater. Some idea of this confusion can be obtained from the following incomplete list of names, all of which have been applied to macaques:

Cynamolgus, Cynomolgus, Cynomolgos
Gymnopyga
Inuus
Lyssodes
Macaca, Macacus, Macaco, Macaquo
Magotus
Magus
Maimon
Nemestrinus
Ouanderou
Pithecus
Pithes
Pithex
Rhesus
Salmacis, Salamacis
Silenus
Simia
Sylvanus
Vetulus
Zati

Aside from these names, used at one time or another for macaques as distinct from other monkeys, macaques have also been combined with other forms in inclusive genera, such as *Papio* or *Cercocebus*, so that altogether (disregarding variant spellings) macaques have been placed in at least 25 different genera or subgenera, yet it is the present consensus that all belong in one genus with perhaps three subgenera, requiring a total of three names, only one of generic (and hence also subgeneric) rank. The confusion here exemplified extends to the nomenclature and arrangement of the whole group. In the present classification the arrangement follows the apparent consensus of competent recent students, and the generic nomenclature is an attempt to follow the Code and Opinions without deviation.

Pocock, 1926, and some others give the Cercopithecidae and Colobidae family rank, a valid system, but the differences between the two are not so great as is usual between mammalian families, and some fossil forms seem to be related to both groups and to suggest that a definitive family arrangement would not follow just these lines. The more usual subfamily separation is, therefore, retained pending further discoveries.

Perhaps the most disputed names among the higher primates are those of the macaques, guenons, langurs, orang, and chimpanzee, which may be discussed here, although the latter two are hominoids. The principal variant usages are as tabulated below.

Osborn, 1910, is given as the usual nomenclature, the one probably most familiar and widespread in textbooks, etc.

Allen has shown beyond any question that *Macaca* (of which *Macacus* is merely an invalid variant) is the correct generic name of the macaques, and Elliot was almost the only writer to doubt this even before Allen wrote. *Cercopithecus* is apparently preoccupied, but the Commission has suspended the Rules (Opinion 104) and made its use in this sense officially valid, superseding Elliot's otherwise necessary change. *Semnopithecus* is preoccupied and is generally abandoned by careful recent students. As between *Pithecus* and *Pygathrix*, there is a serious question on the basis of the Rules, but this need not be further discussed since the Commission has suppressed *Pithecus*, removing it altogether from zoological nomenclature (Opinion 114). If all the langurs are united in one genus, this apparently makes *Pygathrix* the valid name, as Elliot maintained, but there is some reason to recognize two groups, to the second (but larger and more typical) of which the name *Presbytis* then applies. Elliot believed that the Linnaean name *Simia* should refer to a

	Osborn, 1910	Elliot, 1913	Pocock, 1925	This Classification
Macaques	*Macacus*	*Simia*, *Pithecus*, and *Magus*	*Macaca*	*Macaca*
Guenons	*Cercopithecus*	*Lasiopyga*	*Cercopithecus*	*Cercopithecus*
Langurs	*Semnopithecus*	*Pygathrix*	*Pithecus*	*Pygathrix* and *Presbytis*
Orang	*Simia*	*Pongo*	*Simia*	*Pongo*
Chimpanzee	*Anthropopithecus*	*Pan*	*Anthropopithecus*	*Pan*

macaque. It would thus include all the macaques, if they are united in one genus as here, but Elliot separated them into three. On this question I follow Pocock who says that Elliot's splitting of the genus has "no ascertainable reasons." Most authors have used *Simia* for the orang. So much ambiguity has arisen that the Commission suppressed the name *Simia* (Opinion 114), thus leaving *Pongo* for the orang and Pongidae for the Simiidae of most authors. *Anthropopithecus* was proposed at least 22 years after *Pan*, so the latter has clear priority, as Elliot established. The Commission was requested to suspend the Rules but would not do so (Opinion 90), and *Pan* is, therefore, the valid name.

In 1924 a group of zoologists announced that they intended to use *Anthropopithecus* for the chimpanzee, *Simia* for the orang, and *Cercopithecus* for the guenons, regardless of the Rules. Nevertheless the Commission refused suspension of the Rules to the first, suppressed the second name, and authorized only the third in the way desired by these zoologists. Undoubtedly for some time to come there will still be rugged individualists who will use these generic names as they please, but uniformity can be achieved, if ever, only by following the established Code and later decisions made in accordance with its provisions. Complete agreement is impossible, and everyone must feel that some of the Opinions have been unfortunate and ill advised, yet this is the only standard that we have or are likely to have and it is surely for the common good to submerge personal desires and promote uniformity by adhering to it. The same considerations apply to the suppression of the name *Pithecus*, which also provoked the indignation of some students.

†*Moeripithecus* is known only from one jaw fragment with two teeth. It is usually considered as a doubtful cercopithecoid, but Gregory, 1916, referred it to the Parapithecidae, and Remane, 1921, doubtfully to the Hylobatidae. †*Apidium*, also based on a single specimen, is equally dubious, but Gregory considers it as related to †*Oreopithecus*. †*Oreopithecus* is a relatively well-known form and is certainly a cercopithecoid primate, but with certain peculiarities that make its position uncertain. It has been placed in a family by itself, which seems an undue distinction, and also in a separate subfamily of Cercopithecidae. The other known fossil cercopithecoids are all rather near the living forms. Most of the known older anthropoids seem to be nearer the hominoids than the cercopithecoids, although definitely more primitive than living apes. This is anomalous in view of the frequent opinion that hominoids may have arisen from cercopithecoids, but the higher primates leave few and poor fossils, and negative evidence in this group can be given little weight.

HOMINOIDEA

Most students now believe that the gibbons, apes, and man form a natural unit, but there are few questions on which wider divergence of opinion is to be encountered. Disregarding those who maintain that man is a separate "creation," which of course is no longer believed by anyone whose opinion need be considered, there are, nevertheless, some students who believe, or at least seem to say, that man's ancestry has been separate from the beginning of primate differentiation. This would presumably place man in a separate suborder or order (which has been proposed). Others would derive him from the tarsioids (e.g., Wood Jones), others from the ceboids (e.g., Ameghino), and indeed almost every primate group has been hailed as including the ancestry of man. It is not possible or necessary to review these controversies here. I believe that Gregory has achieved the most valuable syntheses of the work of others, combined with his own very broad and detailed knowledge, and cite him as recent authority for the conviction that the gibbons, apes, and man are a unit, derived from a common ancestry.

If this is accepted, it does not much matter what rank is given to that unit. In keeping with the general scale of this classification, superfamily rank is most convenient here. Wilder boldly united all these forms in a single family, Hominidae, and Gregory and Hellman (e.g., 1939d) have adopted this arrangement. On the basis of usual diagnostic characters, such as the teeth, viewed with

complete objectivity, this union seems warranted. I nevertheless reject it, for two reasons: (a) mentality is also a zoological character to be weighed in classification and evidently entitling man to some distinction, without leaning over backward to minimize our own importance, and (b) there is not the slightest chance that zoologists and teachers generally, however convinced of man's consanguinity with the apes, will agree on the didactic or practical use of one family embracing both.

†*Parapithecus* has been considered a cercopithecoid and even referred to the Cercopithecidae (as by me in a previous classification, 1931a), but Gregory's repeated and careful analyses emphasize its prototypal hominoid characters, and I, therefore, place it in this superfamily. Alternatively, it may be near the common ancestry of Cercopithecoidea and Hominoidea if, as Gregory and many others believe (but an equal number of distinguished students do not believe), these groups did have a common anthropoid ancestor. Manifestly of great importance, this poorly known genus is quite insufficiently known to give definite answers to this or other questions asked of it.

The new subfamily arrangement of the Pongidae is a development of the ideas of Gregory and Hellman, 1939b, although they have not classified all the genera involved. The arrangement certainly is not definitive and probably is not fully natural, but it is morphologically defensible and seems to be a practical expedient pending better knowledge. The gibbons are a relatively unified and early offshoot of the hominoid stock, and the ancient (Oligocene) †*Propliopithecus* seems already to be on this line and outside the ancestry of the higher apes. †*Paidopithex* is known only from a rather dubious femur but is included for completeness.

The †Dryopithecinae are probably a very heterogenous group which represents a stage in primate evolution rather than a single phylum and its branches. Thus the different Ponginae probably arose from different †Dryopithecinae so that the separation of the subfamilies is not phylogenetic classfication, but the true phyla are not really distinguished at present. Every scrap of a †dryopithecine has been studied and restudied in exhaustive detail, but these fossils are scraps, for the most part, and about all that emerges with sufficient clarity is that this is a complex from which the living great apes, the †australopithecines, and man may have arisen. The ages here given for the Indian (Siwalik) †dryopithecines are younger than claimed by most authors, but I have followed Colbert, whose correlations seem to me more likely than those of Pilgrim.

†*Australopithecus*, together with †*Plesianthropus* and †*Paranthropus* which seem to me only subgenerically distinct, at most, has been considered everything from a direct ancestor of man to merely another sort of chimpanzee. Dart's placing of †*Australopithecus* in a family "Homo-simiadae" (1925) only served to exemplify the total ignorance of zoology so common among the special students of these higher primates (although, of course, Dart's work is excellent in his own field). I accept the opinion of Gregory and Hellman that †*Australopithecus* represents a line of †dryopithecines that evolved more or less in the same direction as man but did so more slowly, resulting in a structural, but not phylogenetic, intermediate stage between man and the surviving great apes.

All specimens of fossil hominids that differ in any discernible way from *Homo sapiens*, and some that do not, have at one time or another been placed in different genera. Almost none of these anthropological "genera" has any zoological reason for being. All known hominids, recent and fossil, could well be placed in *Homo*. At most, †*Pithecanthropus* (with which †*Sinanthropus* is clearly synonymous by zoological criteria) and †*Eoanthropus* (if the ape-like jaw belongs to it) may be given separate generic rank. Perhaps it would be better for the zoological taxonomist to set apart the family Hominidae and to exclude its nomenclature and classification from his studies.

Literature on Primates

Literature on the Primates, including man, exceeds that on all other animals put together, and even the relatively small fraction directly concerned with taxonomy is very extensive. Nevertheless there is no single work in which the classification of all the primates is adequately discussed. A few cita-

tions of authority on particular points have been made, and a few others may be added here.

Elliot's monumental review (1913) has been severely criticized and it has defects, like all the products of man, but it remains the best single source of information on living primates. It does not define supergeneric groups, and it almost completely neglects study of relationships and phylogeny. Gregory, 1915, is an outstanding, succinct study of the classification of the Prosimii. Pocock's papers, 1918a, 1925, 1926, include an important reclassification of living forms. These are usefully reviewed in Weber, 1928, and numerous other books cover particular points or subdivisions, e.g., Le Gros Clark, 1934a; Lyon, 1913; Remane, 1921a and b; Sonntag, 1924.

Most of what was then known of fossil primates was brought together by O. Abel in 1931, whose book is invaluable despite some serious errors and the adoption of a classification now untenable in important respects. Among classic studies on fossil Prosimii may be mentioned Gidley, 1923; Grandidier, 1904; Gregory, 1920; Matthew, 1915; Ossenkopp, 1925; Stehlin, 1912, 1916; Teilhard de Chardin, 1916, 1921. I reviewed the Paleocene and Eocene forms in 1940a. Among the most recent studies of particular genera or groups are John Clark, 1941; Le Gros Clark, 1934a; Heller, 1935a; Jepsen, 1934; Lamberton, 1939; Lewis, 1933; Seton, 1940; Weigelt, 1933.

On †*Homunculus*, etc., see Bluntschli, 1931; Rusconi, 1935.

There is little important recent literature on fossil Cercopithecoidea, but see, for instance, Andrews, 1916; Broom, 1940; Schwalbe, 1915.

Gregory's papers are among the most important studies of fossil Pongidae and the origin of man and they summarize and refer to almost all other work on the subject; see, e.g., Gregory, 1916, 1922, 1934; Gregory and Hellman, 1926, 1939b; Gregory, Hellman, and Lewis, 1938. Also, among many others, W. Abel, 1931; Broom, 1939; Colbert, 1938b; Ehrenberg, 1938; Hopwood, 1933; Koenigswald, 1935; Lewis, 1934; Pilgrim, 1915.

No attempt is made here to cite the literature on fossil men.

†TILLODONTIA

This is one of the several orphan orders of the early Tertiary, stray groups too unlike other known forms for convenient or probable reference to any established order, of unknown ancestry, and without known descendants. The erection of several orders, each comprising only a few genera and of slight importance in the general scheme of mammalian life and history, is necessary and is already well established by usage. Each of these groups is a monument to our ignorance of many of the most basic facts of the development of the Mammalia.

It is believed that the †tillodonts were probably an independent offshoot of the general, broad insectivore group of the Mesozoic, but this is rather hypothetical. In the present classification the order is moved from second place to fifth. This places it near a similar and perhaps really related order, that of the †taeniodonts, and also removes it from the better established collocation of Insectivora, Dermoptera, Chiroptera, and Primates.

Most authorities place the early (†*Esthonyx*) and the late (†*Trogosus*, †*Tillotherium*) †tillodonts in separate families or subfamilies, and Hay (1930) recognized three families (†Esthonychidae, †Anchippodontidae, †Tillotheriidae). There is at present no justification for the latter arrangement and little for the former. Even if not exactly ancestral and descendent, the two recognizable groups are closely similar structurally and differ principally only in that the earlier forms are more primitive, as would be expected. Contrary to my former opinion, I, therefore, think that family separation much overstresses the diversity, and I prefer not to recognize subfamilies on an almost purely horizontal basis and in a group with so few known genera. †*Anchippodus* and †Anchippodontidae have clear priority as generic and family names, respectively, but their basis is very poor and dubious, and it is preferable to follow usage in recognizing the better defined names based on relatively fine material.

No extensive study of the †tillodonts has been undertaken since Cope and Marsh, although the material in hand, partly unde-

scribed, warrants revision and new, intensive investigation. The order is briefly reviewed in Simpson, 1929d, and the older literature is listed in Hay, 1902, 1930.

†TAENIODONTA

The †taeniodonts are another orphan order like the †tillodonts, although the known forms are more varied and cover a longer span. Cope's original belief in their affinities with the †tillodonts is now generally abandoned, and Matthew (1937) explicitly contradicts it, but the subject seems to me still open pending closer study of the †tillodonts. In the meantime this classification follows Matthew and other good recent authorities in maintaining †taeniodonts tentatively as a separate order of proto-insectivore origin. Wortman's thesis (see references in Simpson, 1931c, and Matthew, 1937) that the †taeniodonts were related, or ancestral, to the Xenarthra or Edentata as a whole is generally rejected. Matthew, 1937, maintains, however, the possibility of some more remote, superordinal connection. I tend to reject any relationship closer than through the generalized proto-Insectivora.[1]

Matthew, 1937, has discussed the group as a whole. This arrangement follows him except that he has four subfamilies (†Onychodectinae and †Psittacotheriinae in addition to the two here retained), three of them with only one genus in each. This seems to me to obscure a rather plain double division of the family and to overemphasize the differences between †*Onychodectes* and †*Conoryctes* and between †*Ectoganus* and †*Stylinodon*, differences in each case largely matters of progressive evolution, even though not entirely so.

The Paleocene forms were revised by Matthew, 1937, and added to by Gazin, 1941. Gazin, 1936b, also greatly improved knowledge of †*Ectoganus*. There is no recent study of †*Stylinodon*.

EDENTATA

Confined as they have always been geographically, the edentates are one of the most abundant, varied, and interesting of mammalian orders. Most classifications have separated them sharply from other mammals, some (e.g., Gervais, Thomas, Ameghino) placing them in a distinct subclass, or even maintaining that they were independently derived from reptiles and hence could hardly be considered as true mammals. This extreme view has, however, been abandoned, and now no one seriously doubts that the edentates arose from primitive Eutheria and belong in that subclass. The crucial evidence of the earliest Xenarthra and especially of the †Palaeanodonta strongly suggests that the edentates arose from proto-Insectivora, along with several other archaic orders, about the beginning of the Paleocene.

The Bruta of Linnaeus included *Elephas*, *Trichechus*, *Bradypus*, *Myrmecophaga*, and *Manis*, while the armadillos (all in *Dasypus*) were placed in his Bestiae along with pigs, insectivores, and opossums. Linnaeus cannot be said to have recognized the group Edentata in any form. Storr did make such a recognition in 1780 when he united sloths, armadillos, pangolins, and anteaters in his Mutici (a name historically antecedent to Edentata but now forgotten). The aardvark was long referred to *Myrmecophaga* and placed in the Mutici or Edentata where it was retained even after generic and family separation. The classical conception of Edentata thus includes five well-defined groups of recent animals, sloths, anteaters, armadillos, pangolins, and aardvarks. The extinct †ground sloths and †glyptodonts, when discovered, soon fell naturally into this order as two more distinct groups. Wortman proposed also adding the †Taeniodonta, and this was widely (not universally) accepted for a time but has since been generally abandoned. Most recently Matthew has added the fossil group †Palaeanodonta, which seems surely to belong here, while cumulative evidence has necessitated removing the pangolins and aardvarks, as discussed under their respective orders. Thus the present conception of the contents of the Edentata has arisen, a history summed up in this diagram:

[1] My publication was not available to Matthew, who died soon after it appeared.

Classic Contents, About 1780	Subdivision	Additions	Removals	Present Contents
(Tree) sloths	—	—	—	Tree sloths
Armadillos	—	—	—	Armadillos
Pangolins	—	—	To own order about 1904 and later	
Anteaters	Anteaters,	—	—	Anteaters
	Aardvarks (genus in 1795, family in 1821)	—	To own order about 1904 and later	
		†Ground sloths (1796)	—	†Ground sloths
		†Glyptodonts (1838)	—	†Glyptodonts
		†Taeniodonts (known 1874, added to order in 1896)	To own order in 1876, position here never fully accepted	
		†Palaeanodonts (known 1903, added to order 1904)	—	†Palaeanodonts

†PALAEANODONTA

Matthew, 1918, believed that the †Metacheiromyidae of Wortman were a primitive offshoot from the ancestry of the Xenarthra, and I accepted and substantiated this view in a still more detailed study (Simpson, 1931c). This now seems to be generally accepted and is sufficiently discussed in the two publications cited. †*Epoicotherium* and †*Xenocranium* are puzzling animals, probably aberrant †palaeanodonts, known as yet only from one skull each (Simpson, 1927c; Colbert, 1942).

XENARTHRA

Despite the very strong differences in appearance, caused by the armor of the armadillos and †glyptodonts and the peculiar habitus of the sloths, it is not now seriously questioned that the Xenarthra are related to one another and form a natural group exclusive of any other mammals. They are the nucleus of the classical group Edentata, and they include the only original members of that group still left in it, so that it would be historically correct to call them simply "Edentata" and abandon the name "Xenarthra," especially since its complement "Nomarthra" is not used here. This is, however, inconvenient, because then a name would have to be devised or resurrected for what is here called "Edentata." Moreover, "Edentata" has always meant "Xenarthra plus-" whatever other forms were supposed to belong here, and it is still used in that convenient way, even though the additional content is not what it was originally or until recently.

To an even greater extent than in other South American groups, the fossil Xenarthra have been classified in large part from very fragmentary remains. Perhaps a third of the proposed genera, at most, are well established in the sense of being reasonably well known, with both their generic distinctions and their affinities demonstrated objectively and to sufficient extent. The principal students of these fossils, notably Ameghino, Kraglievich, and Castellanos, have done a remarkably skillful and learned job in sorting out and classifying the almost endlessly varied scutes and limb fragments of ancient armadillos, †glyptodonts, and sloths, and it is no unfavorable criticism of the magnificent results of their patient toil to conclude that a really definitive taxonomic arrangement has not been achieved, and cannot be on such materials. It is, moreover, inevitable that their work has been mainly analytical, necessarily seeking fine distinctions in sorting such specimens, so that their genera are very small in scope and the whole classification finely split, with categories over-valued in comparison with the standards here urged for mammals in general. Synthesis may come later, and is to be hoped from equally competent hands.

With probable accidental omissions, I have tried to list all well-established genera, along with many that are more dubious, at least as

to rank. Without the enormously detailed knowledge requisite for thorough revision, I have ventured to reduce few genera to subgeneric rank, although I do not doubt that many will become subgenera when a more complete synthetic balance is eventually achieved. Probably most of the listed generic names, if not all, belong to real groups, whether or not they will always be considered genera. On the other hand, many proposed genera are here omitted because (unless, again, well-established names have been accidentally overlooked in this large and difficult literature) they seem at present too dubious and too little known to have much value or any interest except, perhaps, to the most extreme specialist. Many of these, too, will probably prove to be real and definable groups, genera in some cases, when they are better known, and omission here is not in itself a denial of possible validity but only of present usefulness to the general student. These remarks apply, indeed, to every part of the present classification, but they are emphasized as regards the Xenarthra because of my admiration for the South American specialists on this group and because the situation is here exaggerated.

PILOSA

The †ground sloths have been classified in a general way according to the views of Kraglievich with some reduction in rank of various groups, in accordance with the greater scope and balance of this classification. Certain of Kraglievich's views, even among those here retained (e.g., the recognition and contents of the †Ortotheriinae), are open to grave doubts, but he is the only recent authority who has gone over most of this superfamily in recent years with a broad knowledge of literature and of specimens—this without prejudice to Scott, Stock, and others who have done as much or more work but concentrated on a lesser part of the superfamily.

The †Nothrotheriinae, as here classified, include the most primitive known members of the superfamily, and some come close to, or actually are, the ancestors of other subfamilies or even families. In addition to this there is a group of relatively conservative phyla surviving into the Pleistocene, so that this subfamily is in part horizontal and in part vertical and is something of a scrap basket for the less specialized †ground sloths. Stock, 1925, places the whole family †Megalonychidae as a subfamily of †Megatheriidae, a valid arrangement and one emphasizing the real peculiarity of the †Mylodontidae but contrary to the consensus and also embarrassing to the taxonomist because of the enormous variety of the genera that would then have to be arranged in a single subfamily.

The †Mylodontidae are highly polyphyletic, and some subfamily division is desirable, but the efforts so far made in this direction seem either to involve innumerable hypothetical collocations or to be little more than the raising of all clearly distinct and well-known genera to subfamily rank. The generic names for the three most discussed genera of this family have been subject to great confusion. Kraglievich maintains that †*Mylodon* and †*Glossotherium* have been reversed in application in most recent work on South American sloths and that the North American form usually called †*Mylodon* is really a distinct genus, for which †*Paramylodon* (although intended by its author to exclude the more characteristic members of this North American group) is the valid name under the Rules. He is regretfully followed in these apparently necessary, radical departures from long-established usage.

Many students exclude the †Planopsinae from the †Megatheriidae, but Scott has shown that a real and perhaps a close relationship does exist, and this is most conveniently expressed as is done here. It may even prove with better knowledge that the subfamily distinction is purely horizontal and that a more phyletic division can be made, but this is not now possible.

The classification of the anteaters and tree sloths is simple and presents no novelties or difficulties. Their right to any special connection with each other and hence the validity of the two-fold division of the Xenarthra have been denied (e.g., by Gill) but are based on much anatomical evidence and are almost universally accepted. The palaeontology of the anteaters and tree sloths is almost a blank, probably because they have always been essentially tropical animals, and the tropical Tertiary faunas of South America

are very little known. It is also possible that neither group is extremely ancient and that both were derived from primitive †ground sloths.

CINGULATA

The name Loricata for the armored edentates is so widely used that the long-prior, strictly synonymous Cingulata would be passed over were it not that Loricata is preoccupied as well as antedated. Loricata was first (by Merrem in 1820) applied to crocodiles and has recently been revived and is now in use in that sense. There is, then, no way to avoid confusion except for mammalogists to resign the name to the herpetologists. It is fortunate that in so doing they can revive an older name, strictly applicable, and of worthy antecedents.[1]

DASYPODOIDEA

The classification of the recent armadillos is based on the able review by Yepes (1928), with some contraction in values. His Cabassoinae and Priodontinae are united, in part to reduce the number of monotypic groups but principally because their type genera are clearly and rather closely related, more nearly so than are, for instance, some of the genera of Euphractini. The Chlamyphorinae are retained, but the other recent subfamilies of Yepes, along with some extinct groups often placed as subfamilies, are reduced to tribal rank. This is believed to represent the finer degrees of known relationships more exactly and to balance better with the rest of the order than do most previous arrangements. Tribes are here introduced not only for this finer discrimination but also in order to break up the very numerous genera that seem best placed in the Dasypodinae, a remarkably differentiated group with relatively little important morphologic diversity.

The now relatively well-known genus †*Utaetus* could be ancestral to almost all other armadillos and is placed in a separate tribe (along with some very poorly known genera) because it is important and distinctive morphologically and cannot be shown to lie in one of the more specialized phyla. After the Eocene, the central and most abundant group was the Euphractini, and later offshoots may have arisen from this varied and relatively unprogressive nucleus. Most early armadillos are known only from isolated scutes, the affinities of which cannot be well established, and a number of these poorly known, wholly dubious, and unimportant genera are omitted.

Scleropleura, sometimes given subfamily separation (e.g., by Osborn), is now believed (after Winge) simply to have been based on a pathological *Euphractus*.

The application of the basic, Linnaean name *Dasypus* is unfortunately subject to confusion. Many writers, probably the majority, have used this name for the quirquinchos, which would be desirable, both to follow usage and because this group of species is the most central and generalized among living forms. In this case the correct name for the nine-banded armadillos would be *Tatu* and so they have widely been called (by me among many others). Oldfield Thomas, however, attempted to fix *Dasypus* as the name for the nine-banded armadillos, making *Euphractus* valid for the quirquinchos. This is apparently gaining in authoritative usage (although it still appears to be open to debate) and is here reluctantly adopted.

The nine-banded armadillos, here classified as Dasypodini, are often held to occupy a rather isolated position, and the five other tribes here united under Dasypodinae might be placed in a separate subfamily Euphractinae, but this would probably overweight the distinction. In any case there seems to be little reason to make them separate families, sometimes done (e.g., Scott, 1903, but subsequently abandoned) but not generally acceptable.

The scheme of Yepes, thus modified, has been expanded and further adapted to include the fossil forms in accordance with numerous studies, among them those of Ameghino, Scott, Castellanos, and Bordas, and my own (mostly unpublished) observations on all the earlier and some later forms.

Various reports of the discovery of fossil armadillos in the Eastern Hemisphere have so far proved to be erroneous.

[1] This change was suggested by Gill in 1910, but apparently has not been adopted by any other author until now.

†GLYPTODONTOIDEA
†GLYPTODONTIDAE

The prior name for this family is †Hoplophoridae, but this is a case where priority in family names is best disregarded. Usage and familiarity are overwhelmingly in favor of †Glyptodontidae. Many students deny the validity of the name †*Hoplophorus* (and hence of †Hoplophoridae) and decline to use it (although it is certainly valid under the International Rules), whereas all accept †*Glyptodon*. †Glyptodontidae is the oldest family name except for †Hoplophoridae (and another name not based on a generic name and hence not available).

The classification of the later †glyptodonts, or most of them, in three major groups has been long established and is not seriously questioned. These are commonly subfamilies in general classifications and families to those concerned only with them—the usual situation in taxonomy. In a broad view of the edentates, and *a fortiori* of the Mammalia, they seem not to warrant family rank. These lines have not been clearly traced back through the ill-known later Miocene transition period, so that the fine earlier Miocene (Santa Cruz) specimens are of somewhat doubtful phyletic positions. Ameghino placed them in a separate family, †Propalaeohoplophoridae, a subfamily in this classification, a horizontal group with primitive allies or ancestors of several or all of the Pliocene-Pleistocene phyla. Scott classifies them in the central subfamily (or family) †Glyptodontinae, except for the more poorly known †*Metopotoxus* which he tentatively places in or near the †Doedicurinae. Probably these forms do show the beginning of later subdivision, but the connections are now almost purely theoretical and Ameghino's arrangement still seems most practical. In any case there would be no good basis for calling these animals †Glyptodontinae rather than †Hoplophorinae, because the typical †Glyptodontinae are the last to appear and in some respects are the most specialized of all the †glyptodont groups.

Later work on †glyptodont phylogeny has been mostly by Castellanos and this has been followed in a general way, although scaled differently and expressed in slightly different terms for uniformity. The tribal subdivision of the †Hoplophorinae would be convenient and is suggested by his work, but at present it would be surely valid for only a few genera and would leave most *incertae sedis* or classified on grounds more theoretical than subjective. The †Glyptodontinae seem to have arisen relatively late, probably from †Hoplophorinae, and the ill-defined †*Paraglyptodon* and well-defined †*Glyptotherium* are only doubtfully placed here and could about equally well be called †Hoplophorinae. Castellanos, indeed, considers †*Glyptotherium* as independently derived from †*Propalaeohoplophorus*, an opinion that might be correct but that lacks objective evidence. It seems at present more conservative and better warranted to place the genus with its collaterally related approximate contemporaries.

The scanty remains referred (many of them doubtfully) to †*Glyptatelus* show little more than that †glyptodonts of some sort were present in the Musters and Deseado formations.[1] †*Palaeopeltis*, made the type of a separate family by Ameghino, is very poorly known, and there is not even assurance that it was a †glyptodont, although it may have been. It occurs surely in the Deseado, doubtfully in the Musters, and not in the Casamayor, rather than being a Casamayor and Musters genus as sometimes stated.

Important recent or summarizing papers on edentates are: for fossil North American forms, Holmes and Simpson, 1931; Matthew, 1918; Simpson, 1927c, 1931c; Stock, 1925; for fossil South American forms, Bordas, 1933, 1936, 1938; Castellanos, 1931, 1937, 1939–1940; Kraglievich, 1923, 1928b; Rovereto, 1914; Scott, 1903–1904a; for recent forms and the Edentata in general, Flower, 1882; Lane, 1910; Pocock, 1924; Schulthess, 1920; Winge, 1915; Yepes, 1928.

PHOLIDOTA

A group to include the pangolins but to exclude other members of the classical Edentata has been suggested and named several times, among the names used being:

[1] Contrary to some authors, they were certainly present in the Musters, and contrary to others, they are as yet quite unknown in the Casamayor.

Squamata Huxley, 1872, *nec* Oppel, 1811; Pholidota Weber, 1904, *nec* Merrem, 1820; Lepidota Lane, 1910, *nec* Vogt, 1851; Squamigera Gill, 1910; Nomarthra Gill, 1884, emend. Gill, 1910. The first three names were preoccupied. The fourth was only mentioned in passing, was not really intended for use, and was abandoned, in the same publication, in favor of Nomarthra. This last was originally proposed and has been in common use to unite both pangolins and aardvarks, so that the proposal to exclude aardvarks was a very essential emendation and one never generally adopted and not now understood under this name by zoologists. The name Effodientia Illiger, 1811, originally the classical Edentata with sloths excluded, was also revived (by Lydekker, 1896, and adopted by a few later taxonomists) in the radically emended sense of pangolins plus aardvarks, hence a synonym of Nomarthra Gill, 1884, which it cannot properly be said to antedate since its emendation to anything like the same conception was later, and in any case it could not well be restricted to the pangolins.

Thus in the strictest view of nomenclature there is no proper name available for this group, despite the many it has received. Instead of proposing a new name, Pholidota is used regardless of its preoccupation. The only prior name is itself preoccupied, is not in current use in this sense, and is in current use in a very different sense. Pholidota is in current use in this sense, is the only name now generally so used, as applied to mammals has always had exactly this sense, and is not now commonly used in its prior application to reptiles.

The pangolins were long placed in the same order with the South American edentates (Xenarthra) and the aardvarks, but with increasing knowledge they were increasingly isolated until Weber (in 1904) made them a separate order, although still retaining them in a Superorder Edentata. This arrangement on varying scales has since been common and is now favored by the consensus. It was adopted (in slightly different form) in my previous classification but is now abandoned. It cannot be denied that the Xenarthra and the Pholidota may have had a common ancestry, but this has not been demonstrated as a fact or even as a real probability, and if it be true, then the common ancestry must have been exceedingly remote (probably before the edentates were differentiated clearly from the proto-insectivores). Thus ordinal separation is fully justified, and superordinal (or ordinal) union is at least as likely to be wrong as right.

This question can be solved only by fossils, which are almost unknown. There are fossil pangolins in the Asiatic Pleistocene, but they are essentially modern and cast no light on origins. Remains of apparent manids have been found at several locations in the Oligocene and Miocene of Europe. The known specimens are most fragmentary and isolated, and their nomenclature cannot be taken very seriously at present, but the latest study by Helbing, 1938, in conjunction with earlier work, leaves little doubt that Pholidota do occur in the European mid-Tertiary. (More doubtful is the description by Kormos of a supposed manid based on a single claw from the European Pleistocene.) Although it has been claimed that the Tertiary remains substantiate the affinities of Pholidota and Xenarthra, I think their evidence entirely inadequate to support that view. Matthew, 1918, thought that the †palaeanodonts (see under Edentata) also tended to support a remote connection of the orders, but this evidence also seems to me equivocal and insufficient (Simpson, 1931c).

The supposed relationship between *Manis* and *Orycteropus*, signalized by the name Nomarthra, is now so generally rejected that no discussion of the point is necessary here.

Seven well-defined species of recent manids are known. Pocock, 1924, divided these into three subfamilies and six genera. These groups are real, but all seven species are actually very much alike and Pocock's arrangement can be considered only an extreme instance of unnecessary and inconvenient taxonomic inflation, giving generic rank to each of the good species of one genus, as Hatt, 1934, and others have concluded. Beside these studies by Pocock and Hatt, Weber's classic monograph, 1894, and Frechkop's more recent study of living manids, 1931, may be mentioned.

LAGOMORPHA

Linnaeus and other early authors did not clearly separate the hares and rabbits from the rodents (or other rodents). Illiger in 1811 separated them as one of eight families[1] of the "Prensiculantia" (=Rodentia) under the name Duplicidentata. The group was raised to subordinal rank, under various names, by Waterhouse, 1842, Gervais, 1849, Brandt, 1855, and most later authors. At first one of several suborders (three in Waterhouse, four in Brandt, etc.), the lagomorph group eventually (Lilljeborg, 1866, and virtually all later taxonomists) came to be contrasted with all other rodents, so that the classical Rodentia or Glires were divided into lagomorphs on one hand and all other forms on the other.

From this contrast of two quite distinct sorts of "rodents" there arose the suspicion, soon becoming a conviction for many specialists, that the origins of the two groups were so different as to make their reference to a single order incorrect. Although this idea dates definitely from Tullberg, 1899, and more vaguely from earlier glirologists, it was first given formal taxonomic expression by Gidley in 1912, who proposed an Order Lagomorpha. The emendation was early approved by American mammalogists and is now virtually universal among them. European students have been slower to adopt the ordinal separation, but they appear now to be coming to this point of view.

Subsequent discoveries have supported Gidley even more than he can have anticipated. Both lagomorphs and rodents, *sensu stricto*, are now known as rarities from the late Paleocene and in some abundance from the Eocene. The groups were then much more primitive than are any of their later or living members, but they were already decisively distinct, and the earliest lagomorphs and rodents are not noticeably more similar to each other than are later forms except as both have more characters prototypal for all placentals. These facts are consistent only with phyletic separation so remote or ordinal ancestry so different as fully to justify the recognition of a distinct order for the lagomorphs.

[1] Illiger's families, of very unequal value, are often suborders and sometimes even orders of modern classification.

The prior name for this group is Duplicidentata (Illiger, 1811), but Gidley called the order Lagomorpha (after Brandt, 1855), and this has come into general use. Duplicidentata is perhaps rejected in this sense because it so strongly suggests the discarded dichotomy of Rodentia into Duplicidentata and Simplicidentata, although the former name obviously was not originally meant to contrast with the latter, being 55 years older.

It is still a moot point whether the Lagomorpha and Rodentia should be placed in a superorder or cohort Glires. Increasing evidence of their distinctness has naturally given many or most students the feeling that they have nothing at all to do with each other aside from being eutherian mammals (see, e.g., Wood, 1940). Their union on any lower level, once accepted as an "obvious" fact, is now only a hypothesis without much evidence, perhaps with no really clear evidence, although the resemblances formerly used to unite them were not, after all, imaginary (see, e.g., Gregory, 1910). The frankly hypothetical union in one cohort is yet warranted on that basis. It has practical and pedagogical advantages and, I think, no disadvantages when accompanied by a statement that it is permitted by our ignorance rather than sustained by our knowledge.

The origin of the lagomorphs, or of the Cohort Glires if this be accepted, is entirely unknown. Despite some earlier theories of deviation from marsupials, or even direct from reptiles, there is now no doubt that they are Eutheria and so derivable from the postulated proto-insectivoran ancestry of the whole infraclass, but this is no more than to repeat that they are Eutheria. Theories of relationship to particular later Eutheria, for instance, the Eocene artiodactyl †caenotheres, are quite untenable at present.

Division of the living lagomorphs into two families is universal, and most students now recognize a total of 10 living genera, as in this classification, although of course some splitters give generic rank to various other species groups. The Ochotonidae are in some respects more primitive than the Leporidae, but the palaeontological evidence does not support the hypothesis that the ochotonids are older.

The late Paleocene Mongolian †*Eurymylus*

now seems to be a lagomorph, but one so primitive that it is nearly prototypal for both Ochotonidae and Leporidae and morphologically quite different from either (see Wood, 1942). Early and middle Eocene forms are not known, and the late Eocene and subsequent fossils seem all to fall properly into one or the other of the living families. Some poorly known extinct genera have been of doubtful family reference, but it seems possible to place these as ochotonids or leporids when they are known in more detail. For instance, †*Desmatolagus* was for some time doubtfully referred to the Ochotonidae or considered a synthetic intermediate, but Burke later (1936) believed it to be definitely, although somewhat aberrantly, leporid. The same doubt exists regarding †*Oreolagus* and †*Amphilagus*, and this group of genera does to some extent bridge the gap between the families.

