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## Ancestry, Paleontology, and Definition of the Name Mammalia

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The various characteristics in which Mammals coincide, and in which they differ from all other animals, are, moreover, of such a kind, that a polyphyletic hypothesis appears in a special degree inadmissible in their case. It is inconceivable that all existing and extinct Mammals have sprung from several different and originally separate root-forms. We are compelled, if we in any way acknowledge the Theory of Evolution, to assume the monophyletic hypothesis, that all Mammals, including Man, must be traced from a single common mammalian parent-form. (Haeckel, 1897, vol. 2:141-142)

As illustrated by the epigraph, the name Mammalia has long been acknowledged as applying to an entity that owes its existence to the biological process of common descent. That realization should have shifted the meaning of the name Mammalia from a Linnaean class founded on characters and contents to a Hennigian unit of descent more in keeping with the goals of the Darwinian Revolution (de Queiroz, 1988). However, the importance still attached to mammalian "defining" character(s), and an apparent inability to separate the name Mammalia from the clade it represents, betrays the typological elements that still persist in current taxonomy. A misplaced emphasis on what a name means in the Linnaean tradition, instead of what it implies about ancestry, has led some paleontologists, either explicitly (e.g., Lucas, 1990, 1992; Lucas and Hunt, 1990; Miao, 1991) or implicitly (e.g., Clemens, 1986; Hopson, 1987, 1991; Benton, 1990; Lillegraven and Krusat, 1991), to reject a definition of the name Mammalia that is explicitly phylogenetic, i.e., the meaning of that name is expressed in terms of the last common ancestor of all extant mammals (Rowe, 1987, 1988; Gauthier et al., 1988a, 1988b, 1989; a node-based definition of a

crown clade sensu de Queiroz and Gauthier, 1990, 1992). Neontologists might wonder that the name Mammalia is controversial at all, given that no one in several centuries has mistakenly assigned a Recent mammal to some other taxon. Nevertheless, paleontologists continue to struggle with the meaning of the name Mammalia, as is evident from the radically different entities to which that name has been applied, even in the most recent literature (Fig. 1).

The meaning of the name Mammalia (Rowe, 1987, 1988), like any other taxon name, is of general interest because secondary properties, such as its inclusiveness, its diagnostic characters, and its distribution in time and space, stem from its primary attribute, namely, its ancestry (Hennig, 1966; Rowe, 1987, 1988; de Queiroz, 1988). Phylogenetic taxonomy, that branch of phylogenetic systematics responsible for communicating the results of phylogenetic analysis, acknowledges the fundamental role of ancestry by incorporating explicit statements about ancestry into the definitions of taxon names (de Queiroz and Gauthier, 1990, 1992). The issue of name definition is central to a general and unified phylogenetic system of taxonomy whose principles and conventions are derived from, or are at least consistent with, the theory of descent (de Queiroz and Gauthier, 1990, 1992). A precise and consistent taxonomy is essential for comparative biologists interested in developing objective, testable methods for investigating the histories of different lineages (e.g., Marshall, 1990; Norell, 1992; Norell and Novacek, 1992). The several

