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THE PRINCIPLES OF CLASSIFICATION AND A CLASSIFICATION OF MAMMALS

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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.

[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.

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.]

†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.

[1] Rhinocerotids are known from the Miocene and Pliocene in Africa, but the Tertiary forms have not been accurately classified.

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.

[1] Of course it is no detraction that oviparous mammals do exist, since these were undiscovered in Ray's day.

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 "non-ruminant 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.

†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: †Baluchitheriinae, †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.

[1] Except the †Alloceropinae, not properly known to him.