Fossil leporids are very abundant in many deposits, and the known extinct members of the family are already more varied than the surviving forms and are constantly increasing in number. The deciphering of their phyletic history is, however, only begun. Dice, 1929, divided the Leporidae into Palaeolaginae, a broadly ancestral and conservative group with three surviving relict genera, †Archaeolaginae, an extinct offshoot, and Leporinae, a late, progressive group including the widespread and typical living genera. Kormos, Schreuder, Wood, and others have considered the †Archaeolaginae as insufficiently distinctive to be separated from Palaeolaginae but have retained a dual division into Palaeolaginae and Leporinae. On this excellent authority, that arrangement is used in the present classification. On the other hand an equally competent student, Burke, has recently (1941) suggested an arrangement that would have subfamilies Mytonolaginae, Palaeolaginae, Megalaginae, Desmatolaginae, Leporinae, and necessarily several others for later Tertiary and Recent forms, which he does not discuss. This able work makes a necessary beginning of phyletic analysis, but its formal use seems impractical at present since it provides no general view of the family and proposes the use of nearly monotypic subfamilies split both vertically and horizontally.

Modern classification of the recent Lagomorpha dates from Lyon, 1903, and intensive study of the fossil forms might be said to begin with Forsyth Major, 1899. Among the increasingly numerous recent papers on fossil lagomorphs there may be noted Burke, 1934b, 1936, 1941; Dice, 1929; Hibbard, 1939; Schreuder, 1936; Wilson, 1937b; Wood, 1940, 1942.

RODENTIA

Every order of mammals is to some extent mysterious and involves taxonomic problems that cannot now be satisfactorily settled, but no other can compare with the Rodentia in difficulty. Living rodents are believed to be as abundant individually and in variety as all other mammals put together. Most of them are small, many are obscure and rare, and local forms are difficult to obtain. Their relationships are involved in an intricate web of convergence, divergence, parallelism, and other taxonomic pitfalls. Their great numbers, their marked mutability and variability, their spread over almost every conceivable environment, their remarkable adaptability, the shortness of their generations, their usual great fertility with overpopulation and severe mortality, and other factors give them the possibility of exceptionally rapid evolution and of phyletic connections remarkably difficult to retrace.

Problems of this sort can be solved finally only by palaeontology, and here knowledge of rodents has been in a peculiarly unsatisfactory condition. Although more than half of living mammals are rodents and although something like this proportion must have prevailed throughout at least the latter half of the Tertiary, less than one-tenth of known Tertiary mammals are rodents. Discovery of them thus lags behind that of most other orders, and the same has been true of the study of the specimens that are known. The inherent difficulty of the subject, its demand for special knowledge and techniques, and its relatively unsensational and, to many palaeontologists, unattractive nature have discouraged and retarded research on fossil rodents. Some earlier progress was made by palaeontologists like Schlosser and Matthew and by zoologists like Forsyth Major and Winge who happened to run into fossil ro-

dents in the course of their more general studies. Recently the whole situation has begun to change radically with the rise of a number of able specialists. Some, like Hinton, apply profound knowledge of recent forms to the interpretation of allied fossils, and others, like Schaub, make a specialty of fossil rodents. In America there is now a new generation of fossil rodent specialists including Wood, Wilson, Burke, and others. These men and others no less able are rapidly transforming the whole subject, so that no part of mammalian classification is more likely to go rapidly and radically out of date than the arrangement of the rodents.[1]

Under these conditions, the classic taxonomy of rodents, based entirely on recent forms, will be profoundly modified. In fact this taxonomy has never been very satisfactory and has been less stable than for most living mammals. Really first-rate summaries of all available knowledge have been exceptional, and it is fair to say that the most recent was that of Tullberg, more than 40 years ago (1899). Of the more important reviews of the whole order since that date, that of Miller and Gidley, 1918, was strikingly original but inadequately supported and based on premises that are usually rejected; that of Winge, 1924, is almost like his classification of 1887 and may really be dated before Tullberg; that of Weber, 1928, is more a compilation than the result of first-hand study (of course the same is true of the present attempt); and that of Ellerman, 1940–1941, despite its great and many merits, is, in my opinion, rather a retrogression than an advance in comparison with Tullberg and others as regards supergeneric groupings. Some particular points about these several outstanding revisions will be more closely examined in the subsequent discussion.

Aside from the lagomorphs, already discussed, the rodents are certainly all related ordinally, and the order is exceptionally clear cut. There is not, even among fossils, any question as to whether a given animal is or is not a rodent, however doubtful its position in the order may be. A few other gnawing forms, like the primate *Daubentonia*, have been placed in the Rodentia, but it can confidently be said that all these are now sorted out.

The classic basic subdivision of the Rodentia into three major groups (four with the lagomorphs) appeared as early as De Blainville. In his classification of 1834, the "grimpeurs," "fouisseurs," and "marcheurs" are, in rudimentary and vague forms, adumbrations of the sciuromorphs, myomorphs, and hystricomorphs, respectively. The three suborders reached essentially definitive form in Brandt, 1855, and have been retained by most authors ever since. There is a growing feeling now that they should be abandoned, or at least supplemented by additional suborders. Such a rearrangement may be expected eventually, but Brandt's suborders have not yet outlived their usefulness. They are certainly real groups and cannot now be replaced by anything better. There are some important divisions of uncertain position with respect to these suborders, notably the groups here called Aplodontoidea, Anomaluroidea, Dipodoidea, and Bathyergoidea, but uncertainty about these rather small groups does not mean that the three-fold division of the great majority of rodents is invalid.

Some of the more noteworthy departures from the triple subordinal arrangement may be mentioned. Thomas (1897) made five primary divisions, adding "Anomaluri" and "Aplodontiae." He did not consider these "as of the same rank as Sciuromorpha and the others," but so places them in his formal list. Tullberg, 1899, made a double dichotomy as follows:

- Simplicidentati
  - Hystricognathi
    - Bathyergomorphi
    - Hystricomorphi
  - Sciurognathi
    - Myomorphi
    - Sciuromorphi

This does not contradict the validity of the triple division but only rearranges the hierarchic ranks slightly, since Tullberg's Hystricognathi, Myomorphi, and Sciuromorphi are the Hystricomorpha, Myomorpha, and Sciuromorpha of other authors.

Miller and Gidley, 1918, abandoned the designation "suborder" but retained the con-

[1] This sentence was written before our entry into the war. Since then all these specialists have had to discontinue their work. It is not necessary to repeat throughout this work that this is also true of many other orders. The interruption is surely temporary.

ception under the name "superfamily," of which they recognized five:

Sciuroidae	[more or less the classical Sciuromorpha]
Muroidae	[approximately Myomorpha]
Dipodoidae	
Bathyergoidae	[Tullberg's Bathyergomorphi]
Hystricoidae	[approximately Hystricomorpha]

Except for the Dipodoidae, this is virtually Tullberg's four-fold division, and with respect to these major subdivisions it is not a radical departure from usual systems, but the Dipodoidae included the aplodontoids, anomaluroids, dipodoids, and several lesser groups (a thoroughly artificial assemblage, beyond any reasonable doubt, and in no way an advance over the method of distributing these dubious groups among the sciuromorphs, myomorphs, and hystricomorphs). The classification of Miller and Gidley in general was based on *a priori* and in part very improbable ideas as to the necessary evolutionary sequences of a few key characters, and it resulted, on all levels, in some separations and some collocations that can hardly correspond with real phylogenetic relationships.

Winge (1924, nearly like his work of 1887) abandoned both the name and concept suborder and divided the rodents into eight families, approximately of the scope of superfamilies in most other classifications:

Haplodontidae	[=Aplodontoidea]
Anomaluridae	[=Anomaluroidea]
Dipodidae	[=†Eomyidae + Dipodidae + Spalacidae]
Myoxidae	[=Gliroidea]
Muridae	[=Myomorpha, with dubious groups removed]
Hystricidae	[=Hystricomorpha]
Sciuridae	[=Sciuroidea+Castoroidea]
Saccomyidae	[=Geomyoidea]

Paraphrasing Ellerman, it may be said that Winge's theory is brilliant but his details are often wrong and his nomenclature is deplorable, and it may be added that, as in many brilliant productions, when the theory did go astray it did so resoundingly, even absurdly. Surely no weaker word is applicable to Winge's derivation of the aplodontoids from the lagomorphs or of the murids from the dipodids, to mention only two completely impossible contentions of this eccentric genius.

Ellerman (1940–1941) resurrected Tullberg's double dichotomy, with exactly the same groups included in each "subtribus" of Tullberg ("Series" of Ellerman), of which there are four. Ellerman calls the three classical suborders unnatural waste-paper baskets, but Tullberg's, and hence Ellerman's, classification differs from the classic arrangement in three suborders only by giving a little greater emphasis to the differences between typical hystricomorphs and the bathyergoids and a little less to those between sciuromorphs and myomorphs. It still recognizes the classical groups as natural. Even the family arrangement of Ellerman is like Tullberg's except that Ellerman consistently uses superfamilies and has considerably rearranged the muroids and hystricoids, a rearrangement that seems to me less natural than Tullberg's system.

Ellerman's monumental work appeared after the present classification was in manuscript, but it has been extensively used in revision and it is proper to acknowledge here that Ellerman's monograph, as regards the characters of genera particularly, has been invaluable, has prevented some oversights, and has suggested several modifications. It must, however, be confessed that Ellerman's work is a disappointment in some other respects. It is a magnificent and, it appears, highly accurate and practical *key* to the genera of rodents, but it makes little contribution to the search for a natural *classification* of rodents. Ellerman classifies characters, not animals. He so entirely lacks the historical and phylogenetic point of view that his work might have been written by an eighteenth century naturalist, given equally good collections. For him a given character has fixed taxonomic value, the same wherever this character occurs (e.g., vol. 1, p. 8, if a character is not diagnostic of superfamilies in insectivores, it cannot be in rodents); the acquisition of a given diagnostic character automatically places an animal in a given group regardless of its history or its other characters (e.g., vol. 1, p. 8, if *Oryzorictes*, a highly specialized tenrecoid insectivore, had taken to gnawing it would automatically have become a member of the Rodentia); similarly the lack of one selected character absolutely

excludes an animal from a given group, regardless of the balance of its resemblance or of the lineage of its ancestors (e.g., vol. 1, p. 97, because the angular process is not distorted outwards in living caviids, they cannot be hystricoids); and, finally, genera recognizable mainly by characters not readily adaptable for use in a general key are not to be distinguished, however distinct they may be genetically (e.g., vol. 1, p. ix, it is wiser not to pay too much attention to names based solely on characters of the skeleton, soft parts, or baculum). As a practical aid for quick identification of specimens in this very difficult group, Ellerman's contribution is magnificent and beyond praise, but his contribution to taxonomy in a broader, more modern sense is less and requires careful scrutiny.

These and other major rodent classifications may be roughly divided into three schools:

1. The explosive (example Winge) with little or no effort at higher groupings.

2. The waste basket (example Miller and Gidley) with one subdivision (in Miller and Gidley the Dipodoidae) comprising a number of groups improbably related to each other and of uncertain position.

3. The orthodox (example Tullberg) recognizing three or four well-established major groups and tentatively distributing the doubtful lesser groups among these, with appropriate caution as to probability.

Perhaps a fourth school, the eclectic, might be added for classifications like that of A. E. Wood (which covers mainly or only North American rodents), which take an orthodox arrangement as a basis, add a slight waste-basket element, and have many left-overs that are exploded into small bits *incertae sedis*. Such an attempt to incorporate the best features of all schools has much of value, and it would be possible to argue that it most truly represents the actual position of current research, but it also partakes of the weaknesses of all schools without fully utilizing the advantages of any one.

The present classification belongs to the third, orthodox, type. It stems from Tullberg although, in intention at least, it takes into account the very extensive work and discovery of the twentieth century and hence does not, at first sight, seem to follow Tullberg closely. The sciuromorphs, myomorphs, and hystricomorphs still seem to me to be the fundamental natural units of the order, even though each must still carry groups *incertae sedis* as an undesirable appendix.

The Sciuromorpha, as here understood, include the most primitive rodents, structurally ancestral to all others, and also various, separate, later lines most visibly derivable from the known early forms and on the whole most conservative of the basic characters of the latter. The Myomorpha and Hystricomorpha represent two main types of more fundamental modification, each arising quite separately from the other, from early sciuromorphs.

SCIUROMORPHA

APLODONTOIDEA

The Aplodontoidea of this classification have been generally recognized as related to one another, and the existence and contents of the group do not now seem to be seriously questioned except for a few details. This is the most primitive group of rodents. It includes the oldest known rodent (a species of †*Paramys* recently discovered in the Upper Paleocene by Jepsen), had its principal deployment in the earlier Tertiary, and includes only one living genus, *Aplodontia*. This group is essentially that called Protrogomorpha by Wood, 1937, reviving a name given by Zittel in 1893 but in a very different sense since Wood excludes or considers as doubtful the majority of the rodents placed here by Zittel (those placed in my Anomaluroidea, plus the Muscardinidae and Dipodidae). Wood makes clear that the group is a natural unit and that it is distinct from most of the later and recent sciuromorphs, but it is still the consensus that the group is really related to these typical sciuromorphs if not actually involved in the ancestry of some of them. Subordinal separation thus appears to be too violent a reaction against the loose and inaccurate phylogenies of the last generation and to obscure a very probable and surely convenient collocation.

The name †Ischyromyidae is used here in the broad way favored by Matthew and many others. Miller and Gidley made families for each division here called a subfamily and even separated some of them widely as if they

were not related aside from being rodents. This separation has not been accepted by the best-informed later students, but some of them, notably Wood and Burke, do accept family rank for these lesser groups. This is, of course, merely a matter of scale and of no fundamental importance. Wilson has pointed out that the actual diversity represented does not exceed that of many families, and the number of valid genera is not so large as to require undue expansion for cataloguing purposes. It seems to be a fact that all the groups here included in the †Ischyromyidae are closely related in the sense of having diverged little from a common ancestry. They are diverging in various different lines, but those lines, at least, that do not lead definitely to later and more distinctive phyla can well be represented as subfamilies.

McGrew, 1941b, has recently shown that the ancestry of *Aplodontia* can be traced back in a fairly complete structural sequence to late Eocene forms that rather closely resembled still earlier †ischyromyids. Despite some inevitable specialization, the sewellel can, then, be considered a living representative of the most primitive rodent stock. According to the same authority, the peculiarly aberrant, quickly specialized, and soon extinct †mylagaulids probably arose from the early aplodontids. A relationship to the †ischyromyids, whether direct or, as in McGrew's theory, indirect has been generally recognized. Wood, 1937, is followed in removing †*Protoptychus* from the Geomyidae, where it is found in most classifications, and placing it nearer the †Ischyromyidae; also in uniting †Eomyidae and †Adjidaumidae and considering them another abortive offshoot of the early sciuromorphs.

Besides papers already cited, see Wilson, 1937a, 1938b, 1940a, b; Burke, 1934a; Matthew, 1910b; Stock, 1935; Simpson, 1941c.

SCIUROIDEA

Two schools of sciurid classification exist, one using the neomammalogists' usual criteria of pelage, skull, and (in a minor way) teeth, the other relying primarily on the male reproductive organs. The results are markedly different in several respects but are not wholly irreconcilable. The now fairly numerous studies of the reproductive tract (see, e.g., Mossman, Lawlah, and Bradley, 1932, and their bibliography) are valuable for the taxonomist in giving him a good additional criterion for distinguishing convergence from affinity, although it can hardly be claimed that a classification based only on these characters would be adequate or certain.

The present arrangement follows Pocock (1923b; see also Thomas, 1909) rather closely as far as he goes. His divisions are here scaled down in rank, since the squirrels in general do not seem to me to be of more than family rank, and this is apparently the consensus. Thus his families are my subfamilies and his subfamilies my tribes. I have moved the Marmotini nearer the Sciurini because these two are surely very closely related and perhaps should not be separated even as tribes. J. A. Allen, 1915, gave a revision of New World tree squirrels in which he recognized 17 genera. More recently, 1938, Howell has reduced six of these to subgeneric or still lower rank, and if the same criteria are extended outside the field of Howell's revision, the list is reduced to only five full genera, as in my arrangement.[1] I have also followed Howell's very able and reasonable revision in the inclusive use of *Citellus*.

The genera of Old World sciurids have also been rather, but less, finely split by Thomas and by Pocock. Regarding the groups given full generic rank, I have generally followed Ellerman. The genera of flying squirrels still seem somewhat too narrow, but I do not know them well, and I find no authority for reducing them to larger but still valid units.

Differences between the "orthodox" method and the "reproductive system" method of classification of Sciuridae are especially noticeable on two points. "Orthodox" students (e.g., Thomas, Miller and Gidley)

[1] On Allen's attitude toward genera and lesser groups, see page 231 of the present work. I quote Howell, 1938, with greater approval: "The same tendency to give generic rank to practically every recognizable group is more or less prevalent today among workers in other branches of zoology. Such a course results in our so-called genera becoming little more than specific groups. The purpose of systematic nomenclature should be to show not only that there are *differences* between various forms but also that there are *resemblances* that indicate relationship. Giving a generic name to every recognizable group emphasizes the difference between related groups but fails entirely to show their similarities."

recognize a subfamily Nannosciurinae for *Nannosciurus*, *Myosciurus*, and *Sciurillus*. Ellerman accepts the grouping (in a different form), but his evaluation of criteria is almost certain to confuse convergence and relationship. Pocock claims in a way convincing to me that these are independent forms in three widely separated areas, convergent in small size and related habitus characters but not especially related. Orthodox students place *Tamiasciurus* as, at most, a subgenus of *Sciurus*. Pocock showed that its reproductive system is wholly unique and made a separate subfamily for it. This was confirmed by Mossman, Lawlah, and Bradley who incline to remove it from the Sciuridae altogether (but they are not taxonomists and this is surely extreme). The distinction is here tentatively given tribal value.

Fossil squirrels have often been reported, but they have not recently been revised or studied in detail, and many of the identifications seem highly uncertain. Probably some records do not really belong in this family or superfamily. *Sciurus* is reported from the Miocene onwards in both hemispheres, but these references, although doubtless correct as to family, must be assumed to be using the genus *sensu latissimo*. The fossil evidence so far gathered does not at all assist in our understanding the divergence of the innumerable living species or in classifying these. Not much more can be said than that true sciurids did appear in the Miocene.[1]

Incidentally, the impossibility of recognizing some apparently natural groups of sciurids (e.g., the Tamiasciurini) except by the reproductive tract shows again that some problems of phylogeny and taxonomy can never be solved by fossils.[2]

[1] †*Diplolophus* Troxell, 1923, of the Middle Oligocene of North America, not classified by its describer, was placed by Hay in the Sciuridae, where it obviously does not belong. Wood, 1937, indicates that it is *incertae sedis*, with some remote chance that it is a geomyoid.

[2] But these permanently insoluble problems are relatively unimportant. Abundant fossils properly studied should not necessarily lead to belief in a non-existent relationship or miss an existent one. They can be confusing or inadequate only as to whether a relationship is more or less distant. *Tamiasciurus*, for instance, is surely related to *Sciurus*, and failure to distinguish them as fossils would not be an error in kind but only in degree. Moreover, bacula are preservable as fossils, so not all these problems are theoretically insoluble.

GEOMYOIDEA

The geomyoids are a purely American group, appearing about as early as any recent group of North American rodents, and now widespread and well differentiated on this continent. There is no serious question as to the collocation of the geomyids and heteromyids or as to their being placed in the Sciuromorpha.

The recent geomyids were revised by Merriam, 1895, and their classification has not since been substantially changed. The few fossil forms were recently discussed by Wilson, 1936, and by Wood, 1936b. Wood, 1935, 1936a, 1937, has revised the Heteromyidae. His arrangement is here followed and his discussions are so full that further comment is unnecessary.

CASTOROIDEA

The Castoridae are arranged according to the recent revision by Stirton, 1935, with some generalization. The principal difference is the division into two subfamilies, recognized as groups by Stirton but not given subfamily rank pending further revision of European fossils. It is, of course, to be expected that further study will change this (or any other arrangement), but these two groups are already widely recognized not merely as subfamilies but as distinct families and their separation is in accord with Stirton's own conclusions as to phylogeny. Their formal designation is, therefore, demanded by current evidence and usage, whatever the future may bring. Stirton has clearly shown that the usual assignment of family rank to these groups is unjustified, and that the separation of a family †Chalicomyidae (as in Miller and Gidley, 1918, and in several later classifications, including mine of 1931a) is still less warranted.

†*Eutypomys*, although well known, is an isolated form of doubtful affinities. Wood, 1937, has recently studied it, and he follows the original describer, Matthew, in tentatively placing it near the beavers, an arrangement here adopted.

The recent members of the family certainly belong in a single genus and present no taxonomic problem on this level. Derivation of the beavers from the same root as the early squirrels seems to be beyond serious doubt.

ANOMALUROIDEA

The various groups here questionably united form probably the most dubious considerable section of this dubious order. As will appear in discussing the various families, it is not certain and is even improbable that all the animals placed here are related to one another in any special way, and not one of them can be said to be of known systematic position. Their placing here and their grouping together follow good authority but are opposed by authority about equally good. The arrangement is one made only *faute de mieux*. Attention is especially directed to this great uncertainty by the present comment and by the queries and the words "*incertae sedis*" inserted in the formal classification, in the hope that students will not take this arrangement as on a respectable plane of probability and will have their attention directed to a particularly useful and important series of problems awaiting their attack.

ANOMALURIDAE

The Anomaluridae are so distinctive that their separation, at least to the extent of forming a superfamily, is not seriously questioned. Where this superfamily (or analogous large rodent group) should be placed and what it should include are problems as yet decidedly unsolved. Alston placed the Anomaluridae in the Sciuromorpha, Tullberg in the Myomorpha, and each has had important followers. Zittel put the anomalurids in his scrap basket, the "Protrogomorpha," and Miller and Gidley placed them in theirs, the "Dipodoidae." Thomas made a primary rodent division, "Anomaluri," for them. Various students (e.g., Schlosser) have connected them with the hystricomorphs through a tenuous series of supposedly intermediate genera. Thus there is good authority for placing the anomalurids anywhere or nowhere with respect to the classic subdivisions of rodents. Evidence and consensus incline slightly to sciuromorph relationships, and I follow, with a query, this faint and quite possibly erroneous lead.

The dual subfamily division of the Anomaluridae is satisfactory and generally accepted. Miller and Gidley made these families and put *Idiurus* and *Zenkerella* in different subfamilies, but this is extreme and unnecessary. Matschie (an outstanding splitter) made four subgenera of *Anomalurus*. Rümmler has well shown that three of these are of even less than subgeneric rank, but that the other, *Anomalurops*, has proper claims to generic rank, and this is recognized. There seem to be no acceptable vernacular names for the anomalurids. Those sometimes given, such as "African flying squirrels," are artificial book names, improper in origin, wrong descriptively, or otherwise at fault.

Numerous fossil genera have from time to time been placed in the Anomaluridae. Review of these warrants the blanket statement that none has been shown to belong here with any reasonable balance of probability and that most certainly do not belong here. The origin and history of the group are at present entirely unknown.

The classic study of *Anomalurus* is Alston, 1875, and a useful recent paper is Rümmler, 1934.

†PSEUDOSCIURIDAE

†*Pseudosciurus* was at first considered to be a sciurid. It so appears in Alston, and Forsyth Major related it to *Sciuropterus*. Zittel threw it into his "omnum-gatherum" Protrogomorpha, without any particular reference to the anomalurids, although the latter were also placed there, and Miller and Gidley did essentially the same in their "Dipodoidae." Winge made the †pseudosciurids a tribe of anomalurids. This collocation was strongly supported by Schlosser and now has the weight of custom and consensus to back it, rather, it would seem, from inertia than from conviction and knowledge. Dietrich, 1929, and Dehm, 1937, have recently treated the group, but without any renewed attempt to determine its affinities or to restudy the skull structure. Dietrich says that differences from Anomaluridae outnumber resemblances and that the supposed connection involves some fantasy but leaves the subject without any expression of settled opinion one way or the other. Dehm does not even go this far. It may be taken as very improbable that the †Pseudosciuridae were especially related to the Sciuridae, as doubtful whether they were true sciuromorphs, and as possible but unproved that they were related to the anom-

alurids. As now known, the family was short-lived and not very diverse, but it was locally and temporarily abundant.

†THERIDOMYIDAE

This family is generally recognized as valid on the basis of †*Theridomys* and its closer European allies. Its limits and its affinities appear to be really unknown. At least, no two authorities agree, differences of opinion are irreconcilable, and none is backed by convincing evidence. It is usually placed either near the anomalurids, as here, or considered as an ancient hystricomorph ancestral or aberrant group, or both. Schlosser (in his last revision of the Zittel "Grundzüge"), for instance, places the group in the Anomaluroidea as of common origin with the †Pseudosciuridae and as ancestral to certain hystricoids (but by inference not to all—a peculiar conception). Miller and Gidley made it a subfamily of Zapodidae, a view contradicted by all other students. Winge strongly opposed hystricoid relationships for these genera and for the anomalurids, nearly related to them in his as in most opinions.

The genera here listed as "?†Theridomyidae *incertae sedis*" certainly do not all belong to this family. Probably none of them does, but all have been placed here at one time or another, in every case doubtfully or with subsequent protest from other students, and none has been shown definitely to have other closer affinities. At least a dozen other genera have also been referred to the †Theridomyidae, but these have been shown to be invalid or have been later referred with sufficient probability to some other family or are relatively unimportant and seem not to require listing.

The study of this large group of doubtful but potentially important animals is perhaps the greatest desideratum in vertebrate palaeontology today. It may well conceal vital evidence on some of the most basic problems of the history of the rodents, such as the origin and dispersal of hystricomorphs, the affinities of the anomaluroids, and many others. So many and such diverse specimens are available that it seems inevitable that more careful restudy of the whole complex with modern methods and conceptions would have useful results, but this has not been done.

It is unnecessary for anyone but the specialist to follow the complicated divergences of opinion for each genus. A few views may be mentioned to show how much disagreement exists. Zittel, 1891–1893, referred all the genera here listed (except the then unknown genera) to the †Theridomyidae, forming the "classic" conception of this group. Winge, 1887, 1924, made two distinct tribes of anomalurids: †Trechomyini for †*Trechomys* and †Theridomyini for †*Theridomys*, †*Issiodoromys*, and †*Archaeomys*, and did not classify the other genera. Schlosser, 1884, at first placed them in three families and finally, 1923, placed most of them (along with †*Rhodanomys* and †*Cylindrodon*, since shown certainly not to belong here) in a subfamily of Anomaluroidea, but he widely separated †*Issiodoromys*, with †*Nesokerodon*, †*Pomonomys*, and †*Diamantomys*, as a subfamily of Hystricoidea. Osborn, 1908, referred †*Phiomys* and †*Metaphiomys* to the †Eomyidae, and Schlosser and others placed them in the †Theridomyidae. Matthew (*in* Osborn, 1910) considered them †pseudosciurids, but most recent students, without detailed review, seriously question whether any of these views are correct. Hopwood, 1929, did not classify †*Apodecter* except by inference and placed the evidently related †*Phthinylla* in the †Theridomyidae, while Hinton (*in* Hopwood) thought both might be primitive murines.

Without renewed research on the originals, no useful conclusion is possible, but the prediction may be ventured that these miscellaneous genera belong in at least two quite different divisions (probably families or higher), one of which may possibly be allied to the Old World hystricomorphs while the other or others may be almost wholly unrelated and may just possibly belong more nearly where Winge and the consensus have placed them.

PEDETIDAE

Like the three preceding families, the Pedetidae have been placed in irreconcilably different systematic positions and are really of quite unknown affinities. There is a majority

in favor of anomaluroid affinities, but this is not based on very strong reasoning or evidence and is at least as likely to be wrong as right, although a compiler has little choice except to follow it in default of better clues. Alston placed the pedetids as a subfamily of Dipodidae in the Myomorpha. Thomas placed them by themselves at the head of the Hystricomorpha. Tullberg referred them to the "Anomaluroidei" in the "Myomorphi." Zittel put them near the anomalurids in the "Protrogomorpha." Winge made them a tribe of Anomaluridae. Matthew placed them in the Anomaluroidea among the myomorphs. Miller and Gidley put them in Dipodoidae with, but not near, the Anomaluridae and near the Dipodidae and Ctenodactylidae. Schlosser put them in the Hystricoidea. Weber considered them anomaluroid sciuromorphs. Ellerman places them among the myomorphs between the ctenodactyloids and muroids.

There is only one living genus, and only one extinct form can be placed in the family with any likelihood. This genus, †*Parapedetes*, is unusually well known but is in some respects even more specialized than *Pedetes* and casts no light on the origin of the group. Stromer considers affinities with †*Issiodoromys* and †*Nesokerodon* as not improbable but not demonstrable.

On †*Parapedetes* see Stromer, 1926; and on *Pedetes*, Hollister, 1919; Pocock, 1922c.

MYOMORPHA

As the rodents are the most abundant and taxonomically difficult of mammals, so the myomorphs are the most abundant of rodents although the difficulties of their classification are not greater than for the Sciuromorpha. As here considered, they are constituted by three fairly distinctive groups, made superfamilies: the Muroidea, which surely belong here and are the nucleus and real basis of the suborder, the Gliroidea, also placed here by the consensus, and the Dipodoidea, probably correctly placed here but open to more question. As discussed elsewhere, there are a few other groups of rodents sometimes called myomorphs but here placed in other suborders for various reasons.

MUROIDEA

The essential or nuclear members of this group are the protean, almost ubiquitous families Cricetidae and Muridae. Each of these has given rise to various specialized lines, some of which are commonly given family rank. The total number of muroid families recognized in recent classifications varies from one (Muridae only) to a dozen or more. The most distinctive and profound morphological modification exemplified in the superfamily is that associated with subterranean life, a specialization that seems to have occurred in extreme form independently at least three and possibly four times within the Muroidea, and that is incipient in several other lines. In this classification two of these most specialized groups are tentatively recognized as families, Spalacidae and Rhizomyidae. It would perhaps be equally good to place both of these as subfamilies or alternatively also to recognize families Tachyoryctidae and Myospalacidae.

Aside from the existence of these and other specialized, aberrant branches of the group and despite the relative scarcity of Tertiary fossils and the impossibility of filling in innumerable details, the broad outlines of muroid history can be reconstructed with some probability. The early cricetids, appearing in the Oligocene of North America, Europe, and Asia, are most primitive and represent the ancestral structure of the muroids. They probably arose from sciuromorphs (*sensu lato*) toward the end of the Eocene. The main theater of cricetid evolution seems to have been Holarctica, with various branches surging southward from time to time as geographic conditions permitted. When these southern migrants were insulated from later murid invasion, e.g., in the Malagasy and Neotropical realms, they radiated and became the dominant small ground rodents. When not so insulated, e.g., in the Ethiopian and Oriental realms, some of them yet survived as a subordinate, relatively little varied faunal stratum among the dominant murids.

The murids probably arose from the cricetids at a relatively late date, most likely toward the end of the Miocene. Their main

theater of evolution, probably also their place of origin, was the Old World tropical zone, from tropical Africa eastward through southern Asia and the East Indies to Australia. Here they soon became the dominant rodents, tremendously differentiated. They did not reach the Western Hemisphere until brought by man, probably because they are primarily tropical animals and the only land connections between New and Old Worlds available since they arose have been in the far north. They have, nevertheless, sent a few relatively hardy migrants northward in Europe and Asia, much as the cricetids sent a few stocks southward. (Doubtless some of these exploring types would eventually have reached the New World even if not brought by man.)

Many authorities do not recognize the Cricetidae and Muridae as separate or natural families (e.g., Ellerman). There seems, however, to be little serious doubt that they are natural units, even though not strictly comparable if, as is probable, the murids are only the most successful and varied of numerous branches of generally cricetid origin. If it were possible or advisable to make all families even approximately equivalent in morphological scope, the cricetids and murids, indeed all the muroids, should unquestionably be referred to a single family. This is, however, a fairly obvious case where it is inadvisable to follow this one rigid criterion of what constitutes a family. Each group is so enormously varied and the two are so distinctive in history and distribution that it is entirely justifiable to recognize them as different families for greater clarity of exposition and for practical convenience.

CRICETIDAE

As elsewhere, extreme splitters and specialists without a broad vista of classification occasionally raise each of the subfamilies and many of the tribes or smaller groups of this classification to family rank, a procedure that is not necessarily wrong but is disproportionate and is not generally adopted. In my previous classification (1931a) I recognized the nesomyines and the †cricetopines as of family rank, but a review of the former has shown me that I overestimated their distinction, while recent studies by Schaub have shown that the latter are much nearer the typical cricetines than Matthew and Granger at first believed.

In the arrangement of the Cricetinae, I have in general followed the excellent studies of Schaub (especially 1925), who has reviewed the more important recent types and most of the numerous fossils, but with considerable change in formal expression and with the insertion or slight alteration of many details. He has indicated the existence of various subdivisions that best become tribes on the present scale.[1] Two of his groups, the "†Anomalomyidae" and the "†Melissiodontidae," are tentatively rejected as not yet conclusively shown to warrant formal designation, and one tribe that lay outside his first-hand studies, the †Eumyini, is added. Wood, 1937, has shown that the three genera here called †Eumyini are a natural group allied but probably not ancestral to the Hesperomyini, much as the †Cricetodontini are allied to the Cricetini. Despite the excellent work of these two and of other students, notably Argyropulo, 1933, much is yet obscure about these phyletic lines, but the present trial classification is warranted by their results.

The Hesperomyini (see, among many others, Coues, 1874, Gyldenstolpe, 1932), the extraordinarily varied native mice of the New World, are well known in detail, but a broader revision and synthesis are decided desiderata. Gyldenstolpe, 1932, suggested that the number of genera proposed is too large, but he did not attempt a synonymy of the superfluous names. Ellerman has, however, reduced a number of proposed genera to subgeneric or lower status, and in this I have usually followed him. The Neotropical Hesperomyini give a clear example of the rapidity of muroid differentiation under favorable conditions. There are (in this classification) 40 recent genera of Hesperomyini

[1] Schaub's publications on morphology and phylogeny are among the most able and useful ever to be devoted to rodents, but his formal taxonomy is unorthodox and erratic. For instance, he considers his †Cricetodontidae and other similar groups to be subdivisions of his Cricetinae, although he gives to the smaller units family names and to the larger a subfamily name. His names in -idae are thus, despite this termination, to be taken as of about tribal rank, which I have formally assigned to them.

confined to the Neotropical realm. It is probable that most of these genera have originated since about the beginning of the Pleistocene, a time so short from an evolutionary point of view that most of the ungulates, for instance, showed only subgeneric differentiation at greatest and in some cases barely specific change. It is, however, also notable that this intense and rapid differentiation was not accompanied by much basic evolutionary progress or morphological change; no well-defined tribal or other subgeneric group of these rodents has originated in South America. The rapid evolution of new genera was more a matter of segregation of characters in a group with great variation than of the origin of significantly new characters.

The question of the Malagasy rats, Nesomyinae of this classification, seemed to be well settled but has been violently reopened by Ellerman, 1941. He insists that the group has no reality and that on the contrary the seven living genera[1] belong in five different subfamilies of radically diverse zoological and geographical affinities. This suggestion evidently requires consideration and renewed first-hand study of the materials, but in the meantime Ellerman's conclusion seems too improbable to be adopted without substantiation. As far as I know all previous competent students, including the most learned, able, and critical specialists on Muroidea, have fully agreed that these Malagasy rodents form a natural unit. They have differed only as to the rank of that unit, whether a family, subfamily, or smaller group. It is, moreover, pertinent that this is precisely the sort of case in which Ellerman's stated and exemplified principles of classification are almost certain to lead to a result that is erroneous from the point of view of classification by natural affinity rather than by accidental resemblance in a rigid and limited set of key or diagnostic characters. If a single line of rodents attained an insular area and there radiated without competition from other rodents, different later members of the phylogenetic unit would inevitably converge toward various different rodents in other parts of the world, and Ellerman's system would then classify them with the form toward which they converged instead of retaining them as a unit because of their common ancestry. It seems probable that this is what happened in this case and that the subfamily Nesomyinae is real and valid, however its members may interfere with the workings of a mechanical generic key.

The individually abundant and basically varied but less highly differentiated (on a generic level) Microtinae have been fully and ably treated by Hinton (especially 1926), and the present arrangement follows his with unimportant changes induced by later work and with the recognition of a third tribe for the relatively distinctive *Ellobius* and its extinct ally †*Ungaromys*.

The gerbils are frequently given family rank between Cricetidae and Muridae, but the consensus places them as a cricetid subfamily. Some 20 genera have been proposed (many in recent years by Thomas), but only six or seven of these are clearly distinct and reasonably of more than subgeneric rank. A recent classification by Heptner, 1933, recognizes the gerbils as a family with three subfamilies, in which 12 genera or subgenera are placed, but the ranks to be assigned to these are not discussed nor is the disposal of numerous other named groups of supposed suprageneric rank clearly indicated. Even Ellerman, sympathetic to the use of more inclusive genera, recognizes 12 genera of Gerbillinae. Of these I have given 10 full generic rank, and I suspect that a more synthetic detailed study would properly reduce this number.

SPALACIDAE AND RHIZOMYIDAE

At various times each of the more distinctive Old World burrowing myomorphs, *Spalax*, *Tachyoryctes*, *Rhizomys*, and *Myospalax*, together with allies of some of these, has been placed in a single family. It has also been claimed that their resemblance is wholly convergent (except that all are admittedly myomorph), and they have been placed in four different families. The question is still open, but it does seem likely that these forms arose from at least three different non-sub-

[1] "Six" in Ellerman, 1940 (p. 57), is apparently a misprint, as his second volume (1941) lists seven genera separately, the same as the genera of this and most other classifications.

terranean ancestors. I have tentatively followed Miller and Gidley in separating the Spalacidae and Rhizomyidae and placing *Tachyoryctes* in the latter family (as also suggested by fossil rhizomyids more or less intermediate in character). Their placing of *Myospalax* in the Spalacidae, although it followed the consensus, was probably wrong, as recent work by Teilhard de Chardin, Leroy (1941), and others suggests that *Spalax* and *Myospalax* are of quite different origin. I tentatively place the latter in a separate subfamily of cricetids, supposing it to have been of cricetid ancestry and not highly divergent.

MURIDAE

The Muridae show in their most exuberant form the extravagant powers of speciation and, one might say, of generation among modern rodents. If ability to survive and multiply and to adapt quickly to a great number of local situations is taken as the criterion, the murids are incomparably the most successful and dominant mammals, not excepting man. In the Murinae alone, as many as 100 living genera are currently recognized by some students (68 in this classification) and a single genus, *Rattus*, has over 500 recognizable, named subspecies and species (more than 560 are listed as valid by Hayman and Holt *in* Ellerman).

Virtually nothing is really known of the obviously extremely complex interrelationships of the many genera of Murinae, and about all that can now be done within the subfamily is to list the genera, trying to keep together forms with particular resemblances in key characters despite the fact that no definitely genetic grouping is thereby achieved. Ellerman, 1941, has given such a list, and I have followed him in most respects. Here and there a probable genetic group emerges, for instance *Conilurus-Zyzomys-Laomys-Mesembriomys* and probably also *Notomys-Mastacomys* (although these are widely separated in Ellerman's artificial arrangement and mine following him), but their distinction is insufficient for subfamily rank, and tribal or other generic groupings cannot yet be consistently made among the Murinae.

A few other groups, although clearly arising from the Murinae, seem to be phylogenetic units, and they have perhaps diverged sufficiently from the stem forms to be called subfamilies. A really consistent scale of values would probably make these tribes of Murinae (except the Hydromyinae), but the present impossibility of a good tribal arrangement for all murines necessitates calling these groups subfamilies if, as convenience dictates, they are to be recognized at all. The groups are not very clear-cut, and in most cases there are genera of doubtful position. For instance, *Echiothrix*, here placed in the Murinae, is also near the Rhynchomyinae, and *Beamys* and *Saccostomus*, here also called murines (following Ellerman), are often and perhaps better classed as Dendromyinae. The extent and validity of the Phloeomyinae are particularly disputed. Some authors (including Ellerman) do not recognize the groups at all, others place only *Phloeomys* here, and others unite six or seven genera as Phloeomyinae. In adopting the latter usage, I follow Tate, 1936.

In view of the extreme abundance of living Muridae and the fact that many of them seem well suited for fossilization in habits and habitat, it is remarkable that they are very rare fossils except in quite late Pleistocene or sub-Recent deposits. No surely identified murids are known before the Pliocene, and only half a dozen genera, each represented by rather few specimens, have been recognized in the Pliocene (see Schaub, 1938). The principal reasons for this are probably, first, that the center of murid evolution has been in the tropical and largely insular regions of the Old World where few terrestrial Tertiary deposits occur or have been discovered and explored, and, second, that the family really is of relatively recent origin and differentiation and, if it existed at all as yet, was highly localized and not abundant until the Pliocene.[1]

[1] Not for the sake of criticizing but only because Ellerman's work is so very useful within its limits and because it will inevitably become the bible of specialists on recent rodents, who may not have the data for forming independent judgments, another weakness in his masterly monograph must be noted here: his peculiar, and in part demonstrably incorrect, ideas of the geographic history of rodents. For instance, he maintains that Cricetinae were present in South America from the beginning of the Tertiary or before and that the present North American forms are recent immi-

The literature of the Muridae is too extensive to cite adequately in this broader review. Besides the papers already mentioned, the following are particularly useful: Wroughton, 1919 (India); Rümmler, 1938 (New Guinea); Neuhäuser, 1936 (Asia Minor); Wood Jones, 1922 (Australia); St. Leger, 1931 (Africa).

GLIROIDEA

Most students believe that the three groups here included, Glirinae, Graphiurinae, and Platacanthomyidae, are related in about the way suggested by this classification. Miller and Gidley, however, make three families and separate them widely, especially emphasizing what they believe to be fundamental differences between *Graphiurus* and the other two groups. Later authors have not accepted this arrangement and have cast doubt on its theoretical basis, so that I tentatively reject it and follow the strong consensus.

Fossil dormice are rather common in Europe but are not very well understood. It is improbable to the point of impossibility that the earlier fossils really belong to living genera, as is usually stated.

This is a decidedly isolated group, and the fossils do serve to show that it has been so since the early Tertiary. Its subordinal position is not wholly certain, but almost all recent students agree that the dormice are myomorphs. On the other hand, inclusion in the Muroidea overemphasizes the resemblance and is contradicted by the evidence that gliroids are about as old and quite as distinctive as muroids.

DIPODOIDEA

Sicista, which does not have the disproportionately long hind legs of the (literally) jumping "mice," was long considered a true murid (e.g., Alston) but is now universally recognized as allied to *Zapus* and *Dipus*. The superficially similar *Pedetes* has been confused with these forms but seems to be purely convergent. The dipodoids (except *Sicista* and with *Pedetes*) were placed at the end of the Myomorpha by Alston, and this was followed (in essentials) by Thomas, Tullberg, and many others and is still the consensus. Dobson, however, had already, before Alston, argued for hystricomorph affinities. Winge achieved the modern content of the group, excluding *Pedetes* and including *Sicista*, and implied a position near both anomaluroids and muroids. Miller and Gidley, 1918, are among the few competent modern students who have seriously questioned the myomorph affinities of this group. They make it typical of a major division of rodents ("Dipodoidae") to which they also refer such diverse and, in the opinion of virtually all other students, unrelated groups as the Ischyromyidae, Aplodontidae, Anomaluridae, Ctenodactylidae, and Pedetidae.

The arrangement within the superfamily follows Pocock, 1922c, except for the addition of fossil records (mostly as reviewed by Schaub, 1930b) and the insertion of the two recent genera described since 1922 (*Stylodipus*, here considered a subgenus, and *Salpingotus*) and the recognition of a subfamily Cardiocraniinae. Several other extinct genera have been referred to this division of the rodents, notably †*Eomys*, †*Protoptychus*, and †*Paciculus*, but recent students agree in rejecting these references.

This is another old group, as rodents go, and apparently arose along with the muroids and gliroids as the myomorphs were becoming differentiated from the sciuromorphs.

HYSTRICOMORPHA

The pertinence of the ctenodactylids and bathyergids to this suborder is not established and is rather improbable, as will be noted in

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grants from the south. This is so completely wrong that it is not worth while to argue the matter, although it does seem necessary to insist on the correction. He also maintains that the Muridae are among the most archaic of mammals, which is a relative statement but is relatively untrue even if, as he does, one includes the Cricetidae, which are on the whole more archaic than the Muridae, *sensu stricto*. The Muridae, or Murinae, are about the least archaic of mammals and one of the last families to arise. He holds that a large section of the Muridae evolved in Australia and migrated hence to Asia, rather than the reverse. It is certainly true that several types of murids, still confined to Australia and the adjacent islands, became differentiated in that region, but one still must believe that their ancestors, already definitely murids, somehow migrated from Asia, and it is quite clear that this must have occurred (or rather, begun, for there were probably several such migrations) in the late, not early, Tertiary. Complete ignoring of the fossil evidence and lack of a phylogenetic, rather than purely morphological, viewpoint make valid historical zoogeography impossible.

discussing them. Eighteenth century and early nineteenth century naturalists did not recognize a group including the other, or the unquestioned, hystricomorphs of modern classification, and they distributed their broad genera (approximately superfamilies on the present scale) among the rodents according to resemblances in superficial appearance. Illiger, 1811, took a step in the modern direction when he made a group, "Aculenta," for porcupines and spiny "rats" and another, "Subungulata," for other South American hystricomorphs, and De Blainville, 1816, had one group, "marcheurs," that was essentially the Hystricomorpha, as was Waterhouse's "Hystricina" (1842). Brandt applied the name Hystricomorpha in 1855. Since then, so far as I know, no student has failed to recognize the group in some form and to place together in it the forms still considered as surely pertinent (with varying usages as to bathyergids, ctenodactylids, and some others still of doubtful reference).

Despite this uncommonly complete agreement, the phylogenetic validity of the arrangement does not seem to me to be beyond question. There is a grave geographic problem for which no satisfactory solution has ever been found. It is reasonably certain that no hystricomorphs occurred in North America until the late Tertiary when the single genus *Erethizon* appeared there, obviously an immigrant from South America. Rodents nominally hystricomorph but quite distinctive in the two places appear mysteriously at about the same time, Oligocene, in Europe and in South America, continents that cannot within reason have had any land connection, however indirect, at or shortly before that time. In spite of their striking similarity, it is probable that New and Old World porcupines developed independently from these unlike beginnings. Doubtful thryonomyids appeared in Africa in the Miocene. The recent *Thryonomys* and *Petromys* of Africa are amazingly like some South American forms, so much so that some students place them in the otherwise South American Echimyidae or Octodontidae, although they are, of course, easily distinguishable in detail and are more often placed in distinctive families. It is extremely unlikely that there has been a land connection between Africa and South America since the Mesozoic, if ever.

As I see it, it is difficult or almost impossible to reconcile these distributional facts and inferences with the morphological facts and inferences suggesting that all these animals had a common and definitely hystricomorph ancestry. Possible alternatives are (a) that there is no natural group Hystricomorpha and that this name really includes two or probably three convergent groups of independent origin (American "hystricomorphs," Hystricidae, and remaining African "hystricomorphs"), (b) that the geographic relationships expressed above are radically wrong, or (c) that more or less primitive hystricomorphs were somehow rafted across the Atlantic without any land connections. There is strong evidence against any one of these alternatives. Some zoologists will object to this argument because in their opinion geographical considerations have no place in zoological classification, but I maintain that classification should be consistent with phylogenetic theory and that geographical factors of this sort have a very definite bearing on phylogeny. Valid palaeogeographic and phylogenetic theories must be congruous. These particular palaeogeographic theories are just as well founded as are the morphological theories of hystricomorph relationships and are just as likely to be correct, especially since the rodents are so subject to structural convergence. As long as the two lines of evidence seem to be discrepant, the unity of the Hystricomorpha must be considered questionable.

The present classification does retain the time-honored and universally accepted union of New and Old World hystricomorphs in one suborder and places the Thryonomyidae and Petromyidae in the Octodontoidea on morphological grounds. With due expression of doubt, it seems preferable not to advocate a radical change until more conclusive evidence is available that another arrangement would be more natural.

Still leaving the Ctenodactylidae and Bathyergidae for later consideration, previous classifications have seldom attempted any grouping of the hystricomorph families. Among the few important exceptions are Miller and Gidley, and Ellerman. Miller and Gidley divided their "Hystricoidea" (=Hys-

tricomorpha) into a "Medialis series," containing the manifestly allied Caviidae and Hydrochoeridae, and a "Lateralis series," uniting all other families. The "Lateralis series" was divided into a "Group A," including all "Lateralis" families except Dasyproctidae, Chinchillidae, and Abrocomidae, and a "Group B," including those three families. This is a "key" arrangement, based artificially on single, supposedly diagnostic characters and quite surely not consistent with the phylogeny of the group. Their "Group B" in the "Lateralis series" seems to be particularly unnatural. Ellerman adopts a less subdivided arrangement but one similar, to the extent that he contrasts Caviidae and Hydrochoeridae (by him united in one family) with all other hystricomorphs.

I have attempted a new superfamily arrangement that is doubtful and not wholly satisfactory in some details but that seems to me to correspond with probable main currents of hystricomorph differentiation. This is based in large part on fossil evidence, which happens to be remarkably full and fairly well analyzed for the South American groups and is in my opinion, although it will not appear so to some students, likewise supported by the anatomy of the living forms. When, or shortly after, the hystricomorphs are first known in South America, in the Oligocene, they can be rather clearly placed in four main types, not then very different but later becoming markedly so. All the later families can be more or less definitely traced back to one or another of these types, which I, therefore, make the basis of superfamilies. Two of them, Erethizontoidea and Chinchilloidea, although as old and as long-lived as the others, never became much varied and include only one family each. The other two, Cavioidea and Octodontoidea, became and are still highly varied, and each includes several families. An additional superfamily, Hystricoidea, is made for the Old World porcupines, which are really markedly unlike the Erethizontidae in spite of the fact that both have spines (as do various insectivores), which appear to be about as old as the Erethizontidae and which were in the Oligocene almost as distinct from the latter as they are now.

This classification lists all the recent genera considered valid and of that rank. The listing of fossil genera is less complete because some genera of no great interest and founded on dubious grounds are omitted, but most of those currently recognized are included. The authors of most of these genera, Ameghino and Kraglievich, were extreme splitters, and I feel that later revision is almost sure to reduce many of their genera to subgeneric rank. Again it may be emphasized that this does not mean that their named groups are considered invalid, but only that less narrow specialists are likely to align them with a different scale of proportions.

HYSTRICOIDEA

This small group involves no great taxonomic difficulties. Like most subsequent classifications, this one essentially follows Lyon, 1907. See also Pocock, 1922b.

ERETHIZONTOIDEA

The short-lived †*Protacaremys*-†*Acaremys* line represents a side branch distinctive enough for subfamily designation, but most of the known erethizontids seem to belong in a single, rather unified and unprogressive phylum, Erethizontinae, already recognizable in the Oligocene. *Chaetomys* probably branched off from early Erethizontinae, but its history is unknown, and all authors agree in distinguishing it, mostly as a subfamily. Miller and Gidley removed it to the Echimyidae, but it is almost certainly much closer to the Erethizontinae. See Pocock, 1922b; Tate, 1935.

CAVIOIDEA

As regards the recent forms, this superfamily is the family Caviidae of Tate, 1935, and some other authors. That arrangement seems unbalanced because it compresses into one family genera about as divergent as those placed in the five or more octodontoid families. It is also inconvenient because of the large number of genera involved, particularly when the fossils are added, and the difficulty of arranging them all in one family. It may also be noted that Miller and Gidley and Ellerman dissociate the cavies and capybaras entirely from the other forms placed in the family by Tate, etc. This is too extreme and is contradicted by excellent evidence, but it

does emphasize the inadvisability of too inclusive use of Caviidae. I have, therefore, followed other authorities in recognizing the Hydrochoeridae, Dinomyidae, and Dasyproctidae as families rather than subfamilies and in inserting three extinct families. The †Cardiomyinae and Dolichotinae, however, are so close to the typical Caviidae that their removal from that family is not justified or necessary. Kraglievich, although an extreme splitter in general, even refers the dolichotines to the Caviinae. Much of the arrangement of this superfamily is based on his careful work, but with some reduction of ranks and other necessary adjustment. Thus he has shown that the once very abundant, widespread, and varied genera here united as †Heptaxodontidae are related to one another and not referable, as is often done, to the Dinomyidae or other recent families, but it seems necessary for balance to reduce his four families to subfamily rank. His genera are here listed, although some are poorly known and not very distinctive. These curious animals represent a Pliocene culmination of the Neotropical hystricomorphs, among them the largest known rodents (†*Phoberomys*). †Heptaxodontidae is the oldest valid family name and is used, although †*Heptaxodon* is a peculiar genus not at all typical of the family as a whole and sometimes (but probably erroneously) believed not to be of common origin with the other genera placed here.

Ellerman widely separates *Cuniculus* and *Dasyprocta*, placing them in different and not consecutive families, in general agreement with Miller and Gidley, 1918, and Pocock, 1922b. I agree with the consensus that the admittedly very striking peculiarities of *Cuniculus* may be of rather recent origin and that the pacas and agutis probably represent derivatives of a single family stock.

On the recent forms of this superfamily, see especially Yepes, 1935; Tate, 1935; Pocock, 1922b; also Ellerman and other general studies of rodents. On the fossil genera, see especially Anthony, 1918, 1926; Kraglievich, 1926b, 1930b, d, 1932a; Scott, 1905.

CHINCHILLOIDEA

The chinchillids have been separate and distinctive since the first known appearance of hystricomorphs, so can properly be granted superfamily rank. Some of the †heptaxodontids were formerly thought to be chinchillids, but special affinity in this direction now seems impossible. See Scott, 1905; Pocock, 1922b; Tate, 1935.

OCTODONTOIDEA

Like most superfamilies, this was formerly considered a family and still is occasionally, but its 65 or more genera are now dispersed among five to 10 families in all but the most compressed and summary classifications. This arrangement accepts the five Neotropical families of Tate and others plus two African families. The known fossil genera fall into living groups as far as they can be definitely placed. The frequent dual subfamily division of the Capromyidae into hutias and nutrias is abandoned because most of the extinct genera cannot be surely divided in this way, and they seem to show intergradation of the subfamilies such that the apparent division may be only recent and superficial, caused by the accidental survival of only two of many closely allied types of capromyids.

The two African genera, *Thryonomys* and *Petromys*, are morphologically octodontoid, and it has even been common practice to refer them to Neotropical families and subfamilies, for instance, placing *Petromys* with *Octodon* and *Thryonomys* with *Capromys*. The family separation is, however, often made and is justifiable morphologically. It is also a conservative precaution in view of the geographic difficulty in distributing identical families of rodents in Africa, South America, and nowhere else. As previously noted, it is possible that †*Phiomys* or some other of the doubtful ?†Theridomyidae are really related to the thryonomyids, but this is wholly conjectural at present. The tentative listing here of †*Neosciuromys*, †*Phiomyoides*, and †*Sayimys* is only a little less conjectural.

On Octodontoidea, in addition to works on hystricomorphs already cited, see especially Chapman, 1901; Rusconi, 1928; Kraglievich, 1927; Miller, 1922.

BATHYERGOIDEA

There are few more doubtful points in classification, concerning animals that are fairly abundant and quite well known, than the affinities of the bathyergoids. Thomas,

1897, placed them in the Myomorpha between Heteromyidae and Dipodidae. Tullberg, 1899, made them a major subdivision of "Hystricognathi," coordinate with "Hystricomorphi," and Ellerman, 1940, followed Tullberg exactly. Miller and Gidley, 1918, made a major division of rodents for them and indicated no closer affinities, as did Weber, 1928. Winge, 1887–1924, made them a tribe of Hystricidae. Everyone agrees that they are extraordinarily isolated among rodents, and those who commit themselves further agree that if they have any special, though distant, affinity it is with the hystricomorphs. Any decisive indications of their ancestry are overlain and obscured by specializations for a highly specific and peculiar mode of life, and a definitive arrangement cannot be expected until less specialized ancestral forms are found. Supposed ancient allies, like †*Tsaganomys* (now believed to be sciuromorph), have been claimed, but it now seems improbable that any are true bathyergoids. While awaiting better evidence, it is considered inadvisable to base a major division of rodents on these few aberrant genera. I do not know any special recent revision of the family, but its generic subdivisions are well established and subject to no particular doubts except for the unimportant point whether *Fornarina* is a genus, subgenus, or synonym. The last is most likely.

CTENODACTYLOIDEA

This group vies with or exceeds the bathyergids in uncertainty. It has been considered hystricomorph (Thomas, 1896; Winge, 1924; Weber, 1928), myomorph (Tullberg, 1899; Ellerman, 1940), and neither (Miller and Gidley, 1918). About all that can be said is that the ctenodactylids are not sciuromorphs, so must be either myomorphs, hystricomorphs, or members of a separate suborder. As with the bathyergids, possible heritage characters are so hidden by the unusual habitus that only the tracing of the actual ancestry is likely to settle the question. The only possibly important fossil discovery is a specimen from the early Pliocene of India referred by Hinton, 1933, to the recent African genus *Pectinator*. This somewhat improbable, but of course possible, identification may be dubious despite Hinton's high authority, because of the fragmentary nature of the specimen, the promised full description of which I have not seen. In any case it does not appear that the discovery casts real light on the origin of the group.

Except for general works, keys, and description of a few local species or subspecies, I do not know any recent restudy of this family. Among older works, that of Peters, 1871, is noteworthy.

LITERATURE ON RODENTS

Papers on special groups and particular points have been cited in the preceding notes. It may be convenient to repeat here references to the most important general classifications that are still useful in varying degree: Tullberg, 1899; Winge, 1887, 1924; Miller and Gidley, 1918; Weber, 1928; Ellerman, 1940–1941. Except for Miller and Gidley, these all include extensive bibliographies. The various regional faunal studies cited elsewhere also are devoted largely to this order. There is no good review of fossil rodents in general. A few of the important papers on particular groups of fossil rodents have been cited in the course of this discussion, and in addition to these Wilson, 1937a, is an exceptionally useful review of the later Tertiary American rodents.

MUTICA

CETACEA

Because of their perfected adaptation to a completely aquatic life, with all its attendant conditions of respiration, circulation, dentition, locomotion, etc., the cetaceans are on the whole the most peculiar and aberrant of mammals. Their place in the sequence of cohorts and orders is open to question and is indeed quite impossible to determine in any purely objective way. There is no proper place for them in a *scala naturae* or in the necessarily one-dimensional sequence of a written classification. Because of their strong specialization, they might be placed at the end, but this would remove them far from any possible ancestral or related forms and might be taken to imply that they are the culmination of the Mammalia or the highest mammals instead of merely being the most atypical. A position at the beginning of the

eutherian series would be even more misleading. They are, therefore, inserted into this series in a more or less parenthetical sense. They may be imagined as extending into a different dimension from any of the surrounding orders or cohorts.

It is clear (see especially the discussion in Kellogg, 1936) that the Cetacea are extremely ancient as such and that none of the various proposals of exact source, such as that deriving them from certain †creodonts, is very probable. They probably arose very early and from a relatively undifferentiated eutherian ancestral stock. On this basis they deserve to rank as a separate cohort, for which a Linnaean name is available and deserves resurrection.

It goes almost without saying that the existence of the natural group now called Cetacea was recognized from the earliest times, but the fact that these are mammals was not at first perceived, and the limits of the order were not unequivocally established until nearly the end of the nineteenth century. The Mutica and Cete of Linnaeus were classed as mammals and were, except for forms since discovered, exactly the Mutica[1] and Cetacea of this classification. Linnaeus nowhere more clearly showed his remarkable insight than in dealing with these animals. In the following century the Cetacea were usually confused with other aquatic mammals. Even after the pinnipeds were associated with the Carnivora, the Sirenia were long considered Cetacea, or an order closely allied to the latter. This idea is to be found as late as the 1890's in the work of so able a man as Cope, but even then this was old fashioned, and no competent student has since accepted it.

Before 1850 it was noticed that a division of cetaceans into those with teeth and those with whalebone could be made. This has ever since been recognized, and there is no serious present doubt that they are valid phylogenetic units and that all later cetaceans enter into one or the other of them. Eocene fossil cetaceans were known as early as 1670, and beginning in 1832 a series of discoveries in southern United States revealed that these are very unlike any later forms. In 1849 Müller referred these early types, the best known of which was and is †*Basilosaurus*, to a distinct order allied to the Cetacea. Gill, 1872, made them a third suborder of Cetacea, and there they remain in what is unquestionably a natural way.[2]

Throughout the order Cetacea there is a noteworthy absence of annectent types, and nothing approaching a unified structural phylogeny can be suggested at present. Successive grades of structure appear in waves without any known origin for each. This is strikingly true in many orders, not only of mammals but of all animals, but within the Mammalia it is perhaps most striking among the Cetacea. Thus the †Archaeoceti, middle Eocene to early Miocene, are definitely the most primitive of cetaceans, but they can hardly have given rise to the other suborders. The Odontoceti, late Eocene to Recent, are on a higher grade than the †Archaeoceti and, on the average, lower than the Mysticeti, middle Oligocene to Recent, but apparently were not derived from the former and did not give rise to the latter. As Kellogg suggests, the early stages of cetacean history may have taken place in local fresh-water streams and lakes, the sediments of which are not preserved. It is also possible that some crucial later parts of the history occurred in the great ocean basins and did not directly involve the littoral waters and epeiric seas where almost all the known fossil cetaceans lived. In the deposits of these environments, cetaceans are locally abundant fossils, especially in the Miocene.

†ARCHAEOCETI

The arrangement of this suborder exactly follows Kellogg, 1936, whose thorough monograph supersedes all earlier work. He, however, rejects from the †Archaeoceti the four dubious genera here called †Archaeoceti *in-*

[1] Scott has recently revived Owen's term "Mutilata," but this seems undesirable. It is considerably antedated by Mutica, it is no more familiar at present, and it was proposed for the purpose of uniting the Sirenia and the Cetacea, an old, persistent error that Linnaeus perspicaciously avoided.

[2] But it has been questioned. In 1889, D'Arcy Thompson proposed removing these †archaeocetes from the Cetacea and placing them near the Pinnipedia, and Fraas, 1904, considered them aquatic †Creodonta. Present greatly increased knowledge makes both these ideas quite incredible.

certae sedis for want of a more likely place to put them. Kellogg calls †*Microzeuglodon* a †squalodont and the other three Odontoceti *incertae sedis*, but all are called †Archaeoceti by Slijper, 1936, and other good authorities. Abel thought that †*Patriocetus* was ancestral to the Mysticeti, but subsequent workers have strongly opposed this view, without establishing the true affinities of the genus.

ODONTOCETI

The division of the Odontoceti into families and the order in which these families are placed closely follow Slijper, 1936, who has carefully reviewed most of the living and many of the extinct genera. Because so many genera and families are now recognized, I have attempted superfamily grouping, but this is not wholly satisfactory. The most doubtful point is probably the union of Ziphiidae and Physeteridae in one superfamily. Colbert (pers. com.) points out that both are highly and differently specialized and that they appear to be about as distant from each other as either is from the Delphinoidea.

The †Agorophiidae are the most primitive odontocetes and may even represent the group ancestral to the other members of the suborder. The †squalodontids were still relatively primitive, but only relatively, and were well off any possible line of ancestry for the contemporaneous and later platanistoids, physeteroids, and delphinoids. The latter all appear at about the same time in the record and represent at least three, quite likely four and perhaps more, quite independent derivatives from the ancestral toothed whales. The number of genera and families has become so large that I have introduced superfamilies for the association of families that appear to be specially related. Kellogg (with others) is followed in placing †*Notocetus* and †*Squalodelphis* in the Ziphiidae and not in the †Squalodontidae as does Slijper. Slijper recognizes their resemblance or relationship to the Ziphiidae but prefers to emphasize their relatively primitive character.

Most small, long-snouted cetaceans have been referred to the Platanistidae, but recent students have recognized this as a habitus character that may have arisen in sharply distinct lines of descent. This has been carried so far that sometimes only *Platanista* is now left in the family. Kellogg, for instance, removed *Inia* and its allies to a remote family Iniidae and puts *Stenodelphis* and its allies in the Delphinidae. Now Slijper has argued at some length and with well-marshaled evidence that the three groups typified by *Platanista*, *Inia*, and *Stenodelphis* are really and specially related and can well be placed in one family. I have followed him in this but have retained the identities of these three rather well-defined groups by making them subfamilies. Slijper has also shown that †*Pachyacanthus*, although usually placed in the Mysticeti, is an ally of *Platanista*.

The arrangement of the Ziphiidae is essentially that of Kellogg, 1928, with which Slijper, 1936, is also in general agreement. No good grouping of the genera within the family has yet been achieved.

In the Physeteridae the distinction of the †Hoplocetinae from the Physeterinae, introduced by Cabrera, 1926, and adopted by Slijper, is horizontal and probably fortuitous in part. Future knowledge may be expected to provide a more natural subdivision, but in the meantime this is a convenient cataloguing device for this miscellaneous group. *Kogia* is often given separate family status (as by Kellogg), but it is clearly related to *Physeter* and scales in equally well as a subfamily (Slijper).

The Delphinoidea of this classification are the Delphinidae of many authors, including Kellogg. As usual, the exact rank of the group is of slight importance, but the great number and wide diversity of the genera included and the complexity of their many phyla justify superfamily rank and make it desirable from a practical point of view. Abel has gone even further, in my opinion too far, and has raised this division to subordinal rank. The present families are those recognized by Slijper and essentially the subfamilies of those who place all in the Delphinidae. Slijper has shown that some of the fossils hitherto referred to *Tursiops* are so distinct as to merit not only generic but also family rank, on his scale, reviving the name †*Hemisyntrachelus* and making a family for this genus.

The name Monodontidae seems on every count except recent usage preferable to

Delphinapteridae, to such an extent that I venture to revive it.

Even as thus restricted, the Delphinidae *sensu stricto* include abundant genera and distinct phyla, and a subfamily division is desirable. Slijper provides such an arrangement: †Kentriodontinae, Orcinae, and Delphininae. These are clearly natural groups as far as their types are concerned, yet the correct distribution of other genera in them is very uncertain, nor is it clear that all the known genera do fall into three, or into these three, coordinate divisions. At present, then, their adoption would leave the greater part of the family *incertae sedis*. The fossils of this family await revision. Possibly some of them belong in other delphinoid families.

MYSTICETI

The classification of the mysticetes is simpler than that of the odontocetes, as the number of genera is fewer. Some subfamily arrangement of the numerous †cetotheres is much to be desired, but it awaits revision of the group.

Miller and Kellogg place *Neobalaena* in a monotypic family, but I have tentatively followed Slijper in leaving it with *Balaena*. Aside from this point, there is no important dispute as to the arrangement of the mysticetes as far as it is here carried. It may be mentioned, however, that Abel and some others recognize a family †Patriocetidae as ancestral mysticetes, which is not inherently improbable but has been seriously questioned and requires substantiation.

The †cetotheres are more primitive than other mysticetes, and the earlier genera may not be far from the common ancestry of the suborder although, again, the later forms are well removed from that ancestry. The other three families represent (at least) that many separate evolutionary lines from a possible Oligocene †cetothere base.

Literature on the Cetacea in general is extensively listed in Kellogg, 1928, 1936, and Slijper, 1936, and those three works are the best sources for a review of the order. Among many other sources may be mentioned the classic by Van Beneden and Gervais, 1880; Beddard's excellent book, 1900; a long series of studies on fossil cetaceans by Abel (mostly cited by Kellogg); Winge's stimulating summary, 1921; a later paper by Kellogg, 1938, not taxonomic but of exceptional interest from an evolutionary point of view; a recent popular review by Fraser *in* Norman and Fraser, 1938; and Howell's fine book on aquatic mammals, 1930. See also good summaries in several general books on mammals, notably Flower and Lydekker and Weber.

FERUNGULATA

The Ferungulata became enormously differentiated during the Tertiary. They include no forms quite so aberrant as the Mutica, they are now, and probably have long been, fewer in individuals and in lesser taxonomic groups (such as genera) than the Glires, and they have not approached the adaptability and mental attainments of the most successful Unguiculata (that is, of man), but they are unrivaled in major structural diversity. This is reflected in their division into 15 orders, as opposed to eight for the Unguiculata, two for the Glires, and only one for the Mutica. This abundance of major groups is inconvenient taxonomically and suggests the advisability of superordinal grouping. The superordinal relationships are not well established and many dubious points remain (as discussed under each superorder), but the data warrant a tentative five-fold division into Ferae, Protungulata, Paenungulata (new term, defined below), Mesaxonia, and Paraxonia, groups of very unequal size but probably of roughly equivalent importance.

The relationships of these superorders are necessarily theoretical since no transitions between them can be traced in detail. There are, nevertheless, known intermediate types, for instance, between Ferae and Protungulata and between Protungulata and both Mesaxonia and Paraxonia. It seems probable that the earliest Ferae and earliest Protungulata represent a primary dichotomy. The ancestral unit, if known, would perhaps be more easily definable as belonging to the Ferae, and in this sense the Ferae may be considered ancestral to the other superorders. The Protungulata include not only the most primitive and most nearly generalized of all ungulates but also several specialized groups derived from these but not sufficiently transformed or varied to warrant separate superordinal rank. Paenungulata, Mesaxonia, and

Paraxonia appear to have been separately derived from Protungulata, the Paenungulata first, and the Mesaxonia and Paraxonia at about the same time, later than the Paenungulata.

FERAE

As in some other cases (e.g., Glires *vs.* Rodentia), it is here possible to salvage a prior but now little used Linnaean name without abandoning the later but now generally employed essential synonym by applying the two names to different grades of the hierarchy. There is no question that the carnivores, even though placed in a single order, should rank as a superorder within this cohort. Their diversity, their antiquity, and, subsequent to the Paleocene, their sharp separation from the other ferungulates (i.e., from the ungulates) cannot be expressed by a lesser rank.

CARNIVORA

For the most part the union represented by this order was grasped intuitively by the earliest naturalists, but there was long difficulty regarding the seals and some others. This was (according to modern ideas) the most completely natural of the Linnaean orders ("Ferae"), essentially including all the animals now referred to it, even the pinnipeds, and excluding all others (in the tenth edition; unfortunately both earlier and later editions had a less natural assemblage). This is an outstanding example of the insight of Linnaeus, and it is noteworthy that some later authors went far astray in seeking to emend the Linnaean arrangement. For instance, Lacépède, 1799, put the ursids, procyonids, and herpestids in an order "Plantigrades," which also included the insectivores, and put the pinnipeds in a subdivision (approximately a superorder) "Empetrés" along with the sea cow. Cuvier in 1800 made much the same arrangement with the additional error of associating some of the marsupials with the Carnivora ("Carnassiers"). Actually it was not until the second half of the nineteenth century that the Linnaean collocation of 1758 was again achieved, e.g., Haeckel, 1866; Owen, 1868; Gill, 1870. The terrestrial carnivores and the marine forms, so long assigned to widely different orders, were still sharply distinguished as suborders or comparable groups. This arrangement has persisted ever since without much question, living carnivores being almost universally classed as Fissipeda and Pinnipedia or equivalent, coordinate groups within the order.

Even after this arrangement was achieved, the position of the extinct forms now usually called †creodonts continued to be disputed. Most of these differ markedly from both fissipeds and pinnipeds. The name "Creodonta" as originally proposed by Cope in 1875b included most of the forms now called †creodonts (also the †Miacidae), but it also included some (not all) living and fossil insectivores and the group was not placed in the Carnivora. Schlosser excluded the insectivores from the †Creodonta in 1886b, but the relationships between †Creodonta and Carnivora continued to be disputed. The idea was not entirely original with him, but it may be said that Matthew's excellent work (especially 1901 and many subsequent studies) led to general acceptance of †Creodonta as a primitive or archaic suborder of Carnivora, coordinate with Fissipeda and Pinnipedia, a system now almost always used and retained in this classification.

Of several suggested changes of this scheme, only that of Gregory and Hellman, 1939a, which is recent and exceptionally able, will be discussed. They propose to abandon †Creodonta, Fissipeda, and Pinnipedia and to use instead a five-fold subdivision of the order: †Procreodi (of Matthew, as a subdivision of †Creodonta; = †Arctocyonoidea of this classification), †Acreodi (of Matthew, as a subdivision of †Creodonta; = †Mesonychoidea), †Pseudocreodi (of Matthew, as a subdivision of †Creodonta; = †Oxyaenoidea except †Palaeonictinae), †Amphicreodi (new in Gregory and Hellman; = †Palaeonictinae), and †Eucreodi (of Matthew, as a subdivision of †Creodonta, but by Gregory and Hellman expanded to include also all the Fissipeda and Pinnipedia). This is a logical phylogenetic arrangement. It is, if not an established fact, at least an acceptable theory that these five divisions are of approximately equal antiquity and represent a basic splitting up of the carnivore ancestry. Yet I feel that the three-fold arrangement is just as consistent with the same phylogenetic theory

and is incomparably more convenient, not to mention the great advantage of familiarity, which I strive to maintain when no error or inconsistency is involved. Logic in classification is not solely concerned with making coordinate units of like antiquity or arising from the same dichotomy—indeed this ideal is completely impractical. There are other essential logical considerations, for instance, the desirability of approximate balance as to evolutionary status and distinctness. To place all the fissipeds and pinnipeds in a group coordinate with one little (four genera), short-lived (late Paleocene and Eocene) side branch of the †oxyaenids (as I think it), mainly because the latter developed shearing blades on two teeth, seems to me definitely illogical from this point of view.[1]

This is a case where a compromise between horizontal and vertical classification is usual and seems to me advisable if not necessary. One group, †Creodonta, includes the most primitive and the structurally ancestral members of the order. From this ancient, more or less central group many lines radiated. The most progressive, most highly modified, longest-lived, and most abundantly varied of these generally derivative groups are set aside as distinct on the same level in the hierarchy. The others, more conservative, more archaic, of shorter duration, and with less morphological and adaptive differentiation are left in association with the ancestral group. The same sort of compromise occurs repeatedly throughout this classification—for instance, among carnivores, on a lower taxonomic level, the relationships of canids to ursids and of viverrids to hyaenids are analogous and the same sort of classification is used—and, indeed, I am convinced that it could not be avoided in practical classification even if it were necessarily desirable to avoid it.[2]

[1] Of course the argument is for this particular case and has the background of probable phylogeny here involved. The desirability of groups roughly comparable in scope can be entirely controvened when, for instance, a single genus is radically distinct phylogenetically and structurally.

[2] In fact, even Gregory and Hellman's arrangement of Carnivora does not avoid this compromise but only transfers it to lower levels. For instance, their †Procreodi are not a phyletic unit but an ancestral group plus its less divergent descendants. The same is true of their Viverridae, from which they separate the Hyaenidae, and of others of their units.

The suborders here recognized can be arranged in linear sequence, †Creodonta > Fissipeda > Pinnipedia, but the actual relationships are more complex and, as usual, cannot be *expressed* in full in a classification but only used as a basis for a classification *consistent* with them. The †Creodonta are a great, ramified complex from within which arose the Fissipeda, in turn becoming a great, ramified complex from within which arose the Pinnipedia, ramifying in their turn.

†CREODONTA

The main outlines of †creodont classification are due mostly to Matthew, whose various studies of early carnivores are deservedly classics of mammalian taxonomy. In an early study (1901), Matthew divided the †creodonts into †Creodonta Primitiva, †Creodonta Adaptiva, and †Creodonta Inadaptiva. He then tentatively excluded the †Miacidae, remarking that they might later prove to be †creodonts. In his great memoir of 1909a, he defined the †Eucreodi (†C. Adaptiva plus †Miacidae), †Pseudocreodi (†C. Inadaptiva minus †Mesonychidae), and †Acreodi (†C. Primitiva plus †Mesonychidae). The next step (Matthew, 1915) was to make a group †Procreodi for the †Arctocyonidae and †Oxyclaenidae, closely related groups hitherto widely separated because of incomplete knowledge of the earlier, transitional forms, leaving only the †Miacidae in the †Eucreodi, †Mesonychidae and †Triisodontidae in the †Acreodi, and †Pseudocreodi as before. Later work kept this arrangement, with some modification as to family relationships and subdivisions.

With a few modifications due to work since Matthew's death in 1930, the present classification closely follows his, the validity and practicality of which have been increasingly apparent to me in the course of considerable research on these animals. Unfortunately it is almost obligatory in scaling this group in with other carnivores to consider Matthew's major †creodont groups superfamilies, and this necessitates the use of names different from his compounds of "-creodi." The most important modification is the removal of the

†Miacoidea (†Eucreodi) to the Fissipeda, as explained later.

The first superfamily, †Arctocyonoidea, includes the oldest and most primitive of all carnivores, along with a few of their least progressive descendants as late as early Eocene. The other superfamilies, †Mesonychoidea and †Oxyaenoidea, represent two more specialized groups that apparently arose independently and at about the same time (early Paleocene?) from the †Arctocyonoidea. The Fissipeda may also have arisen at about the same time and also from †Arctocyonoidea. In this sense the †Mesonychoidea and †Oxyaenoidea are each similar in rank to the whole of the Fissipeda, but these shorter-lived, persistently archaic, and much less varied groups may, and should in a practical classification, be associated subordinally with their ancestry while the Fissipeda are separated and stressed.

The classification of the †Arctocyonoidea is nearly that of Matthew's last work (1937), with minor emendations and additions. Most other authors have separated the group into two, and many into three, families, but none has known the fossils better or presented his evidence more fully than Matthew. The only definite difference of opinion here is that I have rejected the †Chriacinae in Matthew's sense. The †Oxyclaeninae include at least six or seven recognizable small groups and as many or more divergent phyla, of which †*Chriacus* represents one, but they appear to be of less than subfamily rank, the special association of †*Deltatherium* with †*Chriacus* is probably unnatural, and there is little reason to distinguish this small divergent line and not the others, which are about equally distinctive.

The †Mesonychoidea include only one family with a small number of genera among which subfamily divisions are not established or necessary. The general arrangement and many of the details of the †Oxyaenoidea are taken from Denison, 1938, whose presentation is so full, able, and recent that I see no reason to change anything in it. He does not discuss the †Proviverrinae and †Hyaenodontinae, and for these I have collated information from many sources, among them Matthew, 1909, 1915, 1937, etc.; Schlosser, 1887–1890; Martin, 1906; Colbert, 1935c; Scott and Jepsen, 1936; Simpson, 1937a; and others. The only very peculiar feature is the reference of †*Dissopsalis* to the †Proviverrinae, rather than the †Hyaenodontinae, justified by Colbert's study of a skull of this last survivor of the †creodonts.[1] Gregory and Hellman's proposal to remove the †Palaeonictinae to a distinct group, †Amphicreodi, and some of the reasons for not following them in this have already been mentioned.

FISSIPEDA

Aside from the inclusion or exclusion of the †Miacoidea, the recognition and definition of this group have been generally accepted since the pioneer days of taxonomy, although for a time some of its members were confused with insectivores and marsupials. A satisfactory primary subdivison of the suborder has been hard to achieve and probably is not yet available. At first a major difficulty was the plantigrade carriage of a variety of fissipeds then supposed to be related for that reason but now known to be of different origins. Even in the work of Flower, 1869, 1883, still the basis of most classifications of recent carnivores, this ancient concept survived, for he made a basic separation between bear-like and dog-like carnivores ("Arctoidea" and "Cynoidea") as well as between the latter and the cat-like forms ("Aeluroidea"). In 1895 Winge recognized that Flower's "Arctoidea" and "Cynoidea" were very closely allied, indeed he merged their typical families and placed the dogs in the Ursidae, an arrangement not later or now followed, although it has much to recommend it.[2] He thus made only two divisions, Herpestoidei and Arctoidei. This basic arrangement has since been almost universally followed, using a variety of different sets of names. It is followed here, with the names Feloidea and Canoidea. The following diagram shows most of the distinctive arrangements and nomenclatures of the last 70 years:

[1] Colbert did not commit himself as to the subfamily position of this genus, but his clear exposition of its affinities clearly excludes it from the †Hyaenodontinae and allies it with the more primitive group, the †Proviverrinae.

[2] Better in the form of placing the bears in the Canidae.

Flower 1869	Winge 1895	Weber 1904	Matthew 1909	Pocock 1919b	Hay 1930	Simpson 1931	Scott and Jepsen 1936	Scott 1937a	Gregory and Hellman 1939a
Arctoidea Cynoidea	Arctoidei	Arctoidea	Arctoidea	Arctoidea	Ursoidae	Canoidea	Cynoidea	Cynoidea	Canoidea Mustelo- idea
Aeluroidea	Herpes- toidei	Herpes- toidea	Aeluroi- dea	Mungo- toidea	Feloidae	Feloidea	Herpes- toidea Aeluroi- dea	Aeluroidea	Feloidea

There have also been various authorities, among them Beddard and Schlosser, who queried the possibility of valid superfamily grouping and made no divisions between suborder and families.

Taking comparative anatomy and palaeontology together, the most positively established groupings are:

Canidae
Ursidae
Procyonidae

Viverridae
Hyaenidae

The Mustelidae and Felidae are more isolated in position. It is true that primitive mustelids show marked resemblance to canids (and in isolated cases to procyonids), yet in some forms they almost equally resemble what are probably ancient viverrids. Teilhard de Chardin's work, 1915, on the fissipeds of the Phosphorites de Quercy, among the most ancient and primitive known, shows them all to be linked together by a complex web of resemblances, although they probably include prototypal canids, mustelids, viverrids, and felids. They do not flatly contradict and yet do not clearly support a primary fission into canids plus mustelids as against viverrids plus felids. There is even some possibility that the felids became differentiated before the viverrids, although this is improbable. Without attempting to review all the other evidence, there are grounds for each of the following sets of groupings:

Winge and Most Later Authors

Canidae
Ursidae
Procyonidae
Mustelidae

Viverridae
Hyaenidae
Felidae

Scott and Jepsen

Canidae
Ursidae
Procyonidae
Mustelidae

Viverridae
Hyaenidae

Felidae

Possible Split Arrangement on Principle of Accepting only Collocations Proved Beyond Reasonable Doubt

Canidae
Ursidae
Procyonidae

Mustelidae

Viverridae
Hyaenidae

Felidae

Gregory and Hellman

Canidae
Ursidae
Procyonidae

Mustelidae

Viverridae
Hyaenidae
Felidae

After long consideration of all these and others, I have accepted Winge's grouping, which is also that now almost universally current. It unquestionably goes beyond what is really proved, but is not only possible but also probable despite objections to it. Moreover, as the current arrangement, I would hesitate to discard it without stronger reasons than seem to exist. The second arrangement seems to me to be unbalanced in overempha-

sizing the isolation of the Felidae. Their collocation with the viverrids is no more and probably no less doubtful than that of the Mustelidae with the canids. The same objection, from the other direction, applies to the last arrangement. The third arrangement is the best from the point of view of rejecting unproved groupings and is probably as good in general as the current arrangement, but is tentatively dropped because it is not current and because the arrangement that is current is at least not improbable and is more consonant with the usually sound principle of using as few superfamilies as the evidence permits.

Reasons for calling the two superfamilies "Canoidea" and "Feloidea" are given below. To these surviving superfamilies is added a third, †Miacoidea, for primitive forms, as a group structurally ancestral to both the later superfamilies but not diagnostically unitable with either.

†MIACOIDEA

Cope's original definition of †Creodonta in 1875 explicitly included the group later named †Miacidae. When he discussed the †Miacidae some seven years later,[1] he recognized their structurally ancestral relationship to the fissipeds. In 1890 Schlosser considered the †Miacidae as adaptive †creodonts, leading into the Fissipeda. In 1901 Wortman placed the adaptive †creodonts of Schlosser in the Fissipeda (his "Carnassidentia"), indeed referring †*Vulpavus* (in which he erroneously included †*Miacis*) to the Canidae. Matthew (1909a, pp. 320–321, etc.) argued for the retention of Cope's grouping, considering the †Miacidae as †creodonts, in an adaptive section or, in Matthew's own terminology, in a group †Eucreodi, on the grounds that although structurally ancestral to the Fissipeda they still were in fact closer to the inadaptive †creodonts and that their removal from the †Creodonta raised technical difficulties of definition of the groups concerned. Matthew always retained this arrangement, and many others have followed him. Several weighty authorities, however, among them Winge,[2] Scott,[3] and Osborn,[4] have adopted the central idea, although not the details, of Wortman's emendation and have referred the †Miacidae to the Fissipeda.

There is here no difference of opinion as to affinities but only as to their expression in taxonomy. Looking backward, the †Miacidae are closely related to the †Arctocyonidae. Looking, one might say, "sideward," they are near the inadaptive †creodonts. Looking forward, they lead into the Fissipeda. These various affinities cannot all be simply and clearly expressed by any possible classification, and as usual some compromise must be reached. Matthew's view may be paraphrased as an insistence on a consistently horizontal division between †Creodonta and Fissipeda. This has a certain preponderance of pure logic, since the †Creodonta are in any case partly a horizontal group, and horizontally as well as ancestrally the †Miacidae are nearer the †creodonts. The other view is that since the †Miacidae are in a general way ancestral to the Fissipeda and not, like the †Arctocyonidae, also to other †creodonts, it is possible without confusion to array them vertically with the Fissipeda, leaving the †Creodonta as a natural but peculiarly constituted group of various aberrant, non-ancestral lines plus the common ancestry of all. Reversing my former decision, I now follow this latter plan, which seems to be increasingly favored by my colleagues. No change in views as to phylogeny is involved in this purely formal taxonomic modification.

The most radical recent suggestion is that of Gregory and Hellman, 1939a, who not only place the †Miacidae in the Fissipeda (not under that name, which they reject) but also in the Feloidea and as part of the Viverridae. Indeed the †Viverravinae are by them placed in the Viverrinae. It is unnecessary to say that the resemblances and relationships signalized by these authorities are real. The †Miacidae resemble the Viverridae in many

[1] See Matthew, 1937, for résumé and references.

[2] Winge's work on †creodonts shows more than usual of his eccentricity and less of his perspicacity. Few of his innovations regarding †creodonts and †miacoids call for serious review at this date.

[3] In his latest work. He earlier followed Cope and Matthew.

[4] In his last years. This was one of his criticisms of my previous classification, and on discussing the question in 1931 Dr. Gregory, Dr. Granger, and other colleagues concurred.

ways and are almost perfectly prototypal for them, but without apparent exception the resemblances are in characters primitive for all fissipeds, including the canoids. Studying the †Miacidae in connection with the Canidae, rather than the Viverridae, would justify placing them in the Canidae on the same basis, and this has, in fact, been done. Placing them in the Viverridae is nearly equivalent to saying that the Canidae were derived from the Viverridae. Such definitions are legitimate, and given these definitions this sequence and its taxonomic expression are valid. Nevertheless the †Miacidae are diagnostically distinguishable from Viverridae and Canidae and prototypal for both. I prefer to express the relationships by placing the †Miacidae in a separate superfamily from which both Feloidea and Viverroidea arose. As usual, I also give some weight to the fact that this arrangement does least violence to the classification already in general use.

No one has recently revised all the †Miacoidea, an important field for research. The present treatment is based mostly on Matthew, 1909a, 1915, 1937, with various additions and emendations based for the most part on the work of Teilhard de Chardin, 1915, and Simpson, 1937a, plus a few recently described genera and minor points from several other authors.

CANOIDEA

This group has been variously called Cynoidea, Arctoidea, Ursoidae, and Canoidea. Arctoidea and Ursoidae (or Ursoidea) are objectionable because no one considers the bears as nuclear or typical in the group as it is now constituted. Cynoidea (and also Arctoidea) are invalid as superfamily names because they are not based on names of genera or of families belonging in the groups so designated.[1] Thus Canoidea is the most appropriate valid name. Its only fault is unfamiliarity, but Cynoidea is not now any more familiar, Ursoidea is less familiar, and only the name Arctoidea, which is thoroughly objectionable on all other grounds, has a definite advantage in this respect.

Flower's conception of contrasting bear-like and dog-like groups has now been generally and properly abandoned. The bears were almost surely a relatively late offshoot of the dogs and are closely related to the latter. Moreover the classic Arctoidea, consisting of Ursidae, Procyonidae, and Mustelidae, was unnatural because it is impossible that these three families can have had any common ancestry distinct from that of the Canidae.

The primary lines of Canoidea are the Canidae and Mustelidae which are about equally old and, in their earliest forms, about equally primitive, although the Mustelidae later became decidedly more specialized than the Canidae. The other two families, Ursidae and Procyonidae, seem surely to have arisen from the Canidae.

CANIDAE

The Canidae have, of course, been split into two or more families by some students, but their status as a single family is more widely recognized than in most such cases and can be upheld without serious doubt. Fossil canids are very abundant, and this richness is embarrassing since it suffices to complicate rather than to elucidate the subdivision of the family. The whole group is extremely polyphyletic, and few of the phyla are yet positively and clearly worked out.

Many authors recognize a horizontal, primitive subfamily, but I have merged this with the diverging vertical subfamilies. The living canines are remarkably primitive and conservative; they are virtually late Eocene or early Oligocene fissipeds. I have united with them in the Caninae their own unprogressive ancestry which, with a cluster of closely related minor extinct phyla, represents the central line of the Canidae from which the more distinctive subfamilies diverged. This includes genera like †*Daphoenus*, †*Mesocyon*, and †*Tomarctus* that may or probably do represent the ancestry of some other subfamilies. They are not distributed in the latter because they were still generally canine in structure and either because they seem to be about equally related to two or more other subfamilies or because they were as yet so little distinguished that their later connections are not well established.

[1] And if they were not to be used for superfamilies, their superfamily forms would be undesirable.

Despite their world-wide distribution and an abundance of well-distinguished, more or less local species, the recent canines are quite uniform in structure, and it would be justifiable from many points of view to unite them all in a single genus.[1] Most are, indeed, here referred to *Canis*, and it need hardly be said that the *Canis* of this and other reasonably conservative classifications has been split into a dozen or more genera by some mammalogists. The seven other genera of this classification are more distinctive, and their recognition is now really universal.

The nomenclature of the South American dogs here called *Dusicyon* has been peculiarly confused but has finally been reduced to some order by the successive contributions of Kraglievich, 1930a, Cabrera, 1932, Osgood, 1934, and Kühlhorn, 1938. I have followed Osgood. As capable a mammalogist as Cabrera (who is, however, a generic splitter) still recognizes five separate genera in this group, although Kühlhorn has shown that most of the supposed diagnostic characters intergrade. Because of the former nomenclatural confusion I have given the subgeneric classification, contrary to the general rule of this classification. Half a dozen other generic names have been given to fossil (Pleistocene) *Dusicyon*, but it does not seem necessary or worth while to list these.

The Simocyoninae of this classification are surely a heterogeneous group, but the probability is that most of their various phyla are especially related. Better knowledge will doubtless permit a tribal subdivision that will clarify the subfamily, but lacking this it would be disproportionate to set aside single genera (such as *Speothos* or *Lycaon*) in monotypic subfamilies as has been variously proposed. Dogs of this subfamily (or of this adaptive type) appear formerly to have been as widespread and abundant as the canines but now survive only in three limited southern areas. Contrary to frequent similar cases, however, these are on the whole more and not less specialized than their more successful relatives.[2]

Unfortunately the familiar name *Cynodon* belongs to a fish and is flatly invalid in its almost universal use for a fossil dog. The oldest of several synonyms appears to be †*Amphicynodon*, which must, therefore, be used for this genus. This involves changing the subfamily name to †Amphicynodontinae. The name †Hemicyoninae is available, but cannot properly designate the subfamily intended here, because †*Hemicyon* is of doubtful reference to the subfamily. It is probable that the advanced forms †*Hemicyon* and †*Dinocyon* are offshoots of the †*Amphicynodon* group, but it is not certain. Frick, 1926, created his subfamily[3] †Hemicyoninae by splitting off †*Hemicyon* and †*Dinocyon* from their canid ancestors and allies and uniting them with similar but more bear-like forms, e.g., †*Agriotherium*, commonly referred to the Ursidae. The Canidae and Ursidae intergrade almost perfectly through these various genera, and drawing a line is more a matter of taste than of fact. Frick's arrangement is as valid as any other, but in accordance with various studies subsequent to Frick's paper (e.g., Pilgrim, 1931, 1932; Colbert, 1935c; Scott, 1937a), I incline to think that †*Agriotherium* and its closest allies are best referred to the Ursidae. These doubtless arose from animals similar to †*Hemicyon* (probably not from that genus itself), but †*Hemicyon* and †*Dino-*

[1] As is well known, all the wild canines together cover a very much smaller morphological range than do domestic dogs, which are surely referable to one genus if not one species. The comparison is not really valid, however, because human selection has no counterpart in natural evolution and results of an analogous sort never have arisen and never could arise without human agency.

[2] This is an interesting apparent exception to Matthew's rule that disjunctively distributed southern groups of animals are usually primitive stocks formerly Holarctic. This exception and most others disappear when the rule is restated: disjunctive or relict southern groups are usually ancient stocks formerly Holarctic, displaced and extinct in Holarctica either (a) because of replacement by ecologically incompatible progressive groups, or (b) because of secular shift in environmental conditions. In the first case, (a), the southern relicts will as a rule be more primitive than their Holarctic relatives, while in the second, (b), they are likely to be more specialized because it is the most specifically adapted animals that suffer most from environmental change (rule of "the survival of the unspecialized"). The simocyonines apparently are an example of (b). In any case they definitely follow the rule for southern disjunctive distribution that they are of very ancient origin (almost as old as the canines) and were formerly Holarctic.

[3] He calls it a "morphologic group" and disclaims "the implication of an idea of real relationship" or the intention of creating a taxonomic subfamily.

cyon were still somewhat more dog- than bear-like in essential characters. If the canid-ursid line is not drawn at the convenient point between these genera and †*Agriotherium*, there is little logical reason for not referring the whole sequence, from †*Plesiocyon* onward to the Ursidae. This step was actually taken by Pilgrim, 1931,[1] but it leads to such difficulty and confusion in practical taxonomy that I cannot follow it. †*Amphicynodon* and its early allies are completely canid in character with as yet very little hint of their ursid descendants. It is much simpler, more practical, and nearer to probable reality to call these forms canids and to recognize the fact that the ursids arose from the canids. Moreover it is possible that not only the ursids but also the procyonids arose from †amphicynodontine canids (although the procyonids may have arisen from a canine like †*Pseudocynodictis*, as McGrew, 1938, suggests).

At various times most of my †Amphicynodontinae and †Borophaginae and many of the †Simocyoninae have been referred to the †Amphicyoninae, which were then characterized only by a more or less bear-like habitus. It is fairly clear that this was a superficial arrangement bringing together lines merely convergent in adaptive features. This may still be true of my restricted †Amphicyoninae, but it is probably more nearly a natural group. It appears to have been independent of the roughly parallel †Amphicynodontinae since the late Eocene. †*Tomocyon* may represent another such deployment, but if so it is too poorly known and its scope and character are still too obscure for formal recognition.

The genera here set aside as †Borophaginae are large, later Tertiary canids with heavy jaws, rather distantly convergent toward the hyenas and so sometimes called "hyaenoid dogs." The recent excellent study of †*Aelurodon* by VanderHoof and Gregory, 1940, suggests that two (or more) phyla of separate origin may be included, branching off from the canine line in the vicinity of †*Tomarctus*. The present subfamily may, therefore, be polyphyletic in detailed origin, but this is uncertain, the various genera are closely similar, and they must have had a common origin very little, if at all, before the rise of the morphological subfamily.

Nothing is known of the history of *Otocyon*. Its possession of four molars and some other peculiarities have led to its being placed in a separate subfamily or even family, but it is basically not only canid but also canine.[2] Its peculiarities are such as do occasionally appear as mutations or anomalies among canines, and it may thus have arisen suddenly and by saltation. Despite some arguments, this appears to me as one of the very few and exceptional cases in which the sudden appearance in nature of a fully formed new generic or higher group can be considered as at all probable. It is questionable whether such distinctions, not more deeply affecting the generally canine organization, merit subfamily rank, but I follow the consensus in tentatively granting this.

Besides other papers already cited, on Canidae see Teilhard de Chardin, 1915; Scott and Jepsen, 1936; Loomis, 1932, 1936; Matthew, 1930; Matthew and Stirton, 1930a; Pilgrim, 1931, 1932; Viret, 1933; Pocock, 1914; Klatt, 1928; Colbert, 1935c, 1939; Hürzeler, 1940a, b. The literature is very extensive, but most of the older papers are cited in these.

URSIDAE

The bears form one of the most recent groups of mammals generally granted family rank. Indeed, so recent is their origin, so little their distinction from the dogs, and so complete their intergradation with the latter that it is mostly inertia and the custom of more than a century that cause their family separation.[3] Drawing the canid-ursid line where I do, the Ursidae became distinct only well along in the Miocene. If, with Frick, 1926, the line be drawn above †*Agriotherium*,

[1] But he was in fact dealing only with †*Indarctos* and still more definitely ursid genera so may not have visualized perfectly the implications regarding the vastly more primitive genera not in his hands.

[2] Among others, Matthew *in* Osborn, 1910, and Pocock, 1914, have referred it to the Caninae.

[3] Yet Flower separated them still more widely ("Arctoidea" as opposed to "Cynoidea"). Winge united the Canidae and Ursidae, and there is much to be said for this, although his preference for the latter name seems indefensible. Another practical reason for separation is that the canid family is so large even without including the bears.

†*Indarctos*, and †*Ursavus*, they arose about the beginning of the Pliocene.[1] They were almost surely derived from †amphicynodontine (not †amphicyonine) dogs as an omnivorous, relatively gigantic, plantigrade specialization.

Some authors divide the bears into two or three subfamilies. For instance, Kraglievich, 1926, splits off †*Agriotherium* and †*Indarctos* (perhaps also †*Ursavus*, which he does not mention) as "†Hyaenarctinae,"[2] †*Arctotherium*, †*Pararctotherium*, †*Tremarctotherium*, and *Tremarctos* as Tremarctinae, and the remaining genera as Ursinae. Such subdivisions, however, are of very doubtful theoretical validity and of little or no practical convenience. The primitive "†Hyaenarctinae" (or †Agriotheriinae, or †Hemicyoninae) are simply a few transitional forms, on various different lines of descent, between more dog-like and more bear-like stages. It is probable but not certain that †*Arctotherium* and its supposed extinct allies are especially related to each other, and it is only possible and not clearly probable that they are particularly allied to *Tremarctos*. The generic separability of *Tremarctos* from *Ursus* is not universally admitted, and its subfamily separation is clearly excessive. Moreover there is the anomalous position of *Selenarctos*, apparently midway between *Tremarctos* and *Ursus*. All living ursid genera are very closely allied, at least as closely as is indicated by placing in a single subfamily in a balanced classification. There are only a few genera, and their finer grouping is not a practical aid or requirement.

Generic separation between *Melursus* and *Ursus* is adopted by all authors. Regarding other genera, authorities differ widely although, as in all groups, there is a tendency to recognize more and more genera. There are only about eight clearly distinct living species of bears,[3] and each has been made the type of a genus. Closely allied as these are, I have tentatively listed them as separate, except "*Danis*," now universally abandoned, and *Euarctos*, which is often admitted (without critical balancing of the evidence) by American neo-mammalogists but seems to be of no more than subgeneric distinctness by any standards less extreme than those of Merriam.

There has been much difference of opinion and usage regarding the names of arctotheres. The oldest generic name, †*Arctodus* Leidy, 1854, has often been passed over as indeterminate, and a common practice has been to refer all these bears to †*Arctotherium* Bravard, 1857. Kraglievich, 1926a, also recognized †*Pararctotherium* Ameghino, 1904, in South America and demonstrated the generic distinction of the North American forms, calling all of them †*Tremarctotherium* Kraglievich, 1926, believing †*Arctodus* to be a *nomen vanum*. Gidley, however, in 1928 maintained that †*Arctodus* is determinate and is generically distinct both from the South American and from the common Californian arctotheres, confining †*Tremarctotherium* to the latter. I have tentatively followed Gidley, although the question is not definitely answered as yet.

Among the more important recent papers on the taxonomy of bears are Kraglievich, 1926a; Frick, 1926; Pocock, 1914; Davis, 1941. The literature is widely scattered.

PROCYONIDAE

The procyonids have at various times been split into seven different families, that is, each of the seven surely valid living genera has been placed in its own family. Even now most authors split the group into two, many into three, families, but different authors

[1] Frick, himself, believes that they must have been distinct much earlier, at least as early as the Oligocene, although unknown before the Pliocene. On quite different evidence Pilgrim would also make them distinct in the Oligocene, but, as noted above, the known early forms, although structurally ancestral to bears, were still indistinguishable from dogs.

[2] Correctly †Agriotheriinae. This is the group Pilgrim and Colbert intended by the name †Hemicyoninae, since they were dealing not with †*Hemicyon* but with †*Agriotherium*, †*Indarctos*, and †*Ursavus*.

[3] C. H. Merriam distinguished about 90 species of North American bears alone, but he had a (fortunately) unique conception of the character of a species, giving it less scope than most authors give a minor geographic race, not much more than an individual genetic family group. On such a system twin bear cubs could be of different species. It is true that the classic species can be, and commonly are, split up for convenience into several times seven species, but these represent only variations of seven or eight really distinctive types, which were the species of a generation ago and are still for conservative authors.

recognize different families. Pocock (1921a; see also Hollister, 1916) has given an able and useful treatment of the living forms but one that is, like most of his, excessively inflated, with three families, two monotypic, and the third split into five subfamilies, each essentially monotypic (in two he recognizes a second genus often held to be a subgenus). It is highly probable that all these forms have a common ancestry and are more nearly related to one another than to any other carnivores. They fit well into one family, they are not numerous enough to demand splitting for convenience, and to divide them more radically merely obscures their affinities and defeats a prime purpose of classification.[1]

Among the genera here called Procyoninae, *Bassariscus* and *Potos* are the most distinctive, and it has been claimed for each not only that it merits family distinction but also that it is not really allied to the Procyonidae at all but merely a distantly convergent type. *Bassariscus* is an old and conservative genus, so stands quite apart among living forms, but it is so near the early fossil procyonids that I cannot doubt the reality of the relationship. Placing it in a separate subfamily could be justified, but I tentatively prefer to make no distinction here where consistent distinction (short of seven nearly, or quite, monotypic subfamilies) can be made.

The evidence as to *Potos* is very conflicting, and in some respects this genus differs radically not only from all (other) procyonids but also from all canids and ursids (see, e.g., Davis, 1941). Yet I think the balance of the evidence favors derivation from primitive procyonids. It should, in this case, have an independent ancestry since about the Miocene and could then quite well preserve early canoid characters lost not only in the other living procyonids but also in living canids. Such a history is consonant with the probable geographic facts: the isolation of the *Potos* ancestry doubtless dates from the adventitious introduction of procyonids into South America in the Miocene, before the rise of a true land route between North and South America.

†*Sivanasua* is an anomalous form. Schlosser thought it near †*Parailurus* and *Ailurus*, and I tentatively continue this geographically probable and anatomically quite possible arrangement, although Pilgrim believes it quite distinct and probably nearer the Procyoninae. †*Parailurus*, in any event, it is now agreed, is related to *Ailurus*. Few animals have been of more disputed affinities than *Ailuropoda*. It has been considered an ursid, a procyonid, and neither. It has been associated with *Ailurus* and claimed to have nothing to do with that genus. Recently Raven, 1936, has studied the viscera, and Gregory, 1936, the skull and dentition, of *Ailuropoda*. In addition to their own full and careful studies, they have reviewed all previous observations, opinions, and arguments, and they agree that *Ailuropoda* is related to *Ailurus* and that its affinities are best expressed by placing both in a subfamily Ailurinae of the Procyonidae.[2]

Pohle claimed the presence of a bassariscine procyonid in the Oligocene phosphorites of France, †*Pseudobassaris* Pohle, 1917. Given the extreme improbability of such an occurrence, the fact that Pohle had not seen the specimen in question but knew it only from Riggs, who did not think it a procyonid, and the fact that no confirmation has yet appeared, the supposed datum is hardly worthy of record at present.

Among numerous special papers on Procyonidae, some of the most useful are Hollister, 1916; Pocock, 1921a; Gregory, 1936; Raven, 1936; McGrew, 1937, 1938, 1941a; Klatt, 1928; Davis, 1941.

[1] In this connection, and as one of the principles of this whole classification, I applaud the remarks of Matthew, 1924, apropos of the splitting of the Procyonidae, Mustelidae, and Viverridae into many different families: "This procedure appears unnecessary and objectionable. To create new families for each of the minor groups into which the Carnivora are divisible merely serves to obscure the broader affinities which the families are intended to represent. The smaller groups may be well enough distinguished as subfamilies or as phyla without whittling down the scope of the families of current usage."

[2] *Ailuropoda* is often written *Aeluropus* by recent authors. As an amusing sidelight on taxonomy, Matthew and Granger (1923c, p. 579) have a footnote: "*Æluropus* = *Æluropoda* for the purists." Although disclaiming the title of "purist," in this case I see no reason for not using the name originally given to the animal, which was neither that used by Matthew and Granger nor that assigned by them to the purists.

MUSTELIDAE

In the early Oligocene the fissipeds had diverged so little that it is difficult to distinguish at that time between certain of the less-specialized canids, mustelids, viverrids, and felids. Students devoting particular attention to those ancient faunas are thus likely to group together horizontally a great variety of genera, for instance as in Teilhard de Chardin, 1915, despite the subsequent very wide separation of the phyletic groups that they seem to represent. Thus, too, Loomis, 1932, was able to maintain that several extinct American genera were viverrids, although other students (followed in this classification) distribute them among the canids and mustelids. Schlosser, 1923, made a mustelid subfamily, †Stenoplesictinae, for several of these little-differentiated early forms, probably including not only true mustelids but also some viverrids and, perhaps, felids. I believe †*Stenoplesictis* itself to be viverrid, so reject this as a mustelid subfamily.

The situation is the usual one of having innumerable small branches given off near the base of the major splitting of a mammalian group, branches that offer the greatest difficulty to the taxonomist and that can almost equally well be associated with various different later groups or placed in separate divisions of their own. In the Mustelidae the situation is further complicated, as Matthew and others have repeatedly shown, by the fact that the numerous known Miocene and Pliocene mustelids are seldom real forerunners of the living genera, but almost every genus appears to be all that is known of a distinct phylum. A strictly phyletic suprageneric arrangement is not now a practical possibility. Most of the extinct genera are here referred to the recent subfamilies that they most resemble, usually with some doubt and always with the result of making the subfamilies clusters of separate lines as yet not clearly or strongly linked together. Most of the early forms as well as divergent genera of doubtful status are placed in the central subfamily, Mustelinae.

Pocock, 1922a, recognizes 15 living subfamilies. On the same scale the known fossil forms would add at least 15 more subfamilies. This is begging the question and does not result in a true or useful classification. All students separate the Mustelinae and Lutrinae, groups surely of subfamily rank. Most also separate the Melinae. The separation of the skunks, as Mephitinae, from the badgers, Melinae, is more open to question, but the groups are reasonably well defined and I have tentatively accepted this division. Further separation of the badgers into different natural groups seems to me impossible or at least premature now.

Mellivora and its one known extinct ally †*Eomellivora* also stand out as decidedly isolated from any other mustelids, and their group is tentatively ranked as a subfamily. The extinct, somewhat raccoon-like †*Leptarctus*, †*Craterogale*, and †*Mephititaxus* are still more sharply distinct and cannot be denied the subfamily separation given them by Gazin, if subfamilies are to be used at all in this family. I have kept the whole miscellany of other known genera in the Mustelinae, since with both recent and fossil genera to deal with I cannot detect in present knowledge a rational means of making consistent and useful supergeneric groups. It is tempting to recognize at least the Guloninae, but it seems almost impossible to define such a group properly, and it is doubtful whether its concept (unless the subfamily be simply equated with a single genus) is really more than that of a habitus variously acquired by a number of different mustelines. Indeed the mustelids are almost rodent-like in their extreme polyphyly and convergences and offer taxonomic difficulties like those of the Rodentia on a smaller scale.

There are some excellent reviews of parts of the family, but no one has studied and revised it as a whole, a problem that should be particularly attractive for some future student. The present review is based largely on Pocock for the recent forms, although his formal expression of the taxonomy has been decidedly altered in accordance with a more conservative and synthetic viewpoint. For the fossil forms, a synthesis has been made of scattered data given by more than 20 authors. The recent literature includes, and much more of it is cited in, Helbing, 1936; Gazin, 1936a; Hall, 1930a, 1936; Pohle, 1919; Pocock, 1921b, 1922a.

FELOIDEA

The name "Aeluroidea" is still that most commonly applied to this superfamily, but it is quite invalid as a superfamily name since its group includes no genus *Aelurus*. It is still more objectionable because there is a genus *Aelurus* (or *Ailurus*) which is not an "aeluroid" in the classical sense but a canoid ("cynoid" or "arctoid"). Recognizing these facts, Winge proposed to call the group "Herpestoidei." Believing (incorrectly, or at least very doubtfully) that *Herpestes* is an invalid name, Pocock replaced this term by "Mungotoidea." The serious objections to the use of Herpestoidea are that few students recognize a family Herpestidae and that most prefer to follow the intention and concept of Flower, more important than the superficial point of his nomenclature, and keep the cats as the nucleus of the group. This leaves no valid and logical alternative to the term "Feloidea."

A few students, like Scott and Jepsen, 1936, split the group into two: one division, "Herpestoidea" (better Viverroidea), for Viverridae and Hyaenidae, and one, "Aeluroidea," *sensu stricto* (better Feloidea, *sensu stricto*), for Felidae.[1] This is a natural division, since the viverrids and hyaenids are nearer to each other than to the felids, but these subdivisions are probably not coordinate with Canoidea ("Arctoidea" or "Cynoidea"), and the arrangement seems unbalanced unless the latter group also is split (at least into Canoidea and Musteloidea) and the whole concept of fissiped taxonomy now generally accepted thus abandoned. I am not at present inclined to take this step.

VIVERRIDAE

Pocock (numerous short papers, 1915a–d, to 1937) attacked the unity of the classic family Viverridae, maintaining that authors place in this family all "aeluroids" (feloids) not manifestly cats or hyenas, regardless of their true affinities. He, therefore, placed the forms here considered viverrids in four different families. Gregory and Hellman (1939a) included Pocock's Nandiniidae in the Viverridae but recognized the Herpestidae as separate and placed Pocock's Cryptoctidae in the Felidae.

Although I do not differ in any very important way from Gregory and Hellman's phylogenetic conclusions or even (with more exceptions) from Pocock's, I retain the broader classic conception of the Viverridae. This is one of many cases in which the same phylogenetic scheme is consistent with numerous different classifications, and, as usual, granted such consistency, I prefer the classification that preserves the most familiar usages, that most clearly suggests the broader relationships, and that uses families in a relatively inclusive and balanced way. The viverrids, in this broad sense, are an old group of carnivores that include many different lines of specialization, a horizontal grouping of the oldest, most generalized forms plus such vertical lines as depart least radically from this basis. The two among these many lines that depart most radically are separated on that account as families: Felidae and Hyaenidae. As I see it, the arrangement of Gregory and Hellman is no more "natural" than this and is a compromise between this familiar arrangement and a more radical, strictly phylogenetic or vertical scheme, which should, according to their views of affinities, have five coordinate groups (families?): (1) their Hyaenidae plus Viverrida, (2) their Paradoxurida plus Hemigalida, (3) their Galidictida, (4) their Herpestidae, and (5) their Felidae. This, again, would be entirely valid and consistent with probable phylogeny, but it is an unnecessary complication and does not seem to me to have much, if any, advantage over the present arrangement.

The present classification is based almost entirely on the work of Gregory and Hellman, which in turn drew heavily on that of Pocock but modified it considerably. Only the scale of units is here changed. Their "sections" of Viverridae and their family Herpestidae are made subfamilies, and their subfamilies are made tribes. I have, in addition, retained Schlosser's †Stenoplesictinae, a horizontal and structurally ancestral group, because its members do not seem to me sufficiently differentiated to refer to any or several of the more characteristic later lines.

[1] But in the following year ("History of land mammals") Scott abandoned "Herpestoidea" and returned all to the "Aeluroidea."

Gregory and Hellman's reference of the †Miacoidea to the Viverridae has been discussed under †Miacoidea. Their reference of *Cryptoprocta* to the Felidae is rejected but again without much disagreement as to the facts. They have shown that *Cryptoprocta* has some felid characters, while admitting that it is nearer the viverrids in most respects, and they therefore suggest that it is a very conservative survival of the earliest, most viverrid-like stages of felid evolution. It is, in fact, more like the viverrids, and it seems to me just as likely to have arisen from a primitive viverrid, near but distinct from the felid ancestry, like †*Palaeoprionodon*, as from such a closely similar but more cat-like form as †*Proailurus*. Cats and viverrids were closely similar in the early Oligocene and it is not surprising that a survivor should share some of the characters of both.

Viverrids are also known in the middle and later Tertiary, but the fossils throw little light on the details of subfamily and tribal history. The family has evolved mainly in tropical Africa, Asia, and the East Indies (but, rather surprisingly, did not reach Australia), and this, as in the case of the Muridae, probably explains both the rarity of fossils and the fact that viverrids never reached America.[1]

Viverrids are the only native carnivores of Madagascar, and they have there developed peculiar insular forms as did some of the rodents. It appears probable, however, that Malagasy viverrids do represent more than one mainland stock, as the classification suggests, although this is not certainly established.

The mongooses and mierkats are a very ancient offshoot of the general viverrid ancestry, almost as old as the cats and older than the hyenas but not so distinctive as either of these.

As already stressed, the best review of the Viverridae is Gregory and Hellman, 1939a, and this includes an excellent bibliography. Lamberton, 1939; Pocock, 1915a, b, c, d, 1919b; Colbert, 1939; Teilhard de Chardin, 1915, may also be particularly mentioned.

[1] Unless Gregory and Hellman are followed in calling the †miacoids viverrids, or Loomis was right in so identifying some fossils here considered canid and mustelid.

HYAENIDAE

The relationship of the Hyaenidae to the Viverridae is like that of the Ursidae to the Canidae. The hyaenids are a late (probably well within the Miocene) offshoot of the viverrids, just as the ursids are of the canids. Some forms, notably †*Ictitherium*, attest the transition to such an extent that they can almost equally well be called viverrids or hyaenids, just as such forms as †*Agriotherium* can almost equally well be called canids or ursids.

In considering †*Ictitherium* (with †*Palhyaena*[2]) as a hyaenid I have followed Winge, Pilgrim, and Colbert, who seem to me to have demonstrated that it is closer to the typical hyaenids than to any viverrids, much as it still resembles the latter, and so disagree with Schlosser, Dietrich, Zdansky, and others who call it a viverrid. It does, however, seem advisable to signalize its isolated position and non-ancestral character by retaining Trouessart's and Dietrich's subfamily †Ictitheriinae, transferring it to the Hyaenidae.

Proteles is a very peculiar genus, closely similar to the hyenas in aspect and many details, but also similar to viverrids in more obscure characters and unique in many ways. Flower and many later authors assign it to a distinct family. Others maintain that it is a

[2] Also †*Thalassictis* Gervais, 1850, *ex* Nordmann, and some specimens referred (probably in error) to †*Progenetta* Depéret, 1892. Pilgrim, 1931, selects *Mustela †incerta* as type of †*Thalassictis* and as this is also the type of †*Progenetta* the two would then become synonyms. Pilgrim seems, however, to be mistaken in this point. The form in which Gervais referred to †*Thalassictis* makes it evident that he considered †*robusta*, not †*incerta*, as its type, and if any doubt remains it is removed by the positive designation of †*robusta* as type of †*Thalassictis* in 1904 by Palmer. Therefore, this is the type of †*Thalassictis* beyond question and Pilgrim's attempted selection of †*incerta* in 1931 is without effect. Since †*robusta* belongs to †*Ictitherium*, †*Thalassictis* is a synonym of that genus. †*Progenetta* is not a synonym of †*Ictitherium*, since authorities seem to agree that †*incerta* does not belong to that genus. The published data on the real type of this species do not seem to show conclusively whether it, and consequently †*Progenetta*, belong in the Mustelidae, Viverridae, or Hyaenidae. Some true viverrids and some true hyaenids have been referred to †*Progenetta*, but without adequate assurance that they are really congeneric with the very faulty type of the type species of that genus, which may be mustelid. I have, therefore, omitted †*Progenetta* from the formal classification.

viverrid (given subfamily rank) only convergent toward hyaenids. Yet the studies of Flower, Winge, van Kampen, Pocock, Sonntag, Gregory and Hellman, and others seem to show, even when they did not themselves reach this conclusion, that *Proteles* is more probably a specialized, partly degenerate offshoot of primitive Hyaenidae than merely a convergent form.

The unquestioned, typical hyenas show little important divergence and have a short and little-known history, making this one of the smallest of mammalian, and much the smallest of carnivore, families, even with †*Ictitherium* and *Proteles* included.

Important papers on Hyaenidae include Colbert, 1939; Davis, 1941; Pilgrim, 1931, 1932; Zdansky, 1924, 1925a, 1927; Stirton and Christian, 1940 (in my opinion their fossil is doubtfully or not hyaenid); Gregory and Hellman, 1939a; Dietrich, 1927.

FELIDAE

There are irreconcilable differences of opinion regarding the phylogeny, and hence the major taxonomy, of the felids, in addition to the usual many disagreements as to details. According to one view, of which Matthew was the leading proponent, the true feline line arose in (or near) the genera †*Dinictis*-†*Nimravus*-†*Pseudaelurus*, which were placed in the Felinae. Scott and others have held that †*Nimravus*-†*Pseudaelurus* and related forms are neither ancestral felines nor true †saber-tooths, †machairodontines, but form a wholly distinct group, called †Nimravinae. Still others maintain that at least the earlier of these doubtful forms are †machairodontines. My opinion is that †*Pseudaelurus* and †*Metailurus*, at least, are structurally near the feline ancestry and that †*Nimravus* is not far off it at an earlier stage, as Matthew maintained. Nevertheless I have retained the †Nimravinae distinct from the Felinae. This is justifiable even if the Felinae arose from the †Nimravinae, and it has the further virtue of relative independence from doubtful theory because the arrangement may still be valid even if this proves not to be true. It is, for instance, virtually Scott's arrangement, even though we disagree as to phylogeny.

In recognizing the †Proailurinae and placing them in the Felidae, Pilgrim is followed. Schlosser placed these forms (except †*Vinayakia*, not known to him) in the Mustelidae. Others, reviewing recent evidence in more detail, see in these genera resemblances to the viverrids and felids, for instance, Teilhard de Chardin and Viret. Even if it is not certain, it does appear probable, as Pilgrim thinks, that the viverrid characters are primitive, the felid specialized, and hence that the group can be tentatively considered an unprogressive, in part structurally ancestral, offshoot of the earliest felids.

†*Dinictis* is sometimes considered a true †machairodontine even (as in Scott) when †*Nimravus* is not, but it is close to †*Nimravus* and if, as Matthew thought, it stands near the common source of †machairodontines and felines, some †machairodontine characters should occur even if it is a feline or †nimravine. Similarly †*Pseudaelurus* and †*Metailurus* are such nearly perfect transitional types from †Nimravinae to Felinae (see, e.g., Stock, 1934) that they are placed now in one now in the other group, but this is to be expected under (and it supports) Matthew's theory, and the placing of the division line depends on convenience and opinion. If, as here, these genera are placed in the †Nimravinae, few distinct genera of felines, *sensu stricto*, are known and they go back only to the basal Pliocene (or possibly uppermost Miocene).

Contrary to usual custom, the †machairodontines are here placed last because they are no older than the †nimravine-feline combination and their end forms are more specialized. Until recently, almost all the Old World forms were called †*Machairodus*, a usage surely too broad and miscellaneous. Lately some students have swung to the other extreme and recognize every doubtful little difference as generic. I have tried to recognize and to find valid names for such broad but well-defined groups, truly generic on the scale of this classification, as can reasonably be said to have been properly differentiated.

†*Hyainailouros* is a form of very doubtful relationships, but it seems to be feloid and may be an offshoot of the Felidae, but perhaps of one of the other families. If it is a felid, it is certainly very aberrant, so is well placed at the end of the group. Too little is known about it to go to the length of making

a separate family, but this may be necessary when knowledge is increased. The recently described †*Ailuraena* (see Stirton and Christian, 1940) was referred to the Hyaenidae by its authors. It certainly has remarkable resemblances to the hyenas, but it also resembles the cats and is not typically either hyaenid or felid. Among the recent cats, everyone gives generic rank to *Felis* and *Acinonyx*, but that is as far as agreement goes. Some recognize no other genera and some recognize 20 or more other genera. It is, as Pocock has pointed out, curious that the genus most commonly recognized, next to *Felis* and *Acinonyx*, is *Lynx*, which is more nearly a true *Felis* than at least a dozen other proposed genera that are not so commonly recognized as such. In fact, the work of Pocock, Sonntag, Haltenorth, and others shows beyond serious doubt that the most distinctive group of species sometimes included in *Felis, sensu lato*, is that typified by the so-called big cats, lion, tiger, panther, etc., the prior name for which is *Panthera*. This seems to be a good genus by any modern standards, and I have so classified it. Pocock and Haltenorth disagree as to the contents of the genus, and I have followed the latter. His work is later, much more detailed, and is based on what appear to be more reliable taxonomic characters. *Uncia* is recognized by both Pocock and Haltenorth as a distinct genus closely allied to *Panthera*. I have tentatively made it a subgenus of that genus.

In general no attempt has been made in this classification to list subgenera, but in this case the subgenera are so numerous and have been so insistently called genera by splitters that it would be a serious lack to omit them. In 1858 Severtzov placed every well-distinguished species of felid then known in a distinct subgenus. In 1917 Pocock revived most of these names and gave them generic rank. He did group the species to a slight extent, with evident reluctance, and probably most of his groups will be recognized as natural, but hardly any reasonable modern zoologist would agree that they are of generic rank. As a matter of scale, Pocock's felid genera are for the most part here given subgeneric, and his subfamilies generic, rank.

J. A. Allen, 1919, reviewed the small South American cats and not only accepted Pocock's splitting of them but also revived the few supposed genera that Pocock had kept as synonyms (*Noctifelis, Margay, Oncifelis, Lynchailurus*) and proposed a new genus (*Oncilla*). His comment on the lumpers is so diverting and so characteristic of the extreme splitters' viewpoint that it is quoted:

"These groups are given, tentatively and for convenience, the nomenclatural rank of genera. Their evaluation by future investigators will be subject to general equation, from the viewpoint of whether all cats should be placed in *Felis*, because they are neither bears nor wolves, or that a few leading types may be segregated, to show that the domestic pussy is neither a lion, nor quite a leopard, nor a lynx, or whether it is better to indicate that even among the smaller cats there is some diversity of structure and relationship. To illustrate, the latest faunal list of North American Felidae includes 41 forms, of which 16 are placed in the genus *Lynx* and 25 in the genus *Felis*. Of course the merest tyro in natural history will see at a glance that a part are lynxes and the rest are cats, but only a specialist in cat nomenclature will be able to recognize which are big cats (as pumas and jaguars) or small cats, or which are plain-colored and which are elaborately patterned with spots and bands, or what are their natural relationships; except in the case of subspecies where the trinomial is the key. A further use of generic divisions would not obscure the fact that they are all cats but would indicate that at least all cats are not alike, and perhaps inspire interest as to how they differ."

This argument is almost as disingenuous as it is ingenious. In the first place, its whole point of view is that the purpose of classification is to separate things, barely hinting at the vital fact that bringing things together properly is the more useful and important function of taxonomy. In the second place, Allen seems to deplore the existence of any taxonomic grades between subspecies and genera. In fact a careful examination of his classification shows that he does not use the specific grade in any useful way; in his system the genus does the work and takes the place of the species and the next smaller working unit is the "form," subspecies, or local race. As for subgenera, he ignores them altogether.

Thus while insisting on further generic splitting in order to show grades of differences (and, in theory but not in his practice, of resemblances), he throws out the very mechanism by which this can best be done. It is virtually impossible to show such grades if generic, subgeneric, and specific ranks are all leveled out as genera.

Perhaps it is not necessary to emphasize the especially disingenuous touches in this argument. Allen surely well knew that the fact that cats are not bears or wolves is shown (by everyone) by their being placed in a different superfamily, not by their generic allocations. It is also impossible to believe that Allen really thought that it would help "the tyro in natural history" to make him learn seven generic names in place of one, or that, for instance, there is anything in "*Margay glaucula glaucula*" that will convey to the tyro the idea of a small, gray, spotted Mexican cat more clearly than would *Felis tigrina glaucula*. Indeed a tyro would never guess, and not all specialists would know offhand, even that "*Margay*" is a cat, and the name used by Allen shows nothing as to its relationships, whereas the other name reveals at once to the specialist and also in less degree to the tyro a whole sequence of affinities in different degrees.

I have followed Allen only to the extent of listing *Noctifelis* as a possible subgenus, although even on this level I think it might well be merged with *Felis* (*Leopardus*).[1]

Only one recent attempt has been made to review all the Felidae, fossil and recent, that of Kretzoi, 1929a, and this must be called a failure. It is a nearly complete tabulation and compilation of the proposed genera and species and as such is useful, but its phylogenetic and taxonomic conclusions are not convincing. An extreme example of splitting, perhaps the worst yet to appear, it divides the Felidae of other authors into six families, 15 subfamilies, and more than 60 genera. Without first-hand knowledge of the materials, Kretzoi frequently reaches conclusions radically opposed to those of the students who did have a thorough knowledge of them. His generic criteria often seem to be based on individual variations and seldom can reasonably be given more than specific value. In one case he even proposes a genus for material that he himself considers generically indeterminable! His nomenclature has been carefully considered, and much of it is listed (in synonymy) in my classification, but it has been controlled by reference to more solidly founded work. In a few cases he has supplied needed names for real groups previously known but not correctly named, and these names are, of course, used as valid—they amount to only three genera.

A real revision is much to be desired, and it may be hoped that someone will take Kretzoi's ill-advised outline and expand and emend it into a more complete and better founded study.[2]

The literature on this family is enormous. A fairly comprehensive view, or at least an introduction to such, can be obtained from: Haltenorth, 1937; Pocock, 1917; Matthew, 1910c; Brongersma, 1935; Allen, 1919; Stock, 1934; Burt, 1931; Zdansky, 1924, 1925a, 1927; Pilgrim, 1931, 1932; Teilhard de Chardin, 1915; Scott and Jepsen, 1936; Simpson, 1941b; Merriam and Stock, 1932.

PINNIPEDIA

Early classifications inevitably confused the seals with some unrelated marine mammals, but even in Linnaeus they were correctly classified as Ferae, and their common derivation with the land carnivores is now universally admitted and represented by subordinal rank in the Carnivora. Derivation from some †creodonts has been suggested (e.g., by Wortman, from the †Oxyaenidae) but not substantiated. Derivation from, or at least special relationship to, the bears has been supported by a long series of eminent students and may still be the consensus, but Kellogg has argued cogently against it, and

[1] Unfortunately not the name of the leopards, which belong in *Panthera*.

[2] In the same year, Kretzoi published another paper on cats, Kretzoi, 1929b. I have been unable to consult this work, which is in Hungarian and apparently was privately published, but I have seen an abstract by Lambrecht. According to this abstract, Kretzoi here proposed nine more genera and another subfamily. This is confusion worse confounded. I do not think that there is the slightest chance that any of these names merit recognition, even if they can be considered published in a technical sense, and no attention is paid to them in this classification.

it is, indeed, virtually impossible if only because the pinnipeds are certainly a far older group than the bears. As far as it may be valid at all, this theory can, therefore, be upheld only in the form of derivation from preursid canids or canoids, which is possible but hypothetical. Mivart held that the Phocidae were allied to the Lutrinae, and the Otariidae to the Ursidae. Both resemblances exist and are probably significant, but dual origin of the pinnipeds seems unlikely.[1] Orlov holds that †*Semantor*, a relatively late but remarkably primitive form, supports affinities with the Lutrinae. Probably the pinnipeds are an early offshoot of the little differentiated late Eocene and early Oligocene canoid ancestry, paralleled by the otters, which had the same ultimate origin and a similar adaptive trend, and in other features by the bears, also with the same remote origin. In any case their subordinal rank and their position at the end of the Carnivora may be retained in view of the marked specialization and aberrance of the whole group.

†*Semantor* (see Orlov, 1933) is poorly known but so distinctive that family rank may be admitted. It is barely possible that it is a pinniped-like lutrine (or other mustelid) rather than a lutrine-like pinniped. Division of the other pinnipeds into three families is the usual arrangement.

Probably the Otariidae could usefully be subdivided into subfamilies, but they have not been, and I am unable to make a competent arrangement. Kellogg gives family rank to †*Allodesmus*, and Hay does the same for †*Desmatophoca*, but both are admittedly very close to the Otariidae and this radical separation is unnecessary. Perhaps the groups would be good subfamilies, but in the absence of a consistent arrangement of all the otariid genera it is inconvenient to recognize any isolated subfamilies. †*Paleotaria* Leriche, 1910, from the European Middle Oligocene was supposed to belong to this family, and *Otaria*, itself, has been reported there in the Upper Oligocene, but neither record is worthy of credence at present.

[1] It is, however, supported by several capable students, and the possibility is not excluded. All agree that the Otariidae and Odobenidae have a common origin, but it is not certain that the Phocidae are from the same stock. See, for instance, Howell, 1929.

Much unmerited attention has also been given to a supposed occurrence of a recent genus, *Lobodon*, in the Cretaceous of New Jersey. Aside from any theoretical considerations, the completely unreliable data of the supposed discovery make it unworthy of serious notice.

The dispersion of the numerous later Tertiary European pinnipeds among the recent subfamilies follows Allen, largely substantiated by Kellogg, 1922, and with a few exceptions Kellogg, 1922, 1925, 1927, 1931, is followed in general in dealing with the fossils. The arrangement of the recent genera is not in any noteworthy dispute and is substantially that of Weber, 1928, and most other recent students. Howell's excellent book on aquatic mammals in general (1930) includes perhaps the best single discussion of the living pinnipeds from all points of view and also a good bibliography.

PROTUNGULATA

In this superorder are united a broadly structurally ancestral group, the †Condylarthra, and four other orders that may represent archaic products of an old (probably Paleocene) deployment of the †condylarths. As with all the superorders, the collocation is theoretical, but it rests on a reasonable basis of probability. The early †litopterns strongly suggest that they are merely †condylarths continuing their evolution in South America after they became extinct elsewhere, and it is a reasonable, even though a doubtful, conclusion that the †notoungulates, more progressive and diversified yet basically archaic animals, had the same general origin. The †astrapotheres are extraordinarily isolated structurally, but have features pointing distantly to the †litopterns and still more distantly to the †notoungulates. The case of the tubulidentates is less probable, and their being placed here is done only in default of better evidence, but it may prove to be correct.

The name of this superorder is fitting and convenient in meaning, so much so that its technical propriety has become open to question. That is, this obvious name has long and often been used, e.g., by Marsh in 1884, for a hypothetical group ancestral to the

ungulates in general. Marsh defined the group quite exactly, and certain †condylarths nearly fulfill his definition, but there is nothing in his proposal of the name to show that he intended it to apply to any real animals then known. Such hypothetical names have no standing in nomenclature, and the taxonomic name cannot be credited to Marsh. In 1901 (p. 352) Ameghino used the name in a definitely taxonomic way, including in the †Protungulata only the †Caroloameghiniidae. He subsequently followed this usage consistently, but, so far as I recall, no other student has ever adopted it. The †Caroloameghiniidae are now believed to be didelphoid marsupials, and, if priority were strictly followed, Protungulata could not apply to any placental or any Ungulata, but there is no rigid rule as to priority for ordinal or superordinal names. In 1904 Weber quoted the name †Protungulata from Marsh, and considered the †condylarths to be real representatives of the group hitherto hypothetical in this sense. Although Ameghino's entirely different use was prior, this was the first taxonomic use in any sense now acceptable. Later Weber and a few others (e.g., Abel) have used †Protungulata as if synonymous with, and in place of, †Condylarthra. Others have used it more broadly to include †condylarths and other primitive ungulates.

In spite of this peculiar and equivocal history, Protungulata is the most appropriate name for the superorder here under consideration, and it does not seem likely that confusion will result from its use in this way.

†CONDYLARTHRA

The original definition of the †Condylarthra by Cope was based principally on †*Phenacodus* but included also †*Periptychus*, †*Anisonchus*, †*Mioclaenus*, and †*Tetraclaenodon*. Later work by Cope, Osborn and Earle, and Matthew removed the †periptychids and added the †meniscotheres. I have recently argued for the return of the †periptychids to this order, 1937a. It at least seems clear that they are as close to the typical †condylarths as to the more aberrant forms (here called †Pantodonta, formerly, with the †periptychids and others, called †Amblypoda) with which they were long theoretically associated.

As thus constituted, the †Condylarthra are fairly heterogeneous, although less so than many orders. They include three lines that appear simultaneously in the early Paleocene, †Hyopsodontidae, †Phenacodontidae and †Periptychidae, and were then already quite distinct, although similar in the sense that they were very primitive as ungulates go and could have arisen by primary differentiation of an almost immediately antecedent common ancestry. The earliest †phenacodontids and, to less extent, †hyopsodontids are also very close to the contemporaneous carnivores (†creodonts). For instance, †*Protogonodon*, classed as an †arctocyonid †creodont, and †*Desmatoclaenus*, classed as a †phenacodont †condylarth, are difficult to distinguish. This striking fact is part of the evidence for believing that carnivores and ungulates had a common origin not long before the Puercan (early Paleocene of North America).

Some of the †hyopsodontids are very like the first artiodactyls, and some of the †phenacodonts like the first perissodactyls, and this may represent real relationship, although the direct transition was not through known forms and probably occurred outside the areas where pertinent fossils are known. The †didolodonts of South America, although poorly known, appear to be near the †phenacodonts and probably had their origin in or near the latter group. The †didolodonts are probably, in turn, a conservative survival from the ancestry of the other Tertiary South American ungulates, although this is more hypothetical. In a still more distant and doubtful way, the †meniscotheres and †periptychids may be early, conservative, and short-lived offshoots from a stock or stratum of ungulate evolution that also gave rise to the more highly developed paenungulates (which see). The Order †Condylarthra is thus mainly horizontal in definition, but in this horizontal sense the families do seem to be rather closely related, and their relationships to later orders are not certain or specific enough to warrant or permit dispersing the †condylarth families among the latter.

Reference of the very poorly known †tricuspiodonts to this order is particularly uncertain, but they do not fit well elsewhere and have some suggestion of †condylarth characters. Teilhard de Chardin, 1922, has support-

ed the frequently disputed association of †pleuraspidotheres and †meniscotheres. Reference of the †didolodonts to this order, where Ameghino placed them, has also been commonly rejected, but I have restudied Ameghino's specimens, and more, and I believe that he was right (unpublished observations).

On North American †condylarths, see Granger, 1915; Matthew, 1937; Simpson, 1937; Gazin, 1941, and many earlier papers mostly cited in these. On European forms, see especially Teilhard de Chardin, 1922. On South American, see Ameghino, 1906 and earlier, and a revision by me, completed and still in manuscript when this classification was written.

†LITOPTERNA

Ameghino, who described most of the known †litopterns, consistently referred them to the Perissodactyla. This view was controverted by Scott, 1910, and has not since been accepted by any responsible student. Recent authorities agree in seeing in them resemblances and affinities with either the †Condylarthra or the †Notoungulata, or with both. All retain them as a natural group, and most give them ordinal rank, although, for instance, Gregory and Loomis placed them in the †Notoungulata. I believe that they were directly derived from †condylarths and in a sense are merely the post-Paleocene continuation of the †condylarths where these were able to survive because they did not encounter perissodactyl and artiodactyl competition (as they did on other continents) until the end of the Tertiary. They did rapidly succumb when this competition reached them. They underwent such a long history and became so diversified and so distinct from typical †condylarths that it is justifiable and convenient to give them ordinal rank, showing the †condylarth relationship by superordinal collocation.

The resemblance to the †Notoungulata is real but it is not strong, and its nature and extent, as well as the general history of the groups, make it appear the result of derivation from the same general (South American) branch of †condylarths, rather than of any closer connection. This fact, if it is one, or even the fact that this is probable and not disproved, prevents union with the †Notoungulata more closely than with the †Condylarthra and substantiates the placing of all three in a greater division, here called Protungulata.

In this, as in all the extinct South American groups, there are so many invalid names, poorly founded genera, and doubtful affinities that to discuss each or even to go into detail about some of the more important cases would require monographic treatment impossible here. I have listed most of the names that are probably valid, but have simply omitted some that are unfamiliar in any case and that are highly dubious or that I know (from studies still mostly unpublished) to be invalid. Among many details in the present arrangement not clearly based on published opinions, the placing of †*Protheosodon* in the †Proterotheriidae and of †*Notodiaphorus* in the †Macraucheniidae may be mentioned. This double transfer seems to me highly probable on present evidence but cannot here be defended explicitly.

In the early Tertiary (Río Chico to Deseado formations) there is a large, somewhat heterogeneous group of probable †litopterns of very primitive, especially †condylarth-like stamp. Such of these as were not placed in manifestly extraneous groups have generally been believed to be †macrauchenids, for the principal, surely superficial reason that those in which that part is known do not have a marked diastema. Their tooth structure is more nearly †proterotheriid. They probably include some ancestral †proterotheriids, with some nearly allied but divergent early lines, and are little removed from the common †litoptern ancestry. The best taxonomic expression of these probabilities has seemed to me to be placing them in a subfamily of the †Proterotheriidae.

Much of the primary literature on the †litopterns is included in the studies by Ameghino (see his collected works, 1913–1936, original publication there cited). There is no general revision of the order, but Scott's review of the early Miocene forms is fundamental (Scott, 1910). The other literature is widely scattered and includes Rovereto, 1914; Loomis, 1914; Patterson, 1940a. I have completed but not yet published a revision of the pre-Oligocene †litopterns.

†NOTOUNGULATA

This great order has the distinction of having been discovered by Darwin (on the voyage of the "Beagle"). †*Toxodon*, discovered by him, was described by Owen in 1840,[1] the third genus of fossil mammals to be made known from South America. The first two were †*Megatherium* and "†*Mastodon*" (in the old *sensu latissimo*), described by Cuvier. Owen added the related genus †*Nesodon* six years later, and †*Mesotherium* (usually but incorrectly called "†*Typotherium*") was slowly made known over a period of years from 1857 to 1867. In 1882 the Ameghinos started work on these animals, and during the following 25 years Carlos Ameghino discovered, and Florentino Ameghino described, a great number of new forms. They made known at least two-thirds of the valid genera known today, including members of every important group of †notoungulates but one (the non-South American †Arctostylopidae, discovered after the death of F. Ameghino). There is no other example in mammalogy of a large and complex order, knowledge of which was so largely dependent on a single team of workers.

It is ironic under these circumstances that Ameghino[2] never recognized or accepted the existence of this group as such. Other students were also slow to recognize this entity. In the 1890's some, e.g., Lydekker, placed †toxodonts and †typotheres together but excluded the †entelonychians. Others, e.g., Zittel, associated the †toxodonts and †entelonychians but also included the relatively or absolutely extraneous †astrapotheres and excluded the †typotheres. It remained for Roth, in 1903, to recognize the fundamental resemblance of the animals now called †notoungulates and to differentiate them from all others. In the meantime, Ameghino, although he certainly recognized their community of origin, classified these strangely diverse creatures on the basis of resemblances now known to be adaptive and convergent, and he eventually (e.g., in his great summary of 1906) placed them in eight different orders, six of which are mainly Holarctic and are not now believed to occur in South America, except for one (Perissodactyla) that reached that continent by immigration at the end of the Tertiary.

No one now doubts that Roth was essentially right and that all these forms are related to one another and not related (except by very remote common ancestry, not at all in a forward direction) to any of the varied Holarctic ungulates. Concerning the forms that I have included in the order, this can be said to be an established fact, requiring no argument now, but there is still some difference of opinion as to whether the other South American hoofed mammals, the †litopterns, †astrapotheres, and †pyrotheres, belong here. Roth's original definition excluded all of them. Scott at first (e.g., 1913) included the †pyrotheres but excluded †astrapotheres and †litopterns, but now (e.g., 1937a) he excludes all three. Osborn, 1910, included the †astrapotheres and excluded the others. Gregory, 1910, included all three. Loomis, 1914, excluded †pyrothreres and included †litopterns and †astrapotheres. Authority can be found for almost every possible combination, yet the exclusion of all three from the †Notoungulata is favored by the consensus today and is unquestionably the arrangement most defensible on morphological grounds. When these three groups first clearly appear, in the Casamayor, they are already quite distinct from one another and from the †notoungulates. No known †pyrotheres have any diagnostic †notoungulate characters. Some †litopterns and †astrapotheres developed a typically †notoungulate character (transverse entoconid crest) in the lower teeth, but it is a peculiar fact that this was absent in the earliest and most primitive members of both groups, although already universal in contemporaneous †notoungulates, so that this is demonstrated to be convergent. These two groups probably were derived from the same broad †condylarth-like ancestry as the †Notoungulata, a probability expressed by placing all in a superorder Protungulata, but it is improbable that they have any nearer relationship to the †Notoungulata.

[1] As I write these lines, just one century of study of the †Notoungulata has been completed. Another century may possibly suffice to understand the real phylogeny of this amazing group.

[2] I.e., F. Ameghino; by custom, reference is understood to be the more articulate brother, or rather to the publications, almost all of which were written by him. C. Ameghino's contribution was no less important and was, if anything, more solidly enduring. In following this customary form of reference I do not mean to slight the admirable junior member of this unique team.

Until recently a three-fold subordinal division of the †Notoungulata appeared so natural and so firmly established that the classification seemed quite definite to this extent and hardly open to possible question. This was, however, based almost exclusively on the relatively well-known and abundant but stereotyped and little-varied early Miocene (Santa Cruz) and Pleistocene (Pampean) forms. These fall definitely into only five families: †Homalodotheriidae, †Toxodontidae, †Interatheriidae, †Mesotheriidae ("†Typotheriidae" of other authors), and †Hegetotheriidae. Of these the first two are so distinctive that each was placed in a separate suborder, †Entelonychia and †Toxodonta, respectively, while the last three, all small to medium-sized, rodent-like animals, are so apparently similar that they were placed together in the †Typotheria. But even in the early Miocene the evolution of the †Notoungulata was really almost completed, and later changes are of quite minor extent and importance. Fundamental relationships are obscure in these few specialized survivors. Moreover, the group was then already well past its apogee, which occurred in the Oligocene, and the later forms, basis of the "classical" arrangement, give only a faint idea of true †notoungulate diversity.

As against five families in the Miocene, four in the Pliocene, and three in the Pleistocene, there were nine in the Oligocene and at least eight in the Eocene. Some of these earlier families do not fall naturally into any of the three established later suborders, and others tend to contradict the validity of the boundaries placed between those suborders. These vitally important earlier representatives were long very poorly known and virtually neglected except by Ameghino, whose materials were so fragmentary and so varied that he did not achieve, and could not possibly have achieved, a workable synthesis of them. It is only in the last few years, long after the death of Ameghino, that better specimens of many representative genera have been obtained and that renewed study has begun to reduce this inchoate mass to the beginnings of reasonable order. This work is still actively in progress and nothing like a definitive result is yet available, but it permits some improvement and a tentative rearrangement. This is also influenced by recent studies of the internal, especially ear and endocranial, characters of both early and late forms.

Although the present tentative arrangement naturally grew from the classic studies and draws on them, it is different from any yet proposed. There is, as I earlier showed (Simpson, 1934), a basic Paleocene and Eocene group so primitive that it lacks the differentiating characters of any of the later suborders, and with this is associated at least one line (†Notostylopidae) of short-lived specialization outside any other subordinal sequence. These are united as †Notioprogonia.

The most radical change of the present arrangement is in the enlarged scope of the Suborder †Toxodonta. The typical †toxodonts cannot be traced back clearly into the early faunas, principally because of a continuing gap in knowledge between the Eocene Musters and Oligocene Deseado faunas. There are three mainly Eocene families, †Oldfieldthomasiidae, †Archaeopithecidae, and †Archaeohyracidae, that are vaguely †toxodont-like in the broadest sense. They might be considered as †toxodont-like †Notioprogonia, or as more or less aberrant early offshoots of the †Toxodonta. Pending better demonstration of possible links, one way or the other, I have tentatively adopted the latter point of view. It now seems clear that the †Notohippidae are subordinally allied to the †Toxodontidae. The position of the †Leontiniidae is more questionable, but Patterson, 1936, found that the ear structure is fundamentally †toxodont-like, and this seems to be true of the skeletal characters as well (complete skeletons are now known but study has not been quite completed). The teeth are less progressive than in typical †toxodonts, but seem to represent a closely similar ancestral type.

†*Homalodotherium* and its close allies are so extraordinarily and aberrantly specialized in the skeleton (abnormal limb proportions, claws in place of hoofs) that they have always been sharply distinguished from †toxodonts. But Patterson has shown that both the ear structure (1936) and the endocranial characters (1937b) are †toxodontid in all essential features. Moreover the probable ancestral

group, †Isotemnidae, in the Eocene is quite normal in skeletal characters and is structurally almost as good an ancestral type for the †Toxodontidae as for the †Homalodotheriidae (e.g., Simpson, 1936). In other words, the specializations of the latter, strange as they are, were rapidly acquired and merely overlie, without basically altering, the structure of what are otherwise fully characteristic members of the †Toxodonta. The specialization might, nevertheless, be considered striking enough to warrant rather sharp distinction, but the hitherto accepted Suborder †Entelonychia can really be maintained only on the basis of limb structure, and the earlier representatives of what is rather surely the same phyletic group do not have the diagnostic limb structure. Some infraordinal or superfamilial distinction may yet be acceptable, but I have not indicated this. From a phyletic point of view the present evidence suggests that the †Homalodotheriidae are not much if any more distinct from †Toxodontidae than are the †Notohippidae and †Leontiniidae, and the Eocene families would be left either *incertae sedis* or would each require another superfamily, so that superfamilies would not, at present, seem to have any practical value or reason for separate designation.

Although their separation is ancient, the †Interatheriidae and †Mesotheriidae have many fundamental characters in common, and their association as †Typotheria still seems natural. This is not true, however, of the †Hegetotheriidae, hitherto also placed in the †Typotheria. Every new study and discovery has tended to separate this family more sharply, decisively, and anciently from either †toxodonts or †typotheres and to suggest that it is really a basic subdivision of †Notoungulata, despite the fact that it has only three surely separable phyla (corresponding with the three subfamilies of this classification). The †typothere-like aspect of the †hegetotheres is superficial and is apparently due to the rodent-like habitus, independently acquired, a trend that appeared also in other †notoungulates of surely non-†typothere origin. (See, e.g., Patterson, 1936.) I am, therefore, now taking the logical step of giving the †hegetothere group subordinal distinction.

The details of family and subfamily arrangement require little comment. The Eocene families follow studies by me (a monograph still unpublished but essentially completed) and the later families follow mostly Ameghino, Scott, and Kraglievich except for the union or subordination of a few groups now demonstrated to be more nearly related to others than was formerly apparent. Thus the "†Trachytheridae" of authors are simply primitive †Mesotheriidae, the "†Nesodontidae," similarly, primitive †Toxodontidae, the "†Rhynchippidae" very close allies of typical †Notohippidae, etc. In such cases family separation is quite unwarranted, although most of these groups are practically recognizable and can conveniently be called subfamilies.

The basic literature on this order is mostly contained in Ameghino's collected works, plus Roth, 1903. Many later forms are summarized and a rich bibliography is given in Kraglievich, 1934. Classic studies of the Santa Cruz forms are Sinclair, 1909, and Scott, 1912a, b, 1930. Scott, 1913, 1937a, summarizes the whole order. Among the most recent shorter papers of fairly wide scope are Patterson, 1932, 1934a, b, 1936, 1937b; Cabrera, 1939; Simpson, 1933a, b, 1934, 1935 (and extensive work now in manuscript).

†ASTRAPOTHERIA

Ameghino believed the †astrapotheres to be †amblypods, but this is improbable and has been generally abandoned. Later opinion has been divided only as to whether the †astrapotheres are †notoungulates or deserve ordinal separation. There are some curious resemblances to the †notoungulates, as shown by Scott, 1928, but review, especially in the light of the earlier forms, shows that some, at least, of these are convergent and some parallel and does not establish any as sure evidence of special affinity. †*Trigonostylops* has recently become unusually well known (Simpson, 1933a) and, it proves to be very different from the true †astrapotheres, still less like any †notoungulates and surprisingly, although not very thoroughly, like some †litopterns. The general conclusion on this and other evidence is that †*Trigono-*

stylops and the †astrapotheres represent anciently divergent lines, probably related near their base, derived from some †litopternlike and †condylarth-like ancestry, within the South American protungulate complex but quite distinct from the †Notoungulata as such. The arrangement here given is consonant with this complicated but fairly well-documented series of conclusions.

Ameghino placed †*Albertogaudrya* (and some other doubtful or invalid genera) in the †Albertogaudryidae, †*Astraponotus* and the later forms in the †Astrapotheriidae. The division is horizontal in a nearly linear sequence and does not merit family separation. I have very tentatively maintained it as a subfamily distinction, but the line should be drawn between †*Astraponotus* and †*Parastrapotherium*, since this is the major break, and not that between the former and †*Albertogaudrya*.

Many †astrapothere genera have been named, and probably more will eventually be recognized, but at present those listed here are the only ones surely valid and surely referable to this order. I have revised the early forms (1933a, 1934, and unpublished), and the later ones are known best from the works of Scott, 1928, 1937b, and of Kraglievich, 1928a.

TUBULIDENTATA

This order is represented by only one living genus with one (or a few) species, but that has been the subject of so much dispute, discussion, and detailed investigation that it is among the best known of mammals. The earlier collocation of *Orycteropus* with the Xenarthra, the Pholidota, or both has been sufficiently mentioned in connection with those orders. At first believed to belong in *Myrmecophaga*, the taxonomic history of the aardvark has been one of progressive isolation, first as a genus, then a family, then a suborder, then an order of a Superorder Edentata, and finally as an independent order. In recent years this last opinion has prevailed to such an extent that it may now be called unanimous. It is richly documented by the monographs cited below and is supported by the authority of Gregory, Sonntag, Weber, R. Anthony, Frechkop, and many others.

The only fossils surely referable to the order are from the Pliocene of France, Greece, Persia, and India. They belong to the living genus and give little additional evidence as to the origin of the group. Students of the recent species now differ very little on this point, all considering the Tubulidentata to be a very ancient independent offshoot of a protungulate, †condylarth, or unidentified †creodont-†condylarth ancestry.

Several supposed orycteropodids have been described from the Oligocene and Miocene of Europe. It is to be expected that orycteropodids did live then and there, and these may indeed be remains of them, but so far as as has yet been shown the few fragments are practically indeterminate and of unknown affinities, and it would be futile to attempt to place them in formal classification. Schlosser, 1923, went so far as to return *Orycteropus* to the Edentata on the strength of these fossils, contrary to the virtually universal opinion of all other zoologists and palaeontologists.

More important is Jepsen's Lower Eocene form from Wyoming, †*Tubulodon*, based on several fragments of one individual, including parts of the lower jaw with teeth. This resembles *Orycteropus* in several respects and does not appear to belong with any other known group, yet the material is scanty and the differences are pronounced (as would be expected whether the relationship is real or not). Jepsen concludes that †*Tubulodon* does not support the theory of †condylarth or protungulate origin for the Tubulidentata and that it still more increases the isolation of the order. Anthony, 1934a, b, suggests that †*Tubulodon* is consistent with †condylarth affinities for the order, but it is difficult to say how far this view is influenced by his very peculiar ideas of molar evolution. In a more recent, more dependable, and thorough analysis, Colbert, 1941b, has strongly supported †condylarth ancestry for *Orycteropus* and he holds that †*Tubulodon* "certainly . . . is not a tubulidentate" and if related to this order at all can only be so collaterally through a (pre-tubulidentate) common ancestry.

See especially R. Anthony, 1934a, b; Colbert, 1941b; Frechkop, 1937; Jepsen, 1932; Sonntag, Woollard, and Le Gros Clark, 1925–1926.

PAENUNGULATA

The first glimmering of the group here made is visible in De Blainville's remarkably advanced classification of 1834. He united the "Proboscidei" and "Sirenei" as "gravigrades." Unfortunately the Latinized equivalent, †Gravigrada, of this vernacular term has been applied to a totally different group (†ground sloths) and is not available for the present superorder. The concept here adumbrated reappeared periodically during the nineteenth century but usually without formal taxonomic expression. Thus Gill in 1870 indicated that the Hyracoidea, Proboscidea, and Sirenia were especially related, but used no name to include the three. Another hint from a different direction is seen in Cope's classification in which he separated the "†Taxeopoda" (=Hyracoidea, †Condylarthra, and perhaps "†Toxodontia"=†Notoungulata), Proboscidea, and "†Amblypoda" (=†Pantodonta and †Dinocerata) from all other ungulates ("Diplarthra") and showed that his first three groups have important characters in common. His final classification (1891a, 1898), maintained the same distinction but also placed the Primates (as three suborders) in the "†Taxeopoda," a retrogressive step. He gave no common name to his three or four non-diplarthran ungulate groups.

In 1891 Flower and Lydekker took the essence of Cope's anatomical observations and based on them a division of the "Ungulata" into "Ungulata Vera," essentially Cope's "Diplarthra," and "Subungulata." Under this latter term they united the Hyracoidea, Proboscidea, "†Amblypoda" (†Pantodonta and †Dinocerata), †Condylarthra, "†Toxodontia" (†Notoungulata), and apparently with some doubt the †Tillodontia and †Taeniodonta. With various changes in contents, this conception of a subungulate order or group of orders has persisted and periodically reappeared since then. In Schlosser, 1923, the †condylarths, †notoungulates, and "†amblypods" were removed from the group, and "Subungulata" was made to include the †Embrithopoda, Hyracoidea, Proboscidea (with †Barytheria), and Sirenia. Weber, 1928, adopted Schlosser's nomenclature and usage without change.

The Paenungulata of the present classification does not exactly correspond with any grouping hitherto proposed but is a development of De Blainville's "gravigrades," of Gill's unnamed superordinal group, of concepts behind Cope's "†Taxeopoda,"[1] and of Flower and Lydekker's "Subungulata," especially as emended by Schlosser.

If "Subungulata" could be dated from Schlosser, it would be an acceptable name for the present group, which is Schlosser's expanded and emended, but it cannot. Schlosser received the term from Flower and Lydekker, and their conception was essentially unlike Schlosser's and still less like that of this classification. Even this might not be wholly deterrent, but in fact the name "Subungulata" in formal taxonomy dates from Illiger, 1811, and his vastly prior usage was absolutely different: in his work it designates a group of rodents, essentially the Cavioidea.[2] "Subungulata" has also been used repeatedly in a purely descriptive sense and in several very loose and highly varying taxonomic senses. Search of the literature fails to reveal any acceptable alternative, and it is, therefore, necessary to coin a new name, Paenungulata (*paen-*, combining form of *paene*, "almost, near"), which is sufficiently appropriate and retains the desirable features of the familar but unavailable name "Subungulata."

The nucleus of this superorder is understood to be mainly the familiar association of the Proboscidea with various other groups apparently of African origin, †Embrithopoda, Hyracoidea, and Sirenia. The inclusion here of the Hyracoidea is not well established, but still is rather probable than improbable. That these groups had a common protungulate, or more generally proto-ungulate, origin is currently accepted by the best-informed students and warrants tentative acceptance as a probable but unproved theory. The further inser-

[1] But not of Cope's taxonomy, which cannot be reconciled or equated with the present arrangement. Explicitly, Cope's name "Taxeopoda" cannot be applied, since most of its contents, including all the most typical, were not Paenungulata, and the most typical Paenungulata were excluded from it.

[2] Nor was this an isolated usage promptly forgotten. It was, for instance, adopted by C. L. Bonaparte in his important classification of 1831, by J. A. Wagner in 1841, etc.

tion of the †Pantodonta, †Dinocerata, and †Pyrotheria is both reasonable and convenient and merits tentative acceptance despite its being frankly hypothetical. There probably was not a single primitive specifically paenungulate phylum that split up into the seven orders I place here, although this possibility is not excluded. It is probable that there was some protungulate division that tended toward graviportal body build and the various limb and other characters that the paenungulates have in common, and that all these seven orders came from such a protungulate group, whether their exact origin was narrowly monophyletic or only broadly so in this sense. It is possible but does seem improbable that their common aspect is solely the result of convergence from totally different ancestors.

Although the paeungulates retain definite signs of protungulate origin in some of their most primitive members, the placing of any of them in the Protungulata would be difficult to defend on either morphological or phylogenetic grouds. They must all have appeared in the Paleocene[1] and must then already have been sharply differentiated from the contemporaneous representatives of the Protungulata.

The possibly polyphyletic origin of the superorder, the ancient and deeply defined separation of its constituents, and their long histories and great differentiation are such that each must logically be given ordinal rank. Superorders as now used are theoretical or even hypothetical groupings. Orders are the major division of placentals that can reasonably be said to have an established common origin, and by these criteria these are orders, and their collocation is superordinal.

†PANTODONTA

Only nine genera are now referred to this order, one of these somewhat doubtfully, but it is among the most distinctive of mammalian groups, and it evidently played an important rôle in early mammalian history. When it is noted that these few genera occur on three continents, that they have the enormous time range middle Paleocene to middle Oligocene, and that more than half of the known genera have been described since 1930, it becomes clear that discovery includes as yet only a small part of what must have been a greatly varied and far-flung group.

The definition of the order, as now understood, was long delayed by confusion with other early ungulates now known to belong in different orders. An earlier conception, stemming from Cope and finding its most recent expression in Matthew's posthumous memoir of 1937 (representing his ideas of around 1920), was that the †coryphodonts were closely related to the †uintatheres, and the †pantolambdids to the †periptychids. All four groups were usually united in an order †Amblypoda, or (Matthew) the first two were placed in that supposed order and the last two in a different order †Taligrada. On the basis of several previous studies as well as new revision, I (Simpson, 1937a) pointed out that the †pantolambdids and †coryphodonts, so widely separated in Matthew's and some other classifications, seem to be closely related, while the †periptychids really have little or nothing to do with either of these and are close to the †condylarths, and the †uintatheres are a third, very distinct group certainly not derived from †coryphodonts and probably with no special relationship to the latter. Still more recent discoveries of remarkable annectent types and more complete specimens led Patterson (especially 1939) strongly to confirm these opinions, which now seem to be beyond reasonable doubt as a result of his work.[2] As he shows, it is now impossible to maintain even a family distinction between †*Pantolambda* and †*Coryphodon*, while †periptychids and †uintatheres evidently are ordinally distinct from each other and from the †pantodonts. Patterson also discovered and described a second family allied to, but distinct from, the †*Pantolambda*-†*Coryphodon* group.

†*Pantolambdodon* is poorly known and may not be correctly referred to the order, al-

[1] Two of the seven orders are known in the Paleocene, and all the other five are so highly specialized when they appear in the Eocene that they were surely distinct in the Paleocene. The Paleocene of South America is barely known and that of Africa is unknown.

[2] The evidence for this flat contradiction of the views of Osborn, Matthew, and others was mostly discovered after their studies were completed, and the radical revision of their classification thus in no way reflects on their work.

though this position is as likely as any on present evidence.

A classic study is Osborn, 1898b, and the more important recent revisions are Matthew, 1937; Patterson, 1939 (and earlier papers there cited); Simpson, 1937a. On the Mongolian forms, see Osborn and Granger, 1932; Granger and Gregory, 1934.

†DINOCERATA

Although Marsh originally called this group "Dinocerea," he almost immediately corrected this etymologically poor form. The correction has been universally allowed, and there is no impelling reason for returning to the first spelling. The name has always included the forms now placed here and no others, so that its applicability is not open to question. It was formerly believed that the †pantodonts were either ancestral to the †dinocerates or a collateral branch from their immediate ancestry, and they were, therefore, united as "†Amblypoda," a name still current in a variety of senses, usually loose. Now, however, it is almost certain that the two have no closer connection than origin from similar protungulates or remote ancestral paenungulates, and their special union in a single group is no longer warranted

In the year 1872 the rivals Leidy, Marsh, and Cope applied seven different generic names to members of this order and family, all based on material of nearly the same age and from the same region. Later Cope and Marsh proposed three more names each, making 13 in all, for specimens from these same beds These names, with their probable (but disputable) dates are as follows:

†*Uintatherium* Leidy, August 1, 1872
†*Uintamastix* Leidy, August 1, 1872
†*Tinoceras* Marsh, August 19, 1872
†*Lefalaphodon* Cope, August 19, 1872. This was surely a misprint, and the validity of publication is doubtful. = †*Loxolophodon.*
†*Eobasileus* Cope, August 20, 1872
†*Loxolophodon* Cope, August 22, 1872. Probably = †*Coryphodon* and incorrectly applied to †uintatheres.
†*Dinoceras* Marsh, September 27, 1872
†*Octotomus* Cope, January, 1885
†*Ditetrodon* Cope, June, 1885
†*Tetheopsis* Cope, June, 1885
†*Paroceras* Marsh, 1885. (Subgenus of †*Dinoceras.*)
†*Platoceras* Marsh, 1885. (Subgenus of †*Tinoceras.*)
†*Laoceras* Marsh, 1885. (Subgenus of †*Tinoceras.*)

Despite the long interval, no proper revision of genera and species has been made since 1885, and the outcome of this shameful scramble for priority is still uncertain. †*Uintatherium* is certainly a valid name and genus. Probably at least one other valid genus is included, for the more specialized forms that range into the Upper Eocene. It is usually assumed that †*Eobasileus* is the valid name for these, but this is not positively established at present. Probably all the other names of Cope and Marsh, and possibly even this one, are synonyms of †*Uintatherium.* Cook, 1926, has further complicated matters by proposing the name †*Uintacolotherium* for a species probably belonging to the genus commonly called †*Eobasileus*, without comparing it with any of the several supposed species that are likely to be congeneric with it.

As listed, several other genera that are valid have been discovered since Leidy, Cope, and Marsh rushed their synonyms into print. At least as far as American forms go, these all appear to be closely related and to owe their differences, pronounced as they are in some cases, mainly to their being more or less advanced, so that the various family names proposed, or even subfamily divisions, have no good reason for maintenance. The Asiatic †*Prodinoceras* is very close to †*Probathyopsis*, but †*Gobiatherium* is obviously on a different line of descent from the later American forms and might be placed in a distinct subfamily, although this seems an unnecessary complication at present.

Of the various family names proposed, †Tinoceridae has priority but is probably based on an invalid genus. †Eobasileidae is next in priority. It may be based on a valid genus and is sometimes used, but the validity of †*Eobasileus* is still doubtful. The next name, †Uintatheriidae, is, therefore, used here since it is unquestionably based on a valid genus. It is also the most familiar name.

The classic review of the middle to late Eocene forms is Marsh, 1885, supplemented by Scott, 1886, Cook, 1926, and Osborn and Granger, 1932. On the earlier (late Paleocene and early Eocene) genera see, among others,

Osborn, 1913; Matthew, Granger, and Simpson, 1929; Simpson, 1929b; Jepsen, 1930; Patterson, 1939.

†PYROTHERIA

This is one of the smallest and at the same time most distinctive and isolated of mammalian orders. It has a considerable range in South America, although it is nowhere really common. Ameghino thought that the †pyrotheres were proboscideans and Loomis, after studying a good skull, agreed, although he later retracted this conclusion (pers. com.). Gaudry contented himself with pointing out that †*Pyrotherium* cannot enter into any otherwise known order, and most students agree. It has been tentatively suggested that there is some special connection with the †notoungulates, but this is only a guess based on geography, since the known morphology contradicts it strongly.

Special resemblances to the Proboscidea are almost surely convergent, but it remains entirely possible that the †pyrotheres share with the various orders contiguous with it in this classification, including the Proboscidea, a common "subungulate" or paenungulate heritage, as signalized by Ameghino and by Loomis. The early presence and probable diversity of such a stock are further suggested by †*Carodnia* and †*Ctalecarodnia*, very poorly known genera interesting for their unique characters, for their rather distant resemblances to the North American paenungulates and to the †pyrotheres, and for the fact that they are now the oldest known South American mammals.

†*Griphodon* is another poorly known, isolated genus, probably a †pyrothere, a possibility mentioned by its describer although he inclined to believe it a perissodactyl, which now appears extremely unlikely. Patterson, 1942, established its probable status as a †pyrothere.

†*Paulogervaisia*, often placed in this order, does not belong here.

Although it is probable that more than one minimum unit phylum is represented, the very scanty materials do not permit any clear establishment of phylogeny within the order except to show that the earlier forms, †Carolozittelidae of Ameghino, are more primitive than the later and could be directly ancestral to the latter. This is insufficient basis for family distinction.

Among studies of the group are Ameghino, 1902c; Gaudry, 1906; Loomis, 1914; Anthony, 1924; Patterson, 1942. I have completed but not yet published a study of all the known pre-Oligocene specimens.

PROBOSCIDEA

Although this order has living representatives, familiar to all, the two surviving genera are relicts of a dying group, and they have typical southern relict distribution. The order had a much greater rôle in faunal history than one would dream from this impoverished representation, and it formerly occurred in bewildering numbers and variety over the whole of all the continents, except Australia, and on a number of islands.

The unique characters of the elephants were, of course, recognized from the most remote times, but it did not seem proper to the early naturalists to place one genus (as they ranked it) with only two species in a separate order. Linnaeus placed *Elephas* in the "Bruta," along with sirenians, sloths, anteaters, and pangolins—one of the least natural of Linnaean orders. Blumenbach at first placed the elephants with the walrus and later with the tapir, rhinoceros, and hippopotamus. Still later he added the pigs to the assemblage, and this became the classical late eighteenth and early nineteenth century collocation, under the name of "pachyderms," given by Geoffroy and Cuvier in 1795. The concept survives in the vernacular and has been given vitality by its use in circuses and itinerant menageries, a vitality quite remarkable in view of the fact that "pachyderm" was definitely a technical name and that its technical use and the accompanying concept ceased to be accepted more than a century ago, except by a few relatively incompetent students who were decidedly old-fashioned at the time (e.g., Wagner in 1855).

When Illiger gave the name "Proboscidea" in 1811 he applied it only to the living animals now placed in this order, but he did not intend to break up the "pachyderms." For him, the proboscideans were a family of "Multungula," and the "Multungula" were simply the pachyderms (plus hyraxes). De Blainville, however, soon (1816) placed the ele-

phants as unique representatives of an order ("Gravigrades"). This was not immediately adopted by all, but, largely under the influence of Owen, after about 1840 almost everyone accepted the order and used Illiger's "family" name for it.

Fossil proboscideans, because of their size and their abundance in superficial deposits, were probably the first fossils to attract human attention. The ancient Greeks are known to have collected specimens of them. In the eighteenth century, these were the first fossil vertebrates to receive what may properly be called scientific attention, the †Siberian mammoth in the Old World and the †American mastodont in the New. The science of vertebrate palaeontology may be said to have arisen from the study of these animals. The extent of subsequent discovery can be judged by the fact that Osborn's revision recognizes 352 species of proboscideans, of which all but two are known from fossils only!

Classification within the order is obviously a task for palaeozoology rather than neozoology. The palaeontological literature is more extensive for this than for any other order of mammals. Fortunately the truly herculean task of reviewing this enormous and frequently chaotic mass of publications has recently been accomplished by Osborn (1936, 1942, a posthumous publication dating as of 1935, for the most part). The present classification is based primarily and in greatest part on Osborn, although it also takes into account the older literature, either directly or through the extensive quotations and discussions in Osborn's monumental memoir. Publication on the order has, of course, continued since 1935, but it happens that no major discoveries or revisions have appeared since then.

Although it is based on Osborn and accepts his views as to generic and higher affinities with only minor differences of opinion, the present classification of the Proboscidea is formally quite unlike that of Osborn, a fact that requires explanation and perhaps apology. No destructive criticism and no important rejection of Osborn's essential conclusions are involved, but only a rather thorough difference in point of view regarding the relationship between those essential conclusions and the formal arrangement of nomenclature and classification. Osborn's arrangement is as valid as any other, but the principles underlying it are unique. It is not altogether obvious at first glance, but the careful student of Osborn's memoir will find that his formal classification is profoundly and irreconcilably different from any other that has ever been proposed. As Osborn recognized, his differs more from any of the contemporaneous classifications than these do from the system of Linnaeus.

This places the more general mammalian taxonomist in a serious quandary. There are these alternatives: (1) to let the Proboscidea stand as an order classified in quite a different way from any other in the animal kingdom, (2) to reclassify the Mammalia (if not the Animalia) on Osbornian principles, or (3) to take the data so laboriously and brilliantly compiled by Osborn and to use them in the erection of an orthodox, non-Osbornian classification. The first alternative is not acceptable to me or, I believe, to anyone. The expression of taxonomy inevitably varies greatly from group to group, but that its general principles should be the same for all is an ideal too fundamental to permit exceptions. The second alternative may or may not be theoretically desirable, a matter of taste rather than of fact, but this question need not arise because it is certainly impossible at present. There are no more Osborns. His work on the Proboscidea, with ample assistance, occupied much of his research time for about 45 years and almost all of it for the last 15 of these. This is only one of 32 mammalian orders, several of which are considerably larger. A similar reworking of all the orders of mammals—and less work would hardly suffice for true Osbornian revision—is, at best, far in the future under present conditions. Since the first alternative is undesirable and the second impossible, the third is necessarily adopted here.

The fundamental principle of Osbornian classification is the formal recognition and naming of unit phyla of smallest possible scope and (in practice) without connections one with another. The unit phylum in which the only stated relationship is one of direct ancestry and descent (without branching or horizontal affinity) is a subfamily, of which there are a great number in consequence of

this definition (21 in Osborn's classification of the Proboscidea). Genera are segments of subfamilies, usually separated by evolutionary progression in time, rarely by horizontal differentiation. Occasionally an ancestral genus survives for a time with its descendant in the same phylum, but as a rule among contemporaneous genera no two belong to the same subfamily.[1] In generic and specific nomenclature, the Osbornian system discards the law of priority of name and substitutes for it the priority of conception and the conservation of usage as accepted by standard authors (even if erroneous in a technical sense). In practice Osborn adopted the names that seemed to him most suitable and historically important, as a matter of personal opinion that could hardly be reduced to a set of rules. Subfamily, family, and superfamily names have the familiar terminations, but they are not necessarily based on generic names and may be taken from any appropriate Greek or Latin roots, regardless of any included genus.

In translating the Osbornian system into more usual terms, this classification follows the law of priority for generic names and it compounds subfamily and family names from the names of valid, typical, included genera. The unit phylum idea of a subfamily (practicable in the Proboscidea but not in many groups, e.g., the rodents) is given up and subfamilies become the more usual and broader sort of structural sequences, including lines of common origin and similar trend but frequently multiple, narrowly branched, perhaps sometimes anastomosing. Families become bundles of these subfamily sequences according to either their basic splitting from the prototypal proboscideans or their major later divergence.

As regards the primary point of suborder or superfamily division, I agree with Cabrera and others that these should be only three (disregarding the †barytheres for the moment) and not four or five as in Osborn. The differences among †moeritheres, †deinotheres, and †mastodonts-with-†mammoths are clearly very ancient and basic. The †mastodonts and †mammoths, on the other hand, are basically alike and intergrade almost insensibly. I cannot see the profound break or absolute separation that is sometimes supposed to exist here. That Osborn himself had difficulty in placing this division is shown by the fact that he localized it in several different places in his last years, and finally separated out the †stegodonts as another major group, which doubled the difficulty. Although there certainly are gaps in the record, it seems likely that elephants did arise, in the late Pliocene, from †stegodonts, and †stegodonts, in the late Miocene or early Pliocene, from †mastodonts. Despite its branching phyla and the existing gaps between them in the known species, this whole complex has the unmistakable stamp of a progressing unit.

†*Palaeomastodon* and †*Phiomia* are very near to each other and to the common ancestry of all the later proboscideans. I, therefore, classify them tentatively at the base of the principal or central group that followed them. It is not clearly certain that †*Palaeomastodon* is solely ancestral to †*Mammut* or †*Phiomia* to †*Amebelodon*, and even if this should prove to be true, it would not be erroneous to place them at the base of the †gomphothere line and to derive †*Mammut* and †*Amebelodon* from that line.

Most students still differ from Osborn in believing that †*Serridentinus* is very close to †*Gomphotherium*, and some believe the two to be inseparable. They are so similar that no more than generic distinction is morphologically justified, and it is improbable that they are phyletically distant.

†*Gnathabelodon* and †*Eubelodon* are puzzling forms. They do not differ much from the †gomphotheres, but they have some unique characters and they do suggest also some offshoot of the †anancine ancestry. Osborn placed them in different families, but they seem to me to be allied, perhaps even to be the same genus.

The other subfamilies all appear to be aberrant derivatives of an essentially †gomphotheriine ancestry. Perhaps subfamily separation overstresses their divergence, but it is tentatively acceptable. In each there are primitive forms transitional from true but

[1] As is necessary in any working system—and Osborn's does work and is not an impracticable ideal—exceptions are sometimes made, and Osborn did occasionally give generic, rather than subfamilial, rank to unit phyla. Then the successive units are species, rather than genera, and genera tend to be monotypic at any one time.

variously specialized †gomphotheres. While †*Platybelodon* and †*Amebelodon* may have had somewhat different †gomphotheriine ancestors, they have diverged in essentially the same way and have so many peculiarities in common that a real relationship is suggested. Osborn was much impressed by the dentine rods in †*Platybelodon*, but this is probably not so significant as appears at first sight, and as he thought, because it is now known that such rods are also present in other proboscideans. Their stronger development in this genus seems to be a slight progressive mutation, not a profound and ancient difference.

Whether or not †*Mammut* arose eventually from †*Palaeomastodon*, it must have arisen from some similar and about equally primitive, long-jawed, bunolophodont form of essentially †gomphotheriid structure. The ancient separation and the radically different direction of evolution warrant tentative recognition of the †Mammutidae as a family distinct from the †Gomphotheriidae. The most divergent †mammutid species differ considerably from one another, and probably more than one genus will eventually have to be recognized. The differences, however, are not greater than sometimes are embraced in a single modern genus, there are intergradations that obscure possible generic lines, and there is at present no valid and generally acceptable nomenclature for all the probable groups of species.[1] I, therefore, follow Hopwood, 1935, for the time being and refer all to one genus (but call this genus by the name valid under the Rules).[2]

†*Stegolophodon* is a transitional form between the †mastodonts in general and the †stegodonts. Rejecting all such evidence of the derivation of any one proboscidean phylum from another, Osborn had difficulty in fitting this genus into his classification, at first calling it a †stegodontine and later making for it a subfamily of †Mammutidae ("†Mastodontidae"). I have followed his earlier opinion, which is shared by most authorities. It seems probable that the elephantines arose directly from †stegodontines, the †stegodontines from †mammutids, and the †mammutids from primitive †gomphotheriids, and as usual the points where divisions are established must be somewhat arbitrary. (Osborn is, of course, quite right in stressing the absence of known fossils leading continuously from one structural grade to another; this absence is a common phenomenon, and it is readily explicable by considerations other than absence of real affinity.)

Among the elephantines, it is difficult to find a suitable middle ground between the old custom of referring all elephantines to *Elephas* and the excessive splitting into from seven to 12 genera. Osborn has well shown the heterogeneity of the forms lumped as †mammoths. Some, like †*antiquus*, are near the African elephant; some, like †*hysudricus*, near the Asiatic elephant; and others, like the Siberian and the various American †mammoths, are not particularly allied to either one. I have accepted Osborn's views as to affinities, adapting their taxonomic expression to the more usual conception of the scope of a genus. The *Loxodonta*-like forms are here included in *Loxodonta*, and the *Elephas*-like in *Elephas*. The others may be polyphyletic, but probably are more nearly allied to one another than either living genus (a probability expressed by Osborn by placing all in a separate subfamily) and, therefore, are all placed in one extinct genus, the earliest available name for which appears to be †*Mammuthus*. Anyone who has identified extensive Pleistocene collections knows how very difficult it is in some cases to distinguish between, for instance, †*Archidiskodon* and †*Parelephas* and will probably agree in giving these subgeneric rank. The †Siberian mammoth is more distinctive in its typical form, but even it is linked to the others by transitional species and variants.

[1] Since †*Zygolophodon* and †*Turicius* are probably synonyms, and if not, †*Zygolophodon* is indeterminate (see below).

[2] Hopwood reports the presence of †*M. americanus* in the Pontian of Asia and considers that species to be a Pleistocene immigrant in North America. But the evidence falls short of probability, because a fairly direct ancestry of that species can be traced back well into the Miocene in North America (subgenus †*Miomastodon*), and the presence of the American Pleistocene species in the Asiatic Pontian is almost incredible. It is true that the specimens do not surely differentiate the species, but neither do they suffice to demonstrate identity, which is so improbable that it bears the burden of proof. It is, however, probable, as Hopwood suggests, that the †Mammutidae as a whole arose in the Old World and that the oldest known European forms are older than the earliest American record.

Throughout this classification of the Proboscidea I have assumed that Osborn's identification of specimens and generic arrangements of species were correct unless (as happened very seldom) there was strong evidence to the contrary. Thus I have in no sense discarded or neglected his work but have accepted it as a whole and have merely translated it into the more usual sort of classification.

Because of Osborn's great authority and because his monograph will always be the principal basis for further work on the Proboscidea, it will be useful to give his final classification integrally here. This is done in the following table. The first column is an abstract of his system as it is used in the proboscidean memoir. In the second column are given the names that would probably have to be used if Osborn's classification were retained without change but his nomenclature emended to meet the requirements of the Rules. Where no name appears in this column, that used by Osborn appears to be valid under the Rules.[1] In the third column is shown the disposal that I have tentatively made of each of Osborn's groups.

[1] Osborn used 77 names in all, down through genera but exclusive of subgenera, species, and subspecies. Of these 21 appear to be invalid under the Rules, infractions of which were, of course, intentional.

Osborn, 1936	Osborn's Classification with Revised Nomenclature	Equivalents in Present Classification
†Moeritherioidea		†Moeritherioidea
†Moeritheriidae		†Moeritheriidae
†Moeritheriinae		(No subfamilies in this family)
†*Moeritherium*		†*Moeritherium*
†Deinotherioidea		†Deinotherioidea
†Curtognathidae	†Deinotheriidae	†Deinotheriidae
†Deinotheriinae		(No subfamilies in this family)
†*Deinotherium*		†*Deinotherium*
†Mastodontoidea	†Mammutoidea[2]	(Included in Elephantoidea)
†Mastodontidae	†Mammutidae	†Mammutidae
†Palaeomastodontinae		(Transferred to †Gomphotheriidae and included in †Gomphotheriinae)
†*Palaeomastodon*		†*Palaeomastodon*
†Mastodontinae	†Mammutinae	(No subfamilies in this family)
†*Miomastodon*		Subgenus of †*Mammut*
†*Pliomastodon*		Subgenus of †*Mammut*
†*Mastodon*	†*Mammut*[3]	†*Mammut*
†Zygolophodontinae		(No subfamilies in this family)
†*Zygolophodon*	(Name = †*Turicius*, genus has no valid name)[4]	Unnamed subgenus of †*Mammut*
†*Turicius*	†*Zygolophodon*[4]	Subgenus of †*Mammut*
†Stegolophodontinae		(Transferred to Elephantidae and included in †Stegodontinae)
†*Stegolophodon*		†*Stegolophodon*

[2] If this is considered a suborder †Mastodontoidea is a valid name, but as a superfamily it must be called †Mammutoidea.

[3] Everyone now agrees that †*Mammut* is the prior name for the †American mastodont and any forms congeneric with it and that †*Mastodon* is an antedated synonym. Many authoritites refuse to use †*Mammut* simply because they do not want to. I do not want to either but reluctantly set aside personal desires in favor of adherence to the accepted Rules.

[4] †*Zygolophodon* originally included the species †*borsoni*, †*turicensis*, †*tapiroides*, †*pyrenaicus*, and †*ohioticus* (= †*americanus*). In 1918 Matthew selected †*tapiroides* as type. Hopwood, 1935, submits that †*tapiroides* is indeterminate, but Osborn's, 1936, determination of it seems likely to stand. I, therefore, take it that †*tapiroides* as redefined by Osborn is type of †*Zygolophodon*. In 1926 Osborn took †*borsoni* as type, but since the type had already

OSBORN, 1936	OSBORN'S CLASSIFICATION WITH REVISED NOMENCLATURE	EQUIVALENTS IN PRESENT CLASSIFICATION
†Bunomastodontidae	†Gomphotheriidae	†Gomphotheriidae
†Rhynchorostrinae	†Rhynchotheriinae	†Rhynchotheriinae
†*Rhynchotherium*		†*Rhynchotherium*
†*Blickotherium*		Subgenus of †*Rhynchotherium*
†*Aybelodon*		Subgenus of †*Rhynchotherium*
†Longirostrinae	†Gomphotheriinae	†Gomphotheriinae
†*Trilophodon*	†*Gomphotherium*[1]	†*Gomphotherium*
†*Megabelodon*		Subgenus of †*Gomphotherium*
†Gnathabelodontinae		(Doubtfully included in †Gomphotheriinae)
†*Gnathabelodon*		†*Gnathabelodon*
†Amebelodontinae		(Included in †Platybelodontinae)
†*Phiomia*		†*Phiomia* (transferred to †Gomphotheriinae)
†*Amebelodon*		†*Amebelodon*
†Tetralophodontinae		(Included in †Gomphotheriinae)
†*Tetralophodon*		†*Tetralophodon*
†Notorostrinae	†Cuvieroniinae	†Cuvieroniinae
†*Cordillerion*	†*Cuvieronius*[2]	†*Cuvieronius*
†Brevirostrinae	†Anancinae	†Anancinae
†*Anancus*		†*Anancus*
†*Pentalophodon*		Subgenus of †*Anancus*
†*Synconolophus*		†*Synconolophus*
†Humboldtidae	†Stegomastodontidae	(Included in †Gomphotheriidae)
†Humboldtinae	†Stegomastodontinae	(Included in †Anancinae)
†*Eubelodon*		†*Eubelodon* (subfamily uncertain)
†*Cuvieronius*	(Name = †*Cordillerion*, genus has no valid name)[2]	(Name used for "†*Cordillerion*," genus included in †*Stegomastodon*)
†*Stegomastodon*		†*Stegomastodon*
†Serridentidae	†Serridentinidae	(Included in †Gomphotheriidae)
† Serridentinae	†Serridentininae	(Included in †Gomphotheriinae)
†*Serridentinus*		†*Serridentinus*
†*Ocalientinus*		Subgenus of †*Serridentinus*
†*Serbelodon*		Subgenus of †*Serridentinus*
†*Trobelodon*		Subgenus of †*Serridentinus*

been fixed this action was invalid. Also in 1926 Osborn proposed †*Turicius* with †*turicensis* as type and †*tapiroides* as a referred species. Since he referred the true type of †*Zygolophodon* to his new genus, that genus was and is an antedated synonym of †*Zygolophodon*. †*Zygolophodon* of Osborn, not of Vacek as fixed by Matthew, therefore has no valid name. If †*turicensis* is supposed to belong to a different genus from either †*americanus* or †*tapiroides*, it requires a generic name, but I do not propose one because I question its generic distinction.

[1] The question of †*Gomphotherium* as against †*Trilophodon* is one of the most complex in all nomenclature and cannot be fully discussed here. Probably it can be settled only by legal suspension or interpretation of the Rules. After prolonged investigation it appears to me probable, although not quite certain, that †*Gomphotherium*, type †*G. angustidens*, is available under the Rules and certain that it antedates †*Trilophodon* or any other name available for this genus.

[2] After reviewing the question with care and examining many specimens, I am convinced that Cabrera was essentially correct in his taxonomic and nomenclatural treatment of the South American †mastodonts. Osborn's different taxonomy is a matter of opinion, but his nomenclature, as far as it differs from Cabrera, is invalid under the Rules. Cabrera has shown that the type specimen of the type species of †*Cuvieronius* actually belonged to the †Andean mastodont to which Osborn gave the later name †*Cordillerion*. †*Cuvieronius* is, therefore, the valid name of this genus. The supposed genus that Osborn later called †*Cuvieronius* thus has no name. Cabrera did not give it one because he considered it inseparable from †*Stegomastodon*, and in this I follow him.

Osborn, 1936	Osborn's Classification with Revised Nomenclature	Equivalents in Present Classification
†Platybelodontinae		†Platybelodontinae
†*Platybelodon*		†*Platybelodon*
†*Torynobelodon*		Subgenus of †*Platybelodon*
†Notiomastodontinae		(Included in †Cuvieroniinae)
†*Notiomastodon*		†*Notiomastodon*
†Stegodontoidea		(Included in Elephantoidea)
†Stegodontidae		(Included in Elephantidae)
†Stegodontinae		†Stegodontinae
†*Stegodon*		†*Stegodon*
Elephantoidea		Elephantoidea
Elephantidae		Elephantidae
Loxodontinae		(Included in Elephantinae)
Loxodonta		*Loxodonta*
†*Palaeoloxodon*		Subgenus of *Loxodonta*
†*Hesperoloxodon*		Subgenus of *Loxodonta*
†Mammontinae	†Mammuthinae	(Included in Elephantinae)
†*Archidiskodon*		Subgenus of †*Mammuthus*
†*Metarchidiskodon*		Subgenus of †*Mammuthus*
†*Parelephas*		Subgenus of †*Mammuthus*
†*Mammonteus*	†*Mammuthus*[1]	†*Mammuthus*
Elephantinae		Elephantinae
Elephas		*Elephas*
†*Hypselephas*		Subgenus of *Elephas*
†*Platelephas*		Subgenus of *Elephas*
(Not placed in Proboscidea, considered a distinct order, "†Barytheria")	(No previous unpreoccupied name)	†Barytherioidea
		†Barytheriidae
		†*Barytherium*
5 Suborders or superfamilies		(Without †Barytherioidea): 3 Suborders
8 Families		5 Families
43 Genera		22 Genera

[1] As Hopwood, 1935, has shown and as does, indeed, appear from a judicious reading of Osborn's own citations, †*Mammuthus* is the earliest available name for any †mammoth. †*Mammonteus* was reconstructed by Osborn from "Mammonteum" in a Latin work by Camper, but it is perfectly clear that Camper used this only in the vernacular and neither intended nor inadvertently created a real generic name. It is also doubtful whether Camper's "mammonteum" would be available for a †mammoth (and not †mastodont) even if it were a generic name.

†BARYTHERIOIDEA

†*Barytherium* is a puzzling form without any known antecedents, successors, or close allies. Following Andrews, it is commonly supposed to be distantly related to the Proboscidea, which at least is not unlikely, although the degree of relationship is not known. Andrews tentatively placed it in a separate group, *incertae sedis*, †Barytheria.[2] Sometimes this is recognized as an order, and sometimes †*Barytherium* is merely placed in

[2] This name is plainly preoccupied by †Barytheria Cope, 1898, for the †toxodonts. It is more familiar in Andrews' than in Cope's sense, and preoccupation is not absolutely deterrent for ordinal or subordinal names. It is, however, to be avoided as much as possible; Andrews himself abandoned †Barypoda because of a still more obscure and forgotten prior use; †Barytheria is unfortunate in form and meaning as suggesting a major group of Mammalia and as more appropriate for many other animals than for this one; and if, as here, the group is placed in the Proboscidea, †Barytherioidea avoids these difficulties and is parallel with the other names used in this order.

a family of Proboscidea. The present arrangement avoids overemphasis of this poorly known, isolated animal and is as likely as any other, even though questionable.

Literature

The available literature on Proboscidea except †Barytherioidea is so thoroughly summarized and cited in Osborn, 1936, 1942, that no other reference is necessary here. On †Barytherioidea see Andrews, 1906b.

†EMBRITHOPODA

Since the whole Paleocene and most of the Eocene, probably about a third of the Tertiary and perhaps the most important span in the whole history of mammals, are a complete palaeontological blank in Africa, it is not surprising to find some extraordinarily isolated end forms appearing there after this long gap. †*Arsinoitherium* is such an animal, and its high specialization bespeaks a long history totally unknown to us. Andrews put it in a separate order, and no substantial new contribution has been made since he wrote in 1906b. Nor is there any good reason for doubting his conclusions as to affinities which were that there are no close or certain known relatives of †*Arsinoitherium*, that it probably belongs to the section of ungulates including the elephants, hyracoids, †pantodonts, and †uintatheres (i.e., to my Paenungulata), and that within this section (superorder) it may be closest to the Hyracoidea.[1]

Virtually all that is known of this monotypic order is given in Andrews, 1906b.

HYRACOIDEA

Literally ungulates, with rhinoceros-like teeth, but similar to some rodents in body form and some other characters, the peculiar hyracoids have been a taxonomic stumbling block. Linnaeus did not distinguish the obscure living forms. When they were designated as a genus (Storr, 1780) they were at first placed as rodents near *Cavia* (hence the inappropriate name *Procavia*). Cuvier considered them "pachyderms," and this collocation, under various names, was common during the first half of the nineteenth century. This was supported in large part by the rhinoceroid aspect of the teeth,[2] and when the pachyderms were broken up and distributed among Proboscidea, Artiodactyla, and Perissodactyla, the hyraxes were sometimes, on this account, placed in the Perissodactyla (e.g., Owen, 1868). With further study it was soon found that this limited resemblance is contradicted by profound differences in many other respects, and the hyraxes were placed in an order by themselves (Huxley, 1869, 1872; Gill, 1870, etc.). The wider affinities of this order were, and are, uncertain, but the consensus has been that they are paenungulates in the present sense, subungulates of some authors, distantly related to the Proboscidea.

Two other old ideas have recently been revived, that the hyracoids are nearer to the Perissodactyla (revived by Frechkop and others) and that they are specially allied to the †notoungulates (strongly claimed by Ameghino and revived by Stromer). Neither view seems probable enough at present to disrupt the more usual classification, but it must be noted that no one has ever fully examined and logically interpreted numerous resemblances, probably but not surely superficial, to various other groups, notably to the †meniscotheres and the †notoungulates. About all that has been done is to note some resemblances and to jump to conclusions without fully weighing opposing resemblances and profound differences. Whatever the true affinities of the hyracoids, they certainly have a unique complex of convergent and divergent characters with respect to other orders and merit more study, although this might not be conclusive until older forms are discovered.

Andrews divided the hyraxes into one living and two extinct families, and this arrangement is retained here. It now appears, however, from the studies of Matsumoto, Brauer, Hahn, and others that some of the extinct genera, notably †*Saghatherium*, are close to the modern hyracids, while others, like †*Megalohyrax*, represent widely divergent phyla. It is, therefore, better to transfer the former to the Hyracidae, making necessary a change from Andrews' nomenclature,

[1] Winge definitely referred it to the Hyracoidea, but to Andrews and other well-informed students this has appeared a great overestimate of the similarity and of the probability of relationship.

[2] A peculiarity rediscovered by an American president.

since his name †Saghatheriidae must follow its type genus and cannot longer apply to the more aberrant forms that he had principally in mind in making a separate extinct family.

The small extinct family †Myohyracidae is still more aberrant but is basically hyracoid and does not appear to me to merit removal from the Hyracoidea as Stromer suggested.

As far as known, the hyracoids have never spread beyond Africa and the Mediterranean region. Since the group is old, has been locally abundant, and is associated with mammals much more widespread, this implies some peculiar ecological limitation, the nature of which is not clearly apparent.

Among the more important studies of the living forms are Frechkop, 1936; Hahn, 1934; Hatt, 1936. Most of the known fossils are described in Andrews, 1914; Matsumoto, 1926; Stromer, 1926.

SIRENIA

As was inevitable, the Sirenia were long confused with other aquatic mammals. The consensus down to the end of the nineteenth century was that they are closely allied to the Cetacea. Even Linnaeus, however, glimpsed possible affinities with the Proboscidea, De Blainville in 1816 advanced this view more definitely, and it has been gaining ground steadily ever since. It is vaguely supported by the fossil evidence and is now the general opinion, although the relationship must be distant and is not certain. Ordinal rank is now always given the Sirenia, but it is probable that they are paenungulates, perhaps with some special, although distant, connection with the proboscideans.

The classification of the Sirenia here presented is that of an earlier study (Simpson, 1932) slightly modified to accord with new information from Sickenberg, 1934. The opinions and facts involved and references to the literature are so fully given in those two easily accessible publications that little discussion is called for here.

The fact that three of the four trichechiform families and four of the five dugongid subfamilies are monotypic shows how poor is our knowledge of the group and perhaps also shows a failure in recognizing broader affinities.

†*Prorastomus* has often been referred to the Trichechidae as an ancestral manatee, but I have suggested that this is based on no good evidence and that †*Prorastomus* is close to †*Eotheroides* and nearly prototypal to all sirenians. I have, however, now removed †*Eotheroides* from this family in deference to Sickenberg's insistence on a phyletic arrangement and demonstration that the †*Prototherium* (etc.) phylum arose in or near †*Eotheroides*. I have also recognized his †Protosirenidae, although this arrangement of the early forms still is not satisfactory.

†*Eotheroides*-†*Prototherium*-†*Halitherium*-†*Halianassa*-†*Felsinotherium* are a nearly continuous phyletic sequence with †*Thalattosiren* and †*Hesperosiren* as divergent genera near but off the central line of descent. Probably all the more sharply distinct dugongids, †*Miosiren*, †*Rytiodus*, and the two recent dugongid genera, also arose from some part of this general sequence, and they are given subfamily rank only because of their relatively greater divergence.

The systematic position of †*Desmostylus* has been and still is uncertain. Most students have concluded that it is probably a sirenian. Abel, however, concluded negatively that it is not a sirenian and positively that it is a †multituberculate and allied to the monotremes. His original conception of its morphology was fundamentally wrong and was not sufficiently corrected in later papers after he had seen a specimen. His positive conclusions as to affinities are also erroneous beyond any question. Because of these manifest errors, his negative conclusion has not been very seriously considered by the students best qualified to review it. The most detailed consideration of the whole known morphology of †*Desmostylus* is that of VanderHoof, 1937, and he agrees with the consensus that it is a sirenian. Still more recently, however, Sickenberg, 1938, has briefly reviewed the literature and has strongly opposed sirenian affinities, without clearly suggesting any others, and his argument carries much weight even though it cannot be accepted as quite conclusive in the face of almost complete agreement by students of the actual specimens. What stands out in these arguments, considered dispassionately, is:

1. That †*Desmostylus* is certainly very unlike any other known animal, whether si-

renian or not. This is freely agreed by all, including the strongest supporters of sirenian affinities. That an animal has diverged strongly from all others known does not mean, however, that it has no affinities with a known order, but only makes these harder to detect.

2. That it certainly is not an ally of †multituberculates or monotremes.

3. That it probably has something to do with the general proboscidean-sirenian complex, i.e., that it is more likely than not to be a paenungulate.

4. That it may be a highly aberrant offshoot of the Sirenia, as most students think, but that this cannot be accepted as proved or even as definitely probable. It is merely less improbable than any other positive suggestion yet made.

There the question is likely to rest until more specimens are found.[1]

Besides the valid and the other relatively familiar names given in the classification, at least 25 unfamiliar and nearly or quite valueless generic names have been proposed for sirenians, and these do not require listing here. The nomenclature is also confused because even some of the latest and best authorities, e.g., Sickenberg, insist on using misspelled, antedated, or preoccupied names for many of the genera. It is preëminently true in this group that adherence to the Rules now affords the only chance of future stability, and there is little question that the Rules demand the names and spelling that I have given as valid.

The principal recent reviews of the Sirenia, or of some of them, are Sickenberg, 1934, and Simpson, 1932. These give references to the more important older studies. On †*Desmostylus*, see especially VanderHoof, 1937; Sickenberg, 1938; and works cited by them.

[1] There is said to be a skeleton in existence in Japanese hands, but this has not been published and I cannot positively affirm it as a fact.

Perhaps a personal comment here may be forgiven as it has been provoked. I have been involved in this controversy by both sides, as an authority to be followed and as a horrible example to be attacked, both with equal injustice. I have never made a profound, first-hand study of †*Desmostylus* and have never claimed to have an original, well-based opinion. I have merely tentatively accepted one of the two opposed opinions because it was advanced by the students who knew most about the animal and because it was not inconsistent (as a large part of Abel's arrangement was, for instance, but as none of Sickenberg's now is) with such pertinent facts as I did have at first-hand.

MESAXONIA

There is at present no phylogenetic necessity or pragmatic excuse for placing the perissodactyls in more than one order, but as occasionally happens they are unified not only on the ordinal but also on the superordinal level, using superorders as here introduced. Marsh's term Mesaxonia is essentially a synonym of Perissodactyla but it can conveniently be used to designate the superorder containing the single Order Perissodactyla, just as the parallel name Paraxonia will be used for a superorder with the one Order Artiodactyla.

PERISSODACTYLA

Linnaeus did not at all recognize the perissodactyls as a natural group, placing the horses and hippopotamus (with tapirs as a species of hippopotamus) in the Belluae and the rhinoceroses in the widely separate Glires. Brisson, 1762, distinguished the tapirs from the hippopotamus and the rhinoceros from the rodents, but placed these in two distinct orders and the horses in a third, with no suggestion of their relationship. In later eighteenth and early nineteenth century classifications the tapirs and rhinoceroses are usually to be seen, with various unrelated forms, in a division of "pachyderms" or of "nonruminant fissiped ungulates," while the horses are almost invariably sharply differentiated from all other mammals. Among De Blainville's many accomplishments was that he first (1816) classified the ungulates according to whether they had an even or an odd number of toes, so at last permitted the "solidungulate" horse to be placed near the "multungulate" tapir and rhinoceros. His "onguligrades à doigts impairs" were exactly our Perissodactyla except for including the hyrax, an inclusion that in no way lessens the brilliance of the arrangement for that time. The conception was taken over by Owen without any change and given the label Perissodactyla that it has had ever since.

This history emphasizes the fact that tapirs and rhinoceroses resemble one another

more than either group resembles the horses. This dichotomy of the Perissodactyla is reenforced rather than displaced by the known fossil groups. Most of these can be directly associated with the horse, tapir, or rhinoceros groups (within three superfamilies in the present arrangement). Two groups, the †chalicotheres and †brontotheres, cannot be so closely associated with the antecedents of the surviving group, yet it is clear that they are related to one of these, that of the horses, in a way somewhat analogous to the tapir-rhinoceros relationship. The extraordinary clawed feet of the †chalicotheres long obscured this fact as regards them, but there is now little doubt that it is a fact.

If, as is now almost universal, the Perissodactyla are given ordinal rank, the major association within the group suggests the use of two suborders. This was recognized as soon as the bad start made with the †chalicotheres had been corrected, and can be plainly seen, for instance, in some of Osborn's phylogenetic diagrams, but it remained for H. E. Wood, 1934, to give it formal expression, reviving the two old names Solidungula and Tridactyla for this purpose. Because these names are inappropriate, or at least inadequate, in meaning and have been used in conflicting ways, Scott urged the application of new names and Wood provided these, Hippomorpha and Ceratomorpha, in 1937. I agree with Wood's judgment in preferring the redefinition of historic names to the coinage of new ones, but I here adopt the latter because of the better chance that they can be standardized in general use now that they are in print and endorsed by Scott.

Wood intended the redefined name Solidungula and the equivalent new name Hippomorpha to refer to a suborder explicitly including the †chalicotheres. Scott, 1941, however, continues in somewhat different terms to follow the old system of contrasting †chalicotheres and all other perissodactyls. He, therefore, puts the †chalicotheres in a suborder †Ancylopoda and the rest in a suborder Chelopoda, with two sections (on his premises, I would call them infraorders), Ceratomorpha and Hippomorpha. The point is not of great importance, but I prefer Wood's arrangement to Scott's. The facts that the late †chalicotheres had oddly proportioned limbs and claws for hoofs are striking enough, but these obvious distinctions are not profound and do not conceal the fact that †chalicotheres are related not merely to the perissodactyls as a whole but to one basic branch of perissodactyls, the Hippomorpha, from other members of which the early †chalicotheres are difficult to distinguish. This important conclusion is wholly obscured by making a suborder for †chalicotheres alone, and such an arrangement is, indeed, suggestive of the former placing of the horses in a separate suborder or order from all other perissodactyls because their late representatives have such specialized limbs and feet.

HIPPOMORPHA

The members of this suborder, the great majority of which are extinct, fall in the most natural and indeed obvious way into three groups conveniently designated as superfamilies: Equoidea, †Brontotherioidea, and †Chalicotherioidea. The common ancestry of the whole suborder (and only a little more distantly, of the whole order) is nearly represented by †*Hyracotherium*, which, however, is usually, and may best be, placed in the Equoidea. The †Brontotherioidea and †Chalicotherioidea, of nearly equal antiquity and at first very like the Equoidea, diverged relatively rapidly, and the terminal members of the three superfamilies were remarkably dissimilar in aspect.

EQUOIDEA

The main outlines of equoid evolution are better known than those of any other group, but just because of the great mass of data and wide field of achieved knowledge there is considerable diversity in classification. The present arrangement follows Matthew in essentials, with some slight modification. The †Palaeotheriidae include several quite distinct lines, but all are off-shoots of some very primitive equoid, near †*Hyracotherium*, and all are rather similar in direction of evolution, so that their grouping in one family is convenient. The polyphyly could perhaps be shown by subfamily or tribal divisions, but there is now little reason for this because with one or two exceptions each genus represents a different line of descent, all more or less contemporaneous.

Matthew has shown and insisted that †*Hyracotherium* (including †*Eohippus*) is so primitive that it is not much more definitely equid than tapirid, rhinocerotid, etc., but it is customary to place it at the root of the equid group, as I do here and as Matthew himself did in formal classification. The equid subfamilies in common use and here retained are partly horizontal and partly vertical groups. The main line of equid evolution passed successively through the three subfamilies. The first has only one known generic line, in or near the ancestry of all later forms and distinguished by its primitive character and by the absence of branching. The †Anchitheriinae include not only a line leading to the Equinae (†*Mesohippus*-†*Miohippus*-†*Parahippus*) but also divergent branches, persistently primitive in some crucial characters (late †*Parahippus*, †*Archaeohippus*, †*Anchitherium*, †*Hypohippus*, all of which were contemporaneous for most of their histories). The Equinae, in turn, include the common ancestry (in †*Merychippus*) of all the divergent lines in the noteworthy Pliocene radiation of Equidae and also these lines themselves, at least five in number and with one of these (†*Pliohippus*) branching again into the surviving horses and the extinct South American genera.

Horse phylogeny is thus far from being the simple monophyletic, so-called orthogenetic sequence that it appears to be in most texts and popularizations.

This arrangement is the work of almost innumerable hands, but in something like its modern form it can be dated as beginning with Marsh and carried forward by Osborn and, especially, Matthew. The last details as the system now stands are mostly the work of Matthew's student, Stirton. In the recognition and delimitation of American genera I have rather closely followed Stirton's excellent summary (1940). The most important changes from most earlier classifications (partly due to Matthew) are the nominal but necessary placing of the more characteristic forms earlier called †*Protohippus* in †*Calippus*, the removal of this group from the direct line to *Equus*, and the recognition of three distinct genera among the †*Hipparion*-like forms of North America. I follow Stirton in not recognizing the recently proposed genera †*Duchesnehippus* and †*Pediohippus* and differ from him in considering †*Megahippus* inadequately distinguishable from †*Hypohippus*. For conflicting views as to the status of †*Plesippus*, see Schultz, 1936, and Stirton, 1942. I have followed Stirton.

Neozoologists and a few palaeozoologists tend lately to split *Equus* (even without †*Plesippus*) into a number of different genera. There is no question as to the natural validity of such groups as *Asinus* or *Hippotigris*, but I think these groups best treated as subgenera. They are surely all closely related and are basically very nearly alike in structure despite the superficially striking differences in extremes of color pattern. Even between the most completely striped zebras and the most completely self-colored horses, moreover, there are intergradations and intermediate species. On the other hand some supposed genera of Pleistocene equids, like †*Neohippus*, do not seem to me to rest on any objective basis or to be valid on any level in the hierarchy. (See also Stirton, 1942.)

The literature on Equoidea is very large, not only because this is one of the most abundant and widespread groups of fossil mammals and of exceptional importance in stratigraphy but also because it is the standard example and proof of organic evolution. Among publications of the last 30 years, of particular value for one reason or another are Sefve, 1912 (South America); Osborn, 1918b (Oligocene-Pliocene, North America); Matthew, 1926 (general); Loomis, 1926 (general); Matthew and Stirton, 1930b (Pliocene, North America); Haughton, 1931 (Africa); Stirton, 1940 (North America). All of these have references to older publications.

†BRONTOTHERIOIDEA

A specimen of this group first drew attention to the great White River series and its rich faunas and marked, as nearly as any one discovery, the beginning of exploration for Tertiary mammals in western North America. A remarkably full sequence of †brontotherioids, or †titanotheres as they are still usually called in the vernacular,[1] has since been found, from early Eocene to early Oligocene in North America and to middle

[1] Although the generic name †*Titanotherium* is technically invalid.

Oligocene in Asia. It is probable that the group originated as such at about the time of the earliest known fossils, and this is a relatively short span for the whole history of a mammalian family or superfamily. Although the later members were spectacular animals, the amount of fundamental progress, variety, and important novelty in the family is slight. At any given time most †titanotheres were very much alike save for minor differences in size and proportions of various parts, and the evolutionary change from earliest to latest forms is only moderate, involving little more than a limited amount of premolar molarization, with other slight dental changes, development of horns, all much alike except for †*Embolotherium*, and changes directly correlated with simple increase in bulk.

Although the group can thus fairly be called stereotyped, the variation within the limits of its evolutionary path is great and makes classification difficult. It is fairly certain that a number of genera, and quite possible that some subfamilies, have been based on variations that were really sexual, ontogenetic, or individual. The difficulty of handling such bulky specimens and the expense of building up the requisite series of more or less uniform origin have prevented the acquisition and study of any samples really adequate to demonstrate group characters and to provide a proper basis for objective taxonomy; the same difficulty is experienced in some degree in all groups of large, varied mammals, notably the Proboscidea. Of course no two individuals are alike, and subjective criteria have seemed to warrant placing virtually every good specimen in a new species. To add to the confusion, after a rather elaborate phylogenetic scheme for the American Oligocene forms had been founded in their supposed temporal sequence, it was found that this sequence was in large part, if not wholly, fictitious, because of faulty older field records, the chance effects of inadequate sampling, and zoning based on theoretical rather than observational criteria. According to Scott, 1941, no sequence is at present really known for these forms, and all variants appear to occur at all levels.

Most of the literature and observations on most of the known American specimens were brought together by Osborn, 1929, in a great memoir. Osborn's classification is here adopted except for slight formal changes and for additions and emendations necessitated by later work, even though several points in this arrangement are provisional for the reasons already mentioned. The most important changes are the combination of Osborn's 12 American subfamilies to seven and the insertion of many Mongolian genera. These subfamily combinations were, in fact, indicated by Osborn although not formally adopted by him. The Mongolian forms were found only as he was finishing his work and were never thoroughly studied by him. They have now been studied by Granger and Gregory, whose classification (complete but unpublished when these lines were written) has been adopted here (from the manuscript), except that their two proposed new subfamilies are included in others.

†*Lambdotherium* is so primitive and so nearly a generalized ancestral type for all †titanotheres that it is given subfamily status. It is very like the earliest equoids, and especially the †paleotheres. It is quite possible that the †paleothere-equid dichotomy was basic, in the earliest Eocene, and that with subsequent separation of New and Old Worlds, the †paleothere ancestry developed into †titanotheres in the former and into the typical †paleotheres in the latter. The †Palaeosyopinae carried the group on into the middle Eocene, and from somewhere near the base of this subfamily arose what appear to be three main lines running into the late Eocene and, in part, Oligocene: †Dolichorhininae, †Telmatheriinae, and †Brontopinae. The two latter groups also reached Asia and underwent a large radiation there, finally giving rise to the most specialized of all †titanotheres, the †Embolotheriinae, while two likewise relatively specialized terminal branches arose from the same general complex in America, †Menodontinae and †Brontotheriinae, if, indeed, these are two groups, as Osborn maintained and as seems likely, rather than one, as Scott tentatively suggests.

In addition to Osborn, 1929, which will always be the main source for this superfamily, Scott, 1941, and Granger and Gregory (Bull. Amer. Mus. Nat. Hist., still unpublished as this is written) should be consulted.

†CHALICOTHERIOIDEA

When these animals were first found, early in the nineteenth century, the teeth were ascribed to normal perissodactyls (†lophiodonts) and the claws were believed to belong to an edentate. Only when remains were tardily found in unequivocal association could anyone believe that Cuvier's so-called law of correlation could be so utterly wrong in a particular case and that such an anomalous creature as a clawed ungulate could exist. Then it was believed that the †chalicotheres should be placed in a separate order, at least, partly on the argument that claws preceded hoofs and that the †chalicotheres must, therefore, have arisen from a clawed, not hoofed, ancestry. Now, however, it is quite clear that apparent reversion really did occur and that the †chalicothere ancestry had hoofs and was, in all probability, equoid and almost certainly hippomorph. (A trend from hoofs to claws is in fact quite normal in mammalian evolution, as we see it now, and has occurred independently at least three times, in the †notoungulates, perissodactyls, and artiodactyls.)

Although the †chalicotheres were long-lived (late Eocene to Pleistocene), not many valid genera are known and these fall readily into a primitive and an advanced subfamily, the latter with two tribal phyla. This arrangement is due to Colbert, 1935a, who is followed here without change and whose work should be consulted for details and for references to the older literature.

CERATOMORPHA

Tapirs and rhinoceroses were early associated with each other and separated from the horses, and they formed part of the unnatural group of "pachyderms." When their affinities with the horses became clear, they were still commonly distinguished and associated because of their both having more than one hoof on each foot. As it became clear that this basis for grouping was invalid, or at least superficial, most students simply listed three living families of perissodactyls without other grouping. Now the old association has been revived, mainly by Wood, but for a new and better reason: when perissodactyls first appear, they seem to represent two similar but distinguishable main stocks, one of which gave rise to both tapirs and rhinoceroses.

Unlike the hippomorphs, which proved to include two great fossil groups besides the one surviving, all the ceratomorphs can well be placed in the two living superfamilies, although again, most of the members of both groups are extinct and the superfamilies are much more varied than could be imagined from the living relicts.

TAPIROIDEA

Aside from the unimportant question whether the living tapirs should be placed in one genus, as in this classification, or in two, as is frequent, or three, as the splitters now insist, they are so few and so much alike that they present no particular problem, nor do their more or less direct ancestors from the Oligocene in New and Old Worlds. The discovery of a considerable array of early Tertiary genera has, however, complicated matters. Some of these, e.g., †*Colodon*, have been considered rhinoceroses, or at least rhinocerotoids and some, e.g., the †lophiodonts, are often placed more noncommittally as neither tapiroid nor rhinocerotoids. It is, however, probable that they arose from the tapir ancestry. It is not unlikely that rhinoceroses also arose from forms technically tapiroid, because the tapirs are more conservative on the whole, but even in such a case the little-advanced early side lines are more naturally associated with the tapiroids.

The †isectolophids are very primitive and not far removed structurally from the ancestry of all ceratomorphs. From them, or forms like them, the tapirids arose, as well as two early aberrant lines, the †lophiodonts mainly or exclusively in Europe and the †helaletids mainly or exclusively in North America and Asia. Schlaikjer believes that the tapirids arose from †*Heptodon* rather than from a more generalized †isectolophid, but †*Heptodon* is probably nearer †*Helaletes* (Wood). The †helaletids are in turn divisible into two structural groups long since defined as subfamilies and here retained as such.

There is no adequate recent review of the tapiroids as a whole, and information must

be sought in many short papers, essentially those indicated by the authors and dates of generic names. On the Tapiridae alone, see also Schlaikjer, 1937. The present classification owes much to mainly unpublished observations by Wood.

RHINOCEROTOIDEA

The human factor in classification is nowhere more evident than in dealing with this superfamily. It is, as mammalian superfamilies go, well known, but what is "known" about it is so inconsistent in places that much of it must be wrong. Some authorities still recognize "genera" (e.g., †*Orthocynodon*, an †amynodont) that are, beyond much doubt, based on slight individual variation, while others lump together in one genus a whole tribal lineage that must almost certainly include a whole cluster of genera, even if generic lines be drawn as broadly as could be desired (e.g., the supposed European †*Dicerorhinus* line). Some of the most competent students (e.g., Matthew) follow very broad lines, emphasize skull and foot characters, and tend to neglect dental mutations; others (e.g., Wood) split the groups into mainly short, narrow sequences emphasizing minor dental characters and tending to neglect skeletal structure. Much of the published work (aside from that of Matthew, Wood, and some others) is simply incompetent and has not been revised by a properly instructed and judicious student.

Under these circumstances a balanced, sound classification, to the extent that this is possible for any group, would require years of research and much more knowledge of the specimens than I have. Fortunately a considerable part of the superfamily has been revised by Wood, and he has also acquired a better grasp than any other one student of the groups on which he has not yet published. This arrangement leans heavily on his work, both printed and unprinted, although I continue to draw the categories somewhat more broadly than he would prefer, and he is not responsible for my probable failure to grasp all pertinent details.

The small, early families †Hyrachyidae and †Hyracodontidae have been revised by Wood, 1934, 1927. The first is a primitive family near the structural ancestry of the whole superfamily, and the second is a cursorial side branch. The almost equally short-lived, more strongly aberrant †amynodont branch presents no serious difficulties at present, but Wood informs me that work on Asiatic †amynodonts, not yet near enough to printing for inclusion here, will complicate matters by revealing greater branching within the family. The †Aceratheriinae are often combined with the †Caenopinae (Matthew) but seem, as Wood concludes, to be separable as a fairly well-defined Old World phylum.

The †Caenopinae are a varied group probably including not only the general source of more advanced later lines among its more primitive genera but also at least two (and possibly more) divergent descendent groups, those culminating in †*Diceratherium* and in †*Aphelops* and †*Peraceras*. These two are frequently placed in separate subfamilies (Wood, etc.) but they intergrade with earlier †caenopines, and I see no practical value in separating out one or two such rather closely related genera. If the whole phylogeny can eventually be reconstructed a tribal arrangement should be useful.

Almost everyone gives the †*Baluchitherium* group subfamily status. The apparent array of four genera suggests more knowledge and more diversity than are really indicated. It is probable that †*Forstercooperia* is not correctly placed here, and the other three supposed genera, although each has been made the basis of a subfamily, may well be synonymous, or may be best treated as subgenera of one genus. Since †*Paraceratherium* is the only surely valid generic name here, I use the subfamily name †Paraceratheriinae despite its relative unfamiliarity.

The stocky †Teleoceratinae, another aberrant line, are also based essentially on a single genus, with a possibly composite European ally.

Matthew and most others believe the tandem-horned rhinoceroses to belong together and I so place them, but Ringström and a few other splitters would separate a dicerorhine and a dicerine group. It should be mentioned that Matthew's final classification had only three subfamilies: †Baluchitherii-

nae, †Diceratheriinae, and "Rhinocerinae," but the latter seems unduly miscellaneous, and he does recognize, on a different level, the natural groups here called subfamilies.[1]

Ringström's splitting tendencies (which do not spoil the great value and accuracy of his work) are again seen in his insisting on a separate family for the †elasmotheres, a criterion which, as Wood has said, would make †*Baluchitherium* a representative of a separate order. Subfamily recognition is, however, warranted by the peculiar horn and tooth developments.

In the large literature of this group, the following small selection of papers gives an introductory survey, and they will lead, through their citations, to much of the treatment of special points: Abel, 1910; Breuning, 1923; Forster Cooper, 1934; Granger and Gregory, 1936; Matthew, 1931, 1932; Osborn, 1898a, 1900; Ringström, 1924, 1927; Roman, 1911; Scott, 1941; Wood, 1927, 1934, 1941.

PARAXONIA

As with the Perissodactyla, the Artiodactyla form a single, well-defined order, but the group also merits superordinal rank. For the superorder, Marsh's name Paraxonia is revived.

ARTIODACTYLA

The history of the recognition of a natural group corresponding to our Artiodactyla parallels that of the Perissodactyla. Linnaeus and everyone subsequent to him recognized the ruminant group (Cameliformes+Boviformes=Pecora Linnaeus, Ruminantia of most later authors), but Linnaeus placed the suids in the Bestiae, Unguiculata, and the hippopotamids in the Belluae, Ungulata, each with very unnatural associations. Blumenbach, 1779, put *Sus* with the forms now called artiodactyls, but put *Hippopotamus* with the tapirs, elephants, and rhinoceroses. Storr, 1780, however, associated *Sus* with what was essentially the latter group, and this unnatural assemblage, with *Sus* and *Hippopotamus*, long continued to be used, generally under the name "pachyderms." It was De Blainville who first properly sorted these forms out, and his arrangement, given a useful nomenclature by Owen, survives today.

Once the natural order had been recognized as a unit, the organization of the recent forms did not present many serious problems on taxonomic levels from family to order. The arrangement of genera and species within families is, indeed, exceptionally difficult, particularly among the Bovidae, but it was early apparent that nine well-defined families[2] exist: Suidae, Tayassuidae, Hippopotamidae, Camelidae, Tragulidae, Cervidae, Giraffidae, Antilocapridae, and Bovidae. As for larger groupings, many students have distributed the families in two suborders (or analogous subdivision), the non-ruminant families (first three) in one, and the ruminants (last six families) in the other, an arrangement dating (in different terms) from De Blainville and, indeed, already clearly foreshadowed before the two groups were recognized as belonging to a single order. Differences of opinion arose mainly over the questions whether the Camelidae should not be removed from the Ruminantia as a separate suborder, an increasingly accepted change now favored by a consensus, and whether the Tragulidae should not be similarly treated, a change still much disputed without any clear consensus. In Flower's excellent arrangement (e.g., 1883) there are, for instance, four major groups, Suina (="Non-ruminantia"), Tylopoda, Tragulina, and Pecora, while other authors frequently unite the last two and occasionally the last three.

Fossil discoveries have tremendously complicated the clear and simple arrangement based only on recent artiodactyls and have made this taxonomically one of the most difficult orders in the whole animal kingdom, rivaled only by the rodents in this respect among mammals. Most fossil artiodactyls may, it is true, be fitted into the suborders originally based on recent forms, but even these cause difficulty not only in greatly increasing the necessary number of families and other lesser subdivisions but also in making it difficult to draw lines between groups that are completely distinct among recent animals,

[1] Except the †Alloceropinae, not properly known to him.

[2] In the sense here adopted. It need hardly be said that some authors split these families into a much larger number. On the other hand, some students recognize only six families, uniting Suidae and Tayassuidae, Tragulidae and Cervidae, Antilocapridae and Bovidae.

for instance, Tragulidae and Cervidae or Cervidae and Giraffidae. Other extinct artiodactyls, like the †entelodonts and †oreodonts, do not fall readily into any recent subdivision, major or minor. These difficulties have given rise to irreconcilable differences of opinion, with the result that no one system of major artiodactyl subdivisions is now clearly supported by a consensus if fossils are taken into account.

The following table compares three exceptionally capable classifications, each of which has to large extent been an adaptation of that preceding it, and all of which are essentially efforts to fit extinct and recent groups together into an expansion of the classic arrangement of Flower and Lydekker. The present classification, similar in nature and also evolving from these three, is added for comparison.

Osborn, 1910	Matthew, 1929a	Scott, 1940	This Classification
		Non-ruminantia	Suiformes
†"Primitive artiodactyls" (includes †anoplotheres and †anthracotheres)	†Palaeodonta (excludes †anoplotheres and †anthracotheres)	†Palaeodonta	†Palaeodonta
Suina	Hyodonta	Suina	Suina (excludes hippopotami)
†Oreodonta	†Ancodonta (includes †anoplotheres, †anthracotheres, †oreodonts)	†Ancodonta (excludes †oreodonts)	Ancodonta (excludes †oreodonts, includes hippopotami) †Oreodonta
		Ruminantia	
Tylopoda	Tylopoda	Tylopoda (includes †oreodonts, †hypertragulids)	Tylopoda
			Ruminantia
Tragulina (includes †hypertragulids) Pecora	Pecora	Tragulina (excludes †hypertragulids) Pecora	Tragulina (includes †hypertragulids) Pecora

Schlosser (e.g., 1923) divided the artiodactyls into Bunodontia (essentially Osborn's Suina, except that †leptochoerids and †entelodonts are included—classed as "primitive artiodactyls" by Osborn, as †palaeodonts by Matthew, Scott, and me), †Bunoselenodontia (†anthracotheres, †anoplotheres, and †dichobunids) and †Selenodontia (Ruminantia in the broadest sense, including camels, plus †cainotheres and †oreodonts). Based on a single sequence of characters that occurred independently in different groups, this arrangement is unnatural and misleading. Another arrangement based on single tooth characters was produced by Stehlin, 1910, with these three groups: †Hypoconifera (†dichobunids and †entelodonts), †"Cainotheridae" (†cainotheres only), and Euartiodactyla (all others). The first two of these are small, natural groups but of less than subordinal scope as suborders are usually used. The last is a great heterogeneous mass. It is, for instance, quite incredible that the Suidae should be more closely related to the Bovidae than to the †Entelodontidae. Finally, Pearson, 1927, based a primary dichotomy of artiodactyl classification on the condition of the mastoid region, with an "amastoid group" including hippopotami, †anthracotheres, †en-

There are also students who think any subordinal groupings premature or impossible, and there are others who have proposed more radical emendations usually based on one or a few characters theoretically given basic rank. Of the latter, three deserve special mention because they are by able students, have considerably influenced thought on this group, and are still sometimes accepted in essentials.

telodonts, †choeropotamids, and †cebochoerids, and a "mastoid" group including most other artiodactyls. The "mastoid" condition is primitive for artiodactyls, and it happened to be lost (probably independently) only in a few of the old, rather aberrant offshoots. On the other hand, forms that are almost certainly the direct ancestors of these or quite close collaterals did not lose this character, and the line between "mastoid" and "amastoid" is often unnatural from a phylogenetic point of view.

In all three of these classifications, and others like them, the characters used are assuredly of great importance in classification, and the more orthodox arrangements also use them in determining affinities and in defining groups, but stable and practical classification must be based on a balance of considerations. Major subdivisions based on the presence or absence of single characters are almost never natural. Nature simply does not work so accommodatingly.

The three-fold basic (subordinal) division adopted here, into Suiformes, Tylopoda, and Ruminantia, is virtually the same as that common in the nineteenth century. In spite of all the progress of knowledge, this old arrangement still seems as natural as any other and, although it was based primarily on recent artiodactyls, the very extensive fossil discoveries seem to me to strengthen the arrangement, rather than oppose it in any important way—an example of the truth, not always evident to scholastic minds, that old scientific theories are not necessarily wrong simply because they are old.

The arrangement is in part a compromise between horizontal and vertical classification. The three suborders do probably represent a primary division of artiodactyls into three great stocks, early in the Eocene, but quite generalized early forms, near the ancestry of all, and some short, early lines quite different from all the later forms are grouped together with one of these greater stocks in the Suiformes. Perhaps the most questionable major point is the placing of the †oreodonts, which will be discussed on a later page.

The classification in general is based on that of Matthew, 1929a, more than on any other one source, but a number of modifications have seemed advisable. There has been a large volume of new discoveries and of important research since Matthew's death, and this has been taken into account as far as possible. It tends on the whole to support his views, but of course some changes are made necessary, and there are also various details omitted in Matthew's more summary work although known to him.

It is evident that the first three of Matthew's suborders are more nearly related to one another than to either of the last two or than the last two are to each other. In the Eocene it is extremely difficult to distinguish between †dichobunids, †entelodonts, suoids, †anthracotheres, and †anoplotheres, and all these groups, representing three suborders of Matthew's arrangement, are then clearly closely related and near their common origin. On the other hand, the †oreodonts, the camels, and the pecorans were then already fairly distinct from one another and from the varied groups just mentioned. Leaving aside the †oreodonts momentarily, there is thus a clear basic division of the artiodactyls into three, not five, groups. The division of the first of these into three is also real but less fundamental. That this is so was also known to Matthew and can be seen clearly in his phylogenetic chart published by Colbert in 1934 (see Matthew, 1934). I now represent this important fact by making only three suborders and placing Matthew's five suborders as infraorders within these. I add two other infraorders, †Oreodonta and Tragulina, to the five representing Matthew's suborders, for impelling reasons summarized on later pages.

For ease in handling this protean group I have introduced superfamilies, which Matthew did not use. This also permits the correction of another slight discrepancy in Matthew's arrangement: the fact that certain of his families, e.g., Hippopotamidae and "Dicotylidae" (Tayassuidae), are, according to his own views of phylogeny, of less rank than others. A final unimportant divergence from Matthew's classification is that I have felt constrained to recognize some families that he suppressed, either because he united them with other families on dubious or insufficient grounds (e.g., †Choeropotamidae) or because he apparently omitted them from consideration (e.g., †Leptochoeridae).

SUIFORMES

This suborder has long been recognized by various authors and under different names. It is essentially the "Non-ruminantia" of many workers, but that name is here rejected because it is clumsy, because it is purely negative, and because as a result of this latter fact it has generally not been defined but merely used as a repository for odds and ends because they were not something else. I would have preferred the Greek derivative corresponding with Suiformes, since the "*choerus*" derivatives are more suggestive than "*sus*" of the diverse genera included, but Suiformes is already in the literature with this sense, so is retained.

Except, perhaps, for the †oreodonts, there is little doubt that all these animals are of common origin, and a fairly close relationship is suggested by the intergradations of the early, and indeed some of the later, forms. The earliest †Palaeodonta are near the structural ancestry of all artiodactyls. The later †Palaeodonta, the Suina, and the Ancodonta represent three major lines of specialization from this source. They are distinct enough by Miocene times, at latest, but their early members tend to merge and are hard to classify with certainty on that account. The †oreodonts do not show this merging, doubtless because the early forms have not been discovered, but are probably a fourth offshoot from the same ancestry.

†PALAEODONTA

The outline classification of this group follows Colbert, 1938a. The details have not been reviewed by any one author but are filled in by synthesis of the results of many workers, including Stehlin, Sinclair, Peterson, Matthew, Troxell, Pearson, Colbert, and others.

The †choeropotamids and †cebochoerids are usually placed nearer, if not in, the Suidae, and Pearson supports this, but I follow Colbert's later opinion. The question does, however, remain open. The affinities of the †Leptochoeridae are likewise dubious, without offering so clear-cut a choice. The †Palaeodonta, and within this the †Dichobunoidea, are doubtless really natural but in part on a horizontal basis. They are the most primitive of artiodactyls, some incipiently very divergent groups are included, and most or all later artiodactyls can be traced structurally if not phyletically into this complex.

Most of the genera are now well defined, but this is not true of the †entelodonts. Despite many excellent studies, no proper basis of classification in this group has been worked out. The characters commonly used, such as the relative development of jaw and jugal bones and processes, are not only extremely variable but also probably in large part sexual or otherwise non-significant for the definition of genera. Matthew has suggested that all known forms would well be placed in one gēnus. It is, however, noticeable that certain broader morphological features do appear to be associated with major differences in geographic and geologic distribution, and on this basis I tentatively recognize three genera. Some of the many others proposed may be valid, at least as subgenera, but I do not think that this has been truly demonstrated for any of them.

SUINA

Matthew's Hyodonta expressed a hippopotamid-suid association, such as occurs in most previous classifications. Here the hippopotamids are removed, but the nuclear suoid group remains. I do not feel that Matthew's unfamiliar term possesses sufficient advantages over the classic term Suina, with which it is nearly synonymous, to warrant replacing the latter.

The fossil suids known up to that time were well revised by Stehlin, 1899–1900. Pearson has ably worked over early European and some other forms, 1927, 1928; Pilgrim, 1926, revised the very abundant Indian fossils, describing many new types; and Colbert, 1935c, revised all these. For the general arrangement and the Indian fossils I have followed Colbert as the most recent worker, synthesizing all the previous work with extensive new personal observations. His various groups of genera are here formalized as subfamilies, except that the distinctive and highly uncertain †*Lophochoerus* is left as *incertae sedis*, along with two other genera (not treated by Colbert) equally peculiar and of equally unsettled affinities.

Students of recent pigs often tend to sepa-

rate the wart hogs in their own subfamily, or even family, and it has been suggested that they may have been distinct since the Eocene. Even among recent forms, however, it can be seen that *Phacochoerus* is an obvious and not a great modification of *Sus*, and the fossils (see Colbert) suggest that this modification arose in and since the Pliocene, certainly not Eocene. Reviewing all the suids restores a sense of proportion by which *Phacochoerus* (and many closely allied supposed genera) can hardly be placed except as a genus of Suinae. If *Phacochoerus* were given subfamily, *a fortiori* family, rank, really divergent genera like †*Listriodon* could hardly be referred to the same suborder.

Many students have considered the peccaries to be exclusively New World suoids, but Pearson has shown that †*Doliochoerus* surely and "†*Choerotherium*" (†*Taucanamo*) probably are closer to the peccaries than to the pigs despite their Old World occurrence. Colbert adds the poorly known but also probably tayassuid †*Pecarichoerus*. Inadequately known for sure decision, it yet is probable, as Colbert thought, that these are fragments of an Old World line arising from an Eocene suid-tayassuid fission, so I tentatively segregate them in a subfamily.

The evolution of the tayassuids in North America is fairly well known and presents few taxonomic problems as far as genera are concerned. †*Perchoerus* has frequently been considered a true suid, implying a later and strictly American origin of the Tayassuidae, but Pearson's excellent study quite controverts this. The only other unusual feature in this arrangement is the revival of †*Hesperhys*, which is probably the valid name of the genus now always called "†*Desmathyus*" but which has been overlooked by students of the group (even by Peterson who was working on the collection in which Douglass' hypodigm of †*Hesperhys* is preserved). †*Desmathyus* is probably a good subgenus.

ANCODONTA

The nucleus of this group is formed by the †anthracotheres, with which the †anoplotheres are surely related (although, as usual, this has been disputed). The evidence summed up and supplemented by Colbert shows that the hippopotami are probably also closely related to †anthracotheres and might, indeed, be called specialized surviving †anthracotheres. As to the †cainotheres, opinions vary from Matthew, who shows them as †anthracotheres on his phylogenetic chart (but as a separate, related family in his classification), to Stehlin, who separates them subordinally from all other artiodactyls. Both these views are too extreme, and the present arrangement seems a valid compromise, admitting that the ancodont affinities of the †cainotheres are not proved but, on present evidence, as probable as any others.

The early †anthracotheres are so closely similar to †choeropotamids like †*Gobiohyus* and †*Helohyus* that it really seems at first sight ridiculous to place them in different infraorders, and indeed some students (e.g., Schlosser) have placed these more primitive genera in the †Anthracotheriidae. Such situations necessarily arise when the origins of large groups are uncovered. That the ancodonts are considered a large group, infraorder in this system, is amply justified by their later history. The †choeropotamids are near the ancestry but are already too late to be the direct ancestry, and they seem better classified with the group from which the ancodonts (and other artiodactyls) arose than with the latter.

The †anthracotheres proper are manifestly polyphyletic, and two subfamily groups are commonly recognized, one typified by †*Anthracotherium* and the other by †*Bothriodon*. This division is clearly valid as regards the type genera and their closer allies. The situation appears, however, to be more complicated, and subdivision based only on a few dental resemblances to one or the other of these genera would not be clear cut and probably not natural as applied to all †anthracothere genera. Pending a more complete review of the family as a whole, I have, therefore, omitted subfamilies.

Various earlier Tertiary genera have been referred, or considered as ancestral to the Hippopotamidae, but in all cases the gap is great and the relationship too improbable to warrant family reference. If, as I believe, Colbert is right in deriving the hippopotami from late Tertiary †anthracotheres, these references are wrong. The family is, therefore, left with only three genera. Even these

are sometimes considered subgenera of one genus, but †*Hexaprotodon* and *Choeropsis* do seem to warrant generic separation from *Hippopotamus*.

†Cainothere anatomy has recently been studied in painstaking and brilliant detail by Hürzeler, and I accept the six genera listed by him as valid although, as he remarks, †*Procaenotherium* hardly merits more than subgeneric distinction from †*Cainotherium*.

†OREODONTA

†Oreodonts are not known before the late Eocene, when they were already not only distinctly differentiated from all other artiodactyls but also separated into their two families, although, of course, the early genera are primitive and less distinctive than subsequent representatives. This lack of actual annectant types has prevented certain determination of subordinal affinities. The †oreodonts have been placed in each of the three suborders here recognized, and have also been placed as a major group not formally united with any other within the Artiodactyla. Reference to the Ruminantia or Pecora has been rather generally abandoned because it depended on little more than possession of selenodont teeth, and this may, and probably does, represent only convergence from a "bunoselenodont" type like that of some †anthracotheres. The less specialized †oreodonts show considerable resemblance to †anthracotheres throughout the dentition and skeleton, and this is usually accepted as indicative of affinity. For instance, Matthew, 1929a, placed the †oreodonts in the †Ancodonta, although with some hesitation. Rütimeyer, however, long since advocated reference of the †oreodonts to the Tylopoda, and Scott, a leading student of †oreodont anatomy, supported this view in 1899. It was subsequently abandoned by all students, including Scott, but he has now (1940) reasserted it. The evidence has not been very fully presented on either side, and neither opinion can be supported with complete confidence. I tentatively continue to follow the consensus, while recognizing that Scott may well prove to be right.

Union with the Ancodonta would, however, imply a degree of certainty that is not justified by the facts, and regardless of their further affinities the †oreodonts seem to merit infraordinal rank. There is no valid generic name †*Oreodon*, but this familiar term can well be continued in use by calling the infraorder †Oreodonta.

The clawed †agriochoerids are so peculiar that their dissociated parts were originally referred to three different orders: the teeth to the Artiodactyla, the fore limb to the Carnivora, and the hind limb to the "†Ancylopoda" (=†Chalicotherioidea, in the Perissodactyla as now classified). It was not until 1894 that associated material showed that these supposedly very diverse mammals were all of a single genus †*Agriochoerus*. Earlier (late Eocene) genera have since been discovered, and these fully confirm the artiodactyl nature of the †agriochoerids and their close relationship to the †merycoidodonts, the typical †oreodonts. †*Diplobunops* was at first believed to be an †anoplothere (which, incidentally, is another example of the ancodont-like structure of these forms), but its author, Peterson, later recognized its †agriochoerid affinities. The family otherwise presents no special difficulties, and it has few known representatives.

The †Merycoidodontidae, exclusively North American but among the most abundant groups of fossils, have been fully reviewed by Thorpe, 1937, and some important subsequent work has also been done, especially by Scott, 1940, and by Schultz and Falkenbach, 1940, 1941 (and other work in progress). Although much is known of the phylogeny of the group and although more than 20 genera are recognizable, it has not been customary to subdivide the family beyond occasionally setting off †*Protoreodon* because of its primitive nature. Recently Schultz and Falkenbach, 1940, proposed division into †Merycochoerinae, †Ticholeptinae, †Promerycochoerinae, †Eporeodontinae, and †Leptaucheniinae. They have defined and discussed only the first two of these, but the proposal apparently resembles rather closely a subfamily arrangement independently reached in this manuscript before their work appeared. I continue to follow Scott in having a subfamily †Protoreodontinae for the primitive forms not assignable to any specializing sequence. †*Promerycochoerus* seems to be close to †*Merycochoerus*, and I continue to

place them in one subfamily, at least pending the appearance of Schultz and Falkenbach's discussion of the former genus. As elsewhere emphasized, I do not consider it practical to use subfamilies only for absolutely unified phyla. Since Schultz and Falkenbach do not list a subfamily †Merycoidodontinae, which must logically be used in subfamily division of the †Merycoidodontidae, and since †*Eporeodon* is certainly close to †*Merycoidodon*, I continue to use †Merycoidodontinae and to refer †*Eporeodon* to it. I add the †Merychyinae because this line seems to be about as distinctive as the others called subfamilies.

The †Merycoidodontinae represent a sort of central sequence or cluster, rather diverse but including no highly divergent or distinctive lines. Most of the more specialized groups probably arose in or near this central stock, and it becomes a matter of opinion just where divisions should be made. There is, however, little doubt that the genera †*Ustatochoerus*, †*Brachycrus*, †*Merychyus*, and †*Cyclopidius* are terminal forms of an equal number of distinctive lines radiating and becoming specialized approximately contemporaneously.

References

Only a few of the more important works on basic subdivision of the Artiodactyla and on Suiformes can be cited here. On both subjects general works like Osborn, 1910, Scott, 1937a, or Weber, 1928, are to be consulted, and some more special papers like Matthew, 1929a, 1934, Stehlin 1906–1910, Pearson, 1927, Colbert, 1935b, c, Scott, 1940, Pilgrim, 1941a, b. In addition to these, on †Palaeodonta, see Sinclair, 1914; Peterson, 1909, 1919; Colbert, 1938a. On Suina, see also Stehlin, 1899; Pearson, 1923, 1928; Stock, 1937. On Ancodonta see also Stehlin, 1910a; Depéret, 1908; Forster Cooper, 1924; Schmidt, 1913; Hürzeler, 1936; Colbert, 1938b; Pilgrim, 1940. On †Oreodonta, see especially Loomis, 1924; Thorpe, 1937; Scott, 1940; Schultz and Falkenbach, 1940, 1941. The recent Suiformes are so few that there is little to say on their classification above the specific level, and they are merely an appendage on the arrangement of the fossils, so that no special references to the literature on them are needed.

TYLOPODA

The camels are another group in which the survivors are uninterestingly few, two genera with (at most) six species, and they present no superspecific taxonomic problems beyond those involved in the treatment of the abundant and highly varied fossils.

The group is very distinctive and was already vaguely recognizable in the middle Eocene and well distinguished in the late Eocene. It is often included in the Ruminantia, but this is probably not a natural arrangement. The Ruminantia as a whole seem clearly to have arisen from prototypal Tragulina, which gives that suborder its unity. The Tylopoda evidently arose near, but not from, the Tragulina and are as old as the latter. Early Tragulina, notably the more primitive †Hypertragulidae, are certainly very similar to Tylopoda of equal age, but this suggests that they are near their common origin and, indeed, the origin of all specialized Artiodactyla, rather than that either group was derived from the other. Scott, particularly impressed by this real resemblance, has recently (1940) suggested that the †Hypertragulidae be classed as Tylopoda, but I agree with the previous consensus and present likewise authoritative dissenting opinion (e.g., Colbert, 1941a) that the †Hypertragulidae were differentiated from the most primitive Tragulina after their separation from Tylopoda.

The †xiphodonts are so near the base of artiodactyl differentiation that their placing is somewhat arbitrary. There is, however, some evidence that they are closest to the camelid ancestry and they are usually placed in the Tylopoda. Some of the other very primitive forms, notably †*Amphimeryx* (now placed in the Tragulina) have often been associated with them but are perhaps a little nearer the ancestry of other groups. The best discussion of the †xiphodonts is in Stehlin, 1906–1910.

There is no good revision of the Camelidae. The available studies either are so old that they could be correlated with present knowledge only by long special study or treat of only one or a few genera that happen to occur in some given fauna. The present view of the group is thus built up from several dozen

short papers and notes, and no good references can be supplied for the student who wishes to investigate the camels. He should begin with some general work, of which Scott, 1937a, is probably the best for this purpose, and then can find most of the many special studies through Hay's and other bibliographies.

Matthew worked long on the camels and revised those known up to about 20 years ago or somewhat later, but this work was never reduced to definitive form or published. Its broadest results appear in several of his more general works and are a principal basis for the present classification. In post-Oligocene times he recognized a central line, with several short spurs but progressing fairly steadily to the typical Pleistocene and Recent forms, and three more divergent lines typified respectively by †*Pseudolabis*, †*Alticamelus*, and †*Stenomylus*. This four-fold division is here expressed by four subfamilies. The rather clumsy Camelinae would be improved by tribal subdivision, but until competent and detailed revision of the whole group it would be futile to attempt this. The need for such revision is made especially noticeable by the recently discovered giant forms of the latest Tertiary and Pleistocene, the affinities and proper generic arrangement of which are quite unsettled. The proper positions of †*Paratylopus* and †*Miolabis* are also uncertain, since they may not be true †alticamelines.

The Oligocene and Eocene camelids doubtless include the ancestry of some or all of the later lines, but they are themselves a varied lot, and their subsequent phyletic affinities are very uncertain. They are all united by many primitive characters and may, therefore, be retained in a primitive subfamily at least until their phyletic positions are better understood. †*Protomeryx* (and the recently discovered †*Dyseotylopus*, which should perhaps be considered a subgenus of †*Protomeryx*) is usually also classed as a †poebrotheriine, and since the division is horizontal, one place is about as "natural" as another for drawing the line. †*Protomeryx* is, however, distinctly advanced over †*Poebrotherium* and is the first genus that can be said to lead clearly into the later Tertiary central or cameline line, and I, therefore, place it with the latter.

RUMINANTIA

In the Eocene, the perissodactyls were the dominant herbivores, but by the end of that epoch the artiodactyls had caught up with them and, although perissodactyls continued to be fairly abundant and varied until about the Pliocene, the artiodactyls have been dominant since the Oligocene. Since the later Tertiary the perissodactyls have waned to a few relicts, but artiodactyls are now about as abundant as ever. There has, however, been a marked shift of faunal dominance within the Artiodactyla. In the Eocene and Oligocene, groups here classified as Suiformes were dominant. Since then the Ruminantia have gained steadily, and they are now incomparably the most widespread, most highly differentiated, and individually most numerous of ungulates.

There is no doubt as to the unity of the ruminants here classed as Pecora. Some authors also place the Tylopoda in the Ruminantia, a point that has already been discussed. The Tragulina are sometimes excluded from the Ruminantia, but all recent work on the fossil Tragulina seems to support the view that they lie at the base of the Ruminantia and gave rise to the Pecora, as well as to the relatively conservative lines classed as later Tragulina. This agrees with the present consensus and is supported by the recent fundamental studies of Colbert (e.g., 1941a), whose arrangement of the Ruminantia as a whole is followed here with only slight and unimportant exceptions.

TRAGULINA

This group was originally proposed for the living tragulids, generally recognized as the most primitive surviving ruminants. Despite this status, they are, of course, well removed from the actual ruminant ancestry and somewhat specialized on a low level of ruminant organization. They cannot be traced back very far (late Miocene) and seem, indeed, to be a relatively recent group in their present form, but there is a striking variety of genera in the late Eocene and early Oligocene of the Old World, united as †Gelocidae, that are

similar to *Tragulus* in basic structure. The resemblance is mostly in primitive characters and so does not imply direct phyletic connection, but in a broad view the †gelocids seem to represent the ancestry of the Pecora, on one hand, and of the tragulids, on the other. It is thus justifiable to call them Tragulina, placing them with their least modified descendants and postulating that, in this sense, the Pecora arose from Tragulina. The †Gelocidae are a rather heterogeneous group, and it may eventually be possible to pick out lines close to certain later ruminants, but at present this is not possible and they are classified horizontally. The lack of known annectant types must be imputed to the curious scarcity of ruminants in the available later Oligocene and earlier Miocene collections.

Beside these forms, which are considered traguloid by most students, stand the †Hypertragulidae, the position of which is more disputed. The later †hypertragulids, culminating in the weird †*Synthetoceras*, are so unlike any other mammals that they suggest no close affinities. But these can be traced back without any great break into animals so primitive among the Artiodactyla that they have confusing resemblances to the ancestry of such diverse groups as, for instance, †oreodonts, camels, and deer. I have accepted as a working theory the view of Matthew, 1929a, and others, recently strongly reaffirmed by Colbert, 1941a, that †hypertragulids and tragulids arose (in the Eocene) from the same immediately ancestral group. That this ancestry is represented by the poorly known †Amphimerycidae is a less well-supported conclusion, but here, too, I follow Colbert, with greater misgivings. The slightly more definitely †hypertragulid genus †*Archaeomeryx*, in which almost the whole skeleton is known (Colbert, 1941a) is one of the most interesting of fossils because it is clearly very close to the ancestral structure of all the great and dominant group of Ruminantia.

The other †hypertragulids do not differ radically, but the genera are so distinctive that those that are well known have been assigned to separate subfamilies. This seems to me somewhat to exaggerate their divergence, and I have tentatively called the more important apparent lines tribes.

The relationship between the †Protoceratidae and †Hypertragulidae has been denied, and Schlosser, for instance, placed the latter between the tragulids and cervids and put the former in the Giraffidae. The giraffid resemblance seems to be the result of (†hypertragulid) common ancestry and convergence or parallelism, and the †protoceratids almost certainly arose directly from, and are best classified near, the †hypertragulids, as all recent authorities seem to agree. Matthew and some others have made them only a subfamily of †Hypertragulidae. Three subfamilies within the †Protoceratidae have been proposed, but this has little practical value because there are only four genera (in this classification; five are sometimes recognized, and an extreme splitter might find basis for six), and it is not particularly required or justified by the apparent phylogeny, which seems to represent very nearly a unit phylum in the known genera so that the subfamilies are defined almost entirely according to whether the included genus is more or less advanced and not by branching or difference of descent.

There has been no general review and little recent work on the important group †Gelocidae, but see, for instance, Kovalevskii, 1876; Schlosser, 1902; Matthew and Granger, 1925. On †Amphimerycidae, see Stehlin, 1910. On †Hypertragulidae see especially Peterson, 1919; Frick, 1937; Scott, 1940; Colbert, 1941a. On Tragulidae, see Milne Edwards, 1864; Pocock, 1919a; Colbert, 1935c.

PECORA

With Tylopoda and Tragulina excluded, there is singular unanimity of opinion that the groups here called pecoran do belong together and that they fall naturally into three groups typified by deer, giraffes, and cattle, the superfamilies of this classification. The abundant fossils do not add any major extinct groups, although the positions of some of the more primitive fossils within the three superfamilies are disputed.

CERVOIDEA

The classification of the deer presents many difficult, and in large part unsolved, problems. Despite the great abundance of fossil forms, little light is cast by them on the interrelationships of the living forms. The

latter alone are indeed fairly easy to arrange. The exact terminology and ranking of the usual arrangements differ, but those by authors who know only the recent genera are usually more or less compatible.

That cervoids arose from early traguloids is virtually certain, and it is hard to draw a line between the early members of the two groups. On the whole †*Blastomeryx* and †*Palaeomeryx* are, with their allies, including †*Eumeryx*, definitely cervoid despite their primitive characters. In these primitive characters, at least, these genera are much alike, and this warrants reference to one subfamily. All the later cervoids can be traced back structurally into this group, †*Eumeryx*, especially, being an almost ideal ancestor for the diverse later forms. The living musk deer nearly represent this structural stage and deserve subfamily separation from all other cervids.

In America there developed numerous and diverse but clearly related genera that represent a very peculiar group of deer with long bosses but no deciduous antlers, well off the main line of cervid development. These strange animals fall into a natural unit for which the name †Dromomerycinae is available. Until recently they were very poorly known, and they had a checkered taxonomic career. Some were referred to the Antilocapridae and some scattered in other ruminant groups, but now Frick, 1937, has revised them on the basis of enormous new collections and has demonstrated their pertinence to one group and their cervid affinities in a way convincing to me. Still more recently, however, Pilgrim, 1941b, has argued that these genera are nearer the Giraffidae than the Cervidae. This disagreement is not so fundamental as it may seem. There is little doubt that the deer and giraffes had a common ancestry. It is usual to assign that ancestry, or forms generally near it, to the Cervidae and to speak of the Giraffidae as an offshoot of the Cervidae. Pilgrim's arrangement suggests that the common ancestry should perhaps be considered giraffid, with cervids arising from giraffids. The difference is as much one of nomenclature as of interpretation of the facts. In either view, the †Dromomerycinae are an extinct, aberrant offshoot of the common ancestry of deer and giraffes.

This arrangement of the †Dromomerycinae and of other cervids included in his monograph is essentially that of Frick, 1937, with some unimportant changes in nomenclature.[1]

While this group was dominant in North America, the cervids of the Old World were, for the most part, long-pedicled, truly antlered types centering around †*Dicrocerus*. This stage of evolution survives in *Muntiacus*. It is not certain that the relationship is a phyletic one, but it is at worst a convenient morphological grouping to place all these animals in a subfamily Muntiacinae. The peculiar †*Procervulus* and †*Lagomeryx* are usually placed here, but their antlers were not deciduous and they probably are near the giraffids, so that I tentatively remove them to the Giraffoidea.

Deer of truly modern type, with short-pedicled deciduous antlers and various other distinguishing characters, appear in the Lower Pliocene. They fall into two fairly well-established divisions tentatively recognized as subfamilies. The Cervinae are typical of the Old World, only *Cervus* occurring in North America as an obviously recent Asiatic migrant. The other group, sometimes called Capreolinae for historic reasons but here called Odocoileinae because *Odocoileus* is a

[1] It looks so completely unlike Frick's arrangement that this statement requires amplification. Frick's groupings are here accepted without essential change, and only the ranking and terminology of some supergeneric divisions are modified. Frick's taxonomic system is not, and was not intended to be, comparable with that of anyone else. It is convenient and valid in itself, but of course its original nature makes it impossible to fit bodily into a general classification like this. Frick's subfamilies have no equivalent in the work of anyone else but are, on the average, of about generic rank. For instance, he places 15 genera of American Cervidae in 13 subfamilies, and he apparently bases one or more subfamilies on subgenera, without any included genus. Between his subfamilies and his families (which are approximately those of other authors) he has a rank simply called a "group," for which he gives names ending in "-ini," like the names used by most authors for units called tribes and placed below subfamilies in rank. On the scale of the present classification, Frick's groups with names in "-ini" are sometimes of tribal and sometimes of subfamily rank. Frick's genera and subgenera correspond well with those of other authors and are accepted here. His free use of subgenera seems to be particularly useful and is commended as a model to other taxonomists, who too often tend to give every valid group of species generic rank and skip the useful subgeneric grade in taxonomy.

better type than *Capreolus*, is basically circumpolar but has peopled the Americas and has had a particularly striking secondary radiation in South America, where no other deer were present when it entered. Matthew and others have maintained that this group, as a whole or in its most typical form, was of New World origin, and this may prove to be correct, but in recent years it has seemed more and more probable that it represents an Old World cervine offshoot that sent some members into the New World at a relatively recent time, probably well along in the Pliocene.

It has been suggested that some of the South American fossil genera are not correctly associated with *Odocoileus*, Kraglievich placing †*Antifer* near *Alce* and †*Morenelaphus* in the Cervinae. It seems, however, better to leave them in the group with which they have such strong geographic association. Little is known about them except from broken antlers, and these offer no impelling evidence in either direction, although they do validate the genera.

It is possible that the classification given here is slightly unbalanced in ranking living groups a little too high in comparison with fossil groups, but the discrepancy cannot be great and is almost inevitable in view of the vastly better knowledge of the living forms and their affinities and in view of the still greater discrepancy in the work of students of the living genera only.

Progressive classifications of recent cervids are given by Brooke, 1878, Lydekker, 1898, and Pocock, 1923a. Among the more important papers on cervid evolution, fossil cervids, etc., are Colbert, 1936; Frick, 1937; Kraglievich, 1932c; Matthew, 1908; Schlosser, 1924; Stehlin, 1928, 1937; Teilhard de Chardin, 1939; Teilhard de Chardin and Trassaert, 1937; Zdansky, 1925b; Cabrera, 1941.

GIRAFFOIDEA

Aside from the *petitio pricipii* of considering the giraffes as remotely independent and hanging in taxonomic space, they have been considered as close either to the Bovidae or to the Cervidae and are unquestionably related in some way to both. Matthew believed them to be a relatively recent (by implication, Miocene) offshoot of the Cervidae through primitive cervids like †*Eumeryx* and †*Palaeomeryx*. This view is accepted by Colbert and is now well supported. Some of the fossil †dromomerycines, recently described by Frick, support this view in an indirect way by showing †palaeomerycine derivatives in North America following evolutionary side paths that are analogous in some respects to those taken simultaneously by the giraffids in the Old World. I now consider, however, that the reference of the †Palaeomerycidae to the Giraffoidea in my previous classification (1931a) was a mistake in judgment and express a similar concept in what is probably a better way.

The closeness of this relationship inevitably makes uncertain the proper position of various branches from near the dichotomy between Cervidae and Giraffidae. †*Lagomeryx* and its closer allies are such a branch, and I hesitantly adopt Pilgrim's conclusion that they are a little nearer the Giraffidae. They are at the same time quite close to †*Palaeomeryx* and †*Dromomeryx*. †*Heterocemas*, which now appears to be synonymous with or a subgenus of †*Lagomeryx*, was at first considered a possible antilocaprid, but the discovery of more complete materials has negatived this.

The relationships of such peculiar forms as †*Sivatherium* were once disputed, but it has long been established that the giraffids, strictly speaking, are a distinctive and fairly compact family unit. The arrangement here adopted is that of Colbert, 1935b, which in turn draws on the researches of Pilgrim, Matthew, and others (see Colbert's citations) and especially of Bohlin, 1927. For the †Lagomerycidae and a recent discussion of cervoid-giraffid affinities (with which I agree rather closely in principle but not in formal expression), see Pilgrim, 1941a, b.

BOVOIDEA

This enormous group, the members of which now far outnumber all other artiodactyls or, indeed, all other hoofed mammals, appears to be of fairly recent origin and, unlike any other ungulate group, now to be at its apogee. †*Archaeomeryx* of the Upper Eocene, †hypertraguloid by definition, could well be structurally ancestral to the bovoids, and the actual ancestor at that time was undoubtedly

very like that genus. There is, however, nothing known from the Oligocene that can be considered as showing what the bovoid ancestry was then like, *a fortiori* as actually representing that ancestry. True bovoids appear doubtfully at, and definitely above, the base of the Miocene both in the Old World and in the New. This great gap in the record leaves the origin of the group obscure, and its primary internal differentiation is ascertainable only by inference from animals that lived well after this had occurred.

Even when they first appear, the bovoids are clearly divided into two groups, the relatively small, American family Antilocapridae and the enormous, primarily Old World family Bovidae. Despite their almost unparalleled variety, including over 100 known genera, the bovids are all clearly, and even rather closely, related to one another, and it is customary, and in a balanced system is clearly proper, to place them all in one family.

The gap in knowledge of the bovoid ancestry, the greatest gap anywhere in present knowledge of artiodactyl history, prevents a clear view of the divergence of the early antilocaprids from the early bovids, and the present data are rather anomalous. Structurally the antilocaprids certainly resemble the Bovidae more than any other artiodactyls and it is difficult to imagine any other history than that a common bovoid ancestry did split into these two families. But as far as known now the antilocaprids have always been exclusively North American and the bovids were long exclusively Old World and did not reach North America until the end of the Tertiary. Then where did the common ancestry live and how did this radical geographic separation arise? There is no evidence on this problem, and the absence of such evidence is surprising.

Two other possibilities of events within the great gap must be kept in mind. The antilocaprids may, after all, be an offshoot from early American cervoids, distinct from the Old World bovoids. In that case the closeness of resemblance to the bovoids is deceptive parallelism, and the Bovoidea, as here defined, are an unnatural group. Or antilocaprids may have arisen in the Old World, in which case the Bovoidea may or may not be a natural group but must have had a history unlike that appearing on the face of the facts as now envisioned.

ANTILOCAPRIDAE

The antilocaprids are represented by only one living species, but the fossil forms are abundant and varied, showing that the survivor is the relict of a group analogous, on a smaller scale, to the antelopes of Africa. The fossils fall visibly into two divisions definable as subfamilies, one including the ancestry of *Antilocapra* and a few related branches, and the other including older forms more radically different from the true antilocaprines and only very doubtfully or in the most general way ancestral to the latter.

These earlier forms, the †merycodontines, were long of disputed affinities. According to one view, most fully set forth by Hilzheimer, 1922, although strongly supported by numerous earlier students, among them Winge, these animals were not bovoids at all but simply "hypsodont deer." According to the other view, strongly supported at various times by Matthew and finally conclusively established by him (1924), they are antilocaprids. As far as I know this conclusion is now supported by every competent student and it is adopted here. Some of the extinct antilocaprines, especially †*Ilingoceros*, were once also believed to belong to other groups, in this case to the Bovidae, but this was the fault of inadequate knowledge and now that they are better known there is no doubt as to their antilocaprine affinities.

Possible antilocaprids have been described from South America, Europe, and Asia, but so far the evidence is so imperfect that it does not merit much consideration. It would not be surprising if such active and formerly abundant animals had spread to other continents, but there is now no real reason to believe that they did so.

The present arrangement within the family generally follows Frick's elaborate and excellent monograph, 1937, translating his taxonomy as explained for the Cervidae. In this case his groups with names in "-ini" scale in best as subfamilies. In two cases I use different generic names from those adopted by Frick. He has shown that the synonymy of †*Merycodus* and †*Cosoryx* is uncertain. It is, however, probable and it has been almost

universally accepted. The name †*Merycodus* has been used for the genus for some 40 years, and the change to †*Cosoryx* now is neither necessary nor convenient. Stirton, 1938, has shown that †*Sphenophalos* is synonymous with †*Plioceros*, which it long antedates, and not, as Frick tentatively suggested, with †*Ilingoceros*. It should also be noted (for the Cervidae as well as for the Antilocapridae) that the geologic distribution of the forms described by Frick is uncertain, because he does not give the horizons of any of his discoveries except in a very general way and according to a system of subdivisions of the Tertiary different from that of anyone else and of doubtful equivalence to the usual system here employed.

Some important papers on antilocaprid history and classification: Colbert and Chaffee, 1939; Frick, 1937; Matthew, 1924; Stirton, 1938.

BOVIDAE

With the possible exception of some rodents, this is the most difficult of all mammalian families from a taxonomic point of view. In the popular mind and in many of the earlier technical classifications, it includes three groups of animals, oxen, sheep and goats, and "antelopes"—this last term being made to include all bovids not obviously belonging to one of the other two groups. It soon became apparent, however, that the "antelopes" included various groups that have little more in common than do sheep and oxen. Gray, 1872a, went to the opposite extreme of splitting the Bovidae into 16 families (15 without the Antilocapridae[1]). Even this excessive splitting did not prevent him from placing such dissimilar forms as, for instance, *Naemorhedus* and *Hippotragus* in the same division. Later authors almost universally agree in placing all these forms in one family, Bovidae, but there the agreement stops. The groups have been carefully sorted out since Gray's day, but in most cases the kind of arrangement remains the same, using subfamilies where Gray used families. Thus Flower and Lydekker listed nine supposedly coördinate subfamilies, Sclater and Thomas seven for the "antelopes" alone (presumably with three or four more for the more bovine and caprine groups), and Pocock, 1910 to 1919a, raised this to 16 (including all bovids but excluding antilocaprids).

Such an arrangement is very unsatisfactory. It makes a general view of the family impossible, and it expresses no interrelationships within the family, for the evidence does not really suggest that 10 or 15 groups of bovids are coördinate without any special relationship between any two or more of them. It also reduces the basic scope and rank of a subfamily below those of most recognized subfamilies and in a way not fully warranted by the facts or dictated by necessity and convenience.

An important effort to overcome these shortcomings was made by Schlosser, 1904, 1923, who reduced the 12 "subfamilies" seen as valid to about the rank of tribes[2] and divided the Bovidae into two great subfamilies, "Aegodontia" and "Boödontia," largely on dental but also on other characters. The two groups so differentiated are unquestionably natural as to their nuclear types, but the dichotomy represents over-simplification and almost certainly causes some unnatural collocations of lesser divisions. Perhaps on this account it was not widely accepted, and its important basic contribution has not always been appreciated.

Schwarz, 1937, has made a more recent attempt of the same sort, embodying the very extensive new fossil discoveries of the last few years, described by Bohlin, Teilhard de Chardin, Pilgrim, and others. He recognizes nine subfamilies (apart from the "Antilocaprinae") which he arranges in three "sections."[3] The peculiar duikers, Cephalophinae, form one section; the kudu and eland group, Strepsicerotinae, the nilgai group, Boselaphinae, and the oxen, Bovinae, a second; and all others a third. Although differently defined, Schwarz's second and third

[1] The one group now believed really worthy of family distinction from the Bovidae. Many later authors also do refer *Antilocapra* to this family, but the evidence is that its group is really ancient and of true family rank, and it is not further considered in this section.

[2] His formal nomenclature does not follow the accepted conventions, but I believe that I am fairly representing his thought.

[3] An inconvenience of current bovid taxonomy is that no formal rank is assignable to such "sections." They really occupy the place of subfamilies in the system and should be designated as such.

"sections" are essentially Schlosser's "Boödontia" and "Aegodontia," respectively. Schwarz clarified the "boödont" group and probably reduced it to a real and wholly natural division, but he did so at the expense of throwing into the "aegodonts" (not under that name) forms like the oryx group, Hippotraginae, which probably do not belong there, even though Schlosser may have been equally incorrect in uniting them with his "Boödontia."

The most recent original and general classification, that of Pilgrim, 1939, is based on a careful review of the preceding work and also on an intimate acquaintance with a large amount of important new fossil material. It recognizes 11 subfamilies, four placed in a "subfamily section" "Aegodontia," almost exactly Schlosser's group of that name, and three in a "subfamily section" "Tragelaphoidea,"[1] which is exactly Schwarz's "Sektion II." The other four are left floating, with no section assignments.

On review of these and other studies, despite their contradictions, a reasonably consistent and probable, although tentative, view of the broad outlines of bovid relationships does emerge. It is possible to express this in a taxonomic way with more conventional nomenclature and better balance than in the arrangements just cited, without really contradicting their results. In the first place, the "subfamilies" of most recent authors seem to me, as they did to Schlosser (in different terms), as best given less than subfamily, and hence tribal, rank. I tentatively recognize 13 of these, essentially those of the apparently soundest recent work.[2] These may then be grouped into five subfamilies, as follows:

Bovinae
  Strepsicerotini
  Boselaphini
  Bovini
Cephalophinae
  Cephalophini
Hippotraginae
  Reduncini
  Hippotragini
  Alcelaphini
Antilopinae
  Neotragini
  Antilopini
Caprinae
  Saigini
  Rupicaprini
  Ovibovini
  Caprini

Here the Bovinae are Schwarz's "Sektion II," Pilgrim's "Tragelaphoidea," a grouping which Pilgrim, particularly, has established as natural despite the fact that it includes both "oxen" and some "antelopes" of the students of the past century. The Caprinae are Pilgrim's Caprinae plus Ovibovinae and are Schwarz's Caprinae plus *Saiga* and *Pantholops*, which he placed with the gazelles or antilopines and which can almost equally well be placed either there or with the goats and sheep. I subdivide this caprine complex, which Schwarz and Pilgrim did not (at least on this level), perhaps somewhat too strongly, but on what appears to be good evidence. In any case it is highly probable that the Caprinae as here defined are an essentially natural group of about true subfamily rank.

I follow Schwarz, and also in essence Pilgrim, in considering the little duiker group, Cephalophinae, as quite distinct from any other. Its history is completely unknown.

Schwarz, Pilgrim, and indeed almost all students agree that there is some special relationship between the gazelles and the dikdiks, so that my Antilopinae = Neotragini + Antilopini is probably a natural group, but there is disagreement as to its proper limits. Pilgrim, following Schlosser, considered these as divisions coördinate with, and to be grouped beside, the Caprinae. Schwarz inserts them between the "Reduncinae" and "Hippotraginae." It seems to me a convenient and justified arrangement, not really inconsistent with any of these authoritative opinions, to place these "aegodont antelopes" together as a unit in themselves, as I have done.

The Hippotraginae, as I define the sub-

[1] Not acceptable as a name for such a group because it has the form of a superfamily name.

[2] They are those recognized by Schwarz and by Pilgrim except that like Pilgrim (and most previous students) but unlike Schwarz I recognize the gnu group, my Alcelaphini, and the musk ox group, my Ovibovini, and unlike either of them but like many previous workers, I tentatively recognize saigine and rupicaprine groups as distinct both from the gazelles and from the goats.

family, form a tentative group, one not so surely natural as the others here recognized and one not quite like any in previous classifications. Yet each student has provided bits of evidence that tend not only to separate these three tribes from others but also to unite them with one another. Schlosser showed that in the teeth and in some other respects all three have definite, and in part similar, bovine tendencies. Schwarz (relying heavily on Pocock) showed that all three likewise have a series of very gazelle-like characters, to such an extent that he placed the gnus in the Antilopinae (Antilopini of my arrangement). Pilgrim protested against this union and left the three groups separate and without recognized affinities. It is possible that these three groups of what could be called "boödont antelopes" did develop independently, but even if so they are morphologically definable as a single group and there is real, however inconclusive, evidence of their possible common origin.

Some of the tribes of this arrangement are a little unwieldy, with as many as 17 and 18 genera, and a subtribal arrangement would be convenient. Pilgrim has attempted such an arrangement for several of them, notably the Bovini, but the data do not yet suffice to do this well for some of the other tribes that need it more, and I do not make the attempt.

Turning to lesser details, almost every genus has been shuttled about in the classification, and it is impossible to mention more than a few points that have some importance and are still in dispute. It will be noticed that the system is based mainly on recent forms, no tribe being wholly extinct. This probably is somewhat artificial, the fossils being forced into the most nearly similar recent group, but it is also testimony to the relatively recent origin of the groups and the absence of very old fossils. Such few relatively early (Miocene) and primitive forms as are known are inevitably of rather uncertain position, and this is also true of some of the very abundant Lower Pliocene fossils. Without attempting to justify each reference, it can be said that each is based on recent good authority.

Schlosser placed †*Pseudotragus*, †*Tragocerus*, and the many fossil genera associated with each in a "group" (tribe) "†Pseudotraginae," but the †*Tragocerus* group seems, as shown by Pilgrim and others, to be a boselaphine offshoot, while †*Pseudotragus* itself and many similar genera appear to be much closer to the hippotragines, with which they may be united.

It is admittedly difficult to draw a sharp line between the Antilopinae and the Caprinae, and this is emphasized by the fact that the Saigini are usually, and the Rupicaprini frequently, referred to the Antilopinae. On the basis of review and of recent fossil finds, Pilgrim places both in the Caprinae.

Schwarz did not separate the ovibovines at all from the caprines, while Pilgrim separates them sharply (although recognizing a relationship). The present arrangement is not merely a compromise but also seems warranted by the remarkable recent discoveries in this group, which tend to show it as covering a wider geographic and morphological range than previously supposed but also tend to strengthen the evidence of caprine more than antilopine, or particularly bovine, affinities. Placing the takin, *Budorcas*, here, as Teilhard de Chardin does, is tentative but is also consistent with this broader view of the group. †*Criotherium* is commonly referred to the Alcelaphini, even in quite recent work, but Bohlin has rather convincingly argued for its ovibovine affinities.

The evolution of the Caprini is poorly understood, and the few fossil genera placed here are by no means of certain position. Like the rupicaprines, these animals appear to have evolved almost exclusively in mountainous areas, and old mountain faunas are very inadequately preserved—the conditions of erosion making this a great gap in knowledge and one never likely to be well filled.

It is even more difficult for this group than for others to give a reasonably short list of citations which will yet give a student an adequate introduction to the vast literature and support certain recent modifications. The following will at least give some idea of the main points: Bohlin, 1934, 1935a, b, 1937, 1938; Frick, 1937; Gray, 1872a; de Mecquenem, 1924–1925; Pilgrim, 1937, 1939; Pilgrim and Hopwood, 1928; Pilgrim and Schaub, 1939; Pocock, 1918b; Schlosser, 1903, 1904; Schwarz, 1937; Sclater and Thomas, 1894–1900.

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