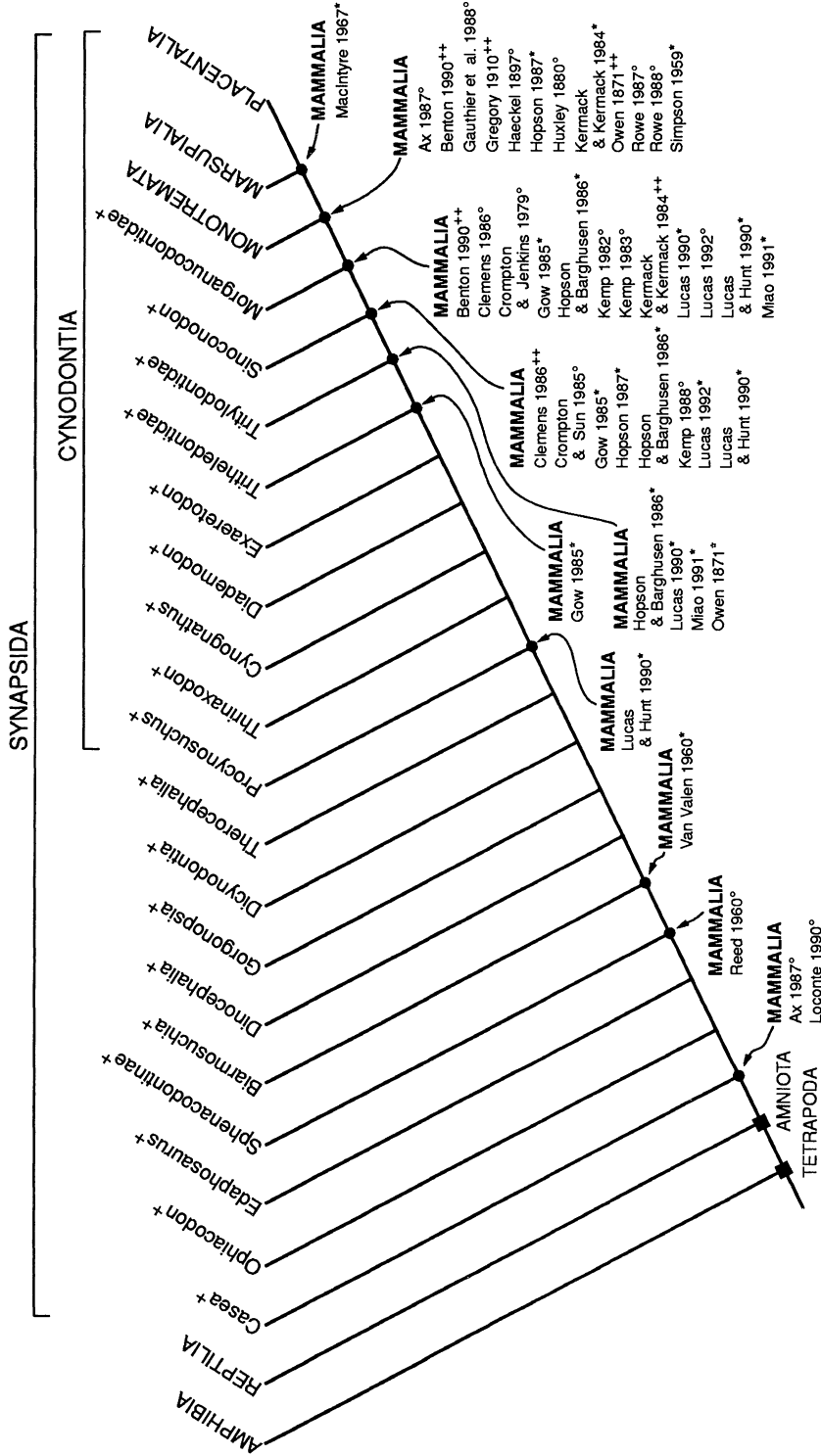


FIGURE 1. Usages of the name Mammalia plotted on a phylogeny of extant and extinct synapsid amniotes (from Gauthier et al., 1988b; Rowe, 1988, in press). ° = name definitions based on ancestry. \* = name defined on characters, shown at the nodes where those characters obtain. \*\* = name defined on some other criterion (usually content) or on unspecified criteria. + = extinct taxa.

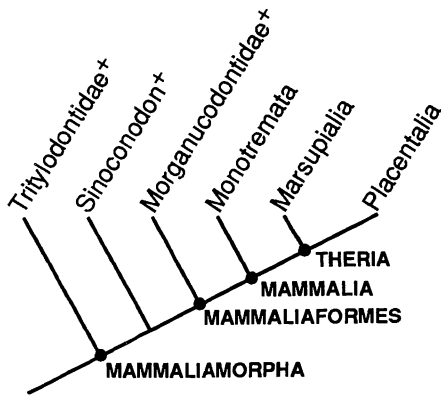


FIGURE 2. A phylogenetic taxonomy of mammalia-morph synspsids (Rowe, 1988, in press; see also Kemp, 1982, 1983, 1988; Crompton and Sun, 1985; Gauthier et al., 1988b, 1989; Lillegraven and Krusat, 1991; Miao, 1991; Wible, 1991; Crompton and Luo, in press).

meanings accorded the name Mammalia in current paleontology thwart such efforts by ignoring the primary goal of phylogenetic taxonomy, which is to precisely and consistently convey information about ancestry (rather than about characters and contents per se, which are likely to change with increasing knowledge; Rowe, 1988; de Queiroz and Gauthier, 1990, 1992).

Objections to a node-based definition that restricts the name Mammalia to the clade stemming from the common ancestor of extant mammals vary in detail, but all have one of the following three elements in common. They assert that such a definition would disrupt the "traditional" meaning accorded the name by paleontologists (presumably in terms of its contents and characters). They object to a definition that fails to acknowledge the importance of "key" characters in the origin and subsequent success of mammals. Perhaps because they are paleontologists, these characters, be they "key," "traditional," or otherwise, are almost invariably among those few that might be preserved in the fossil record. Finally, they accord fossils a special role in delimiting the lower boundaries of taxa. Some of these objections parallel the earliest arguments that arose when the goals of phylogenetic systematics first came into conflict with Linnaean traditions; the rejection of paraphyletic and polyphyletic

taxa evoked equally sharp protests from many paleontologists (e.g., Simpson, 1971; Charig, 1976; Miao, 1991).

Few would deny that if ideas about relationships should change, then a taxonomy should be altered accordingly. But even in the present climate of broad agreement on the most pertinent features of synspsid phylogeny (Fig. 2), there remains a considerable range of more or less inclusive entities to which the name Mammalia is currently applied by paleontologists (Fig. 1). There is consequent disparity in the secondary historical properties represented by the name. For example, some usages place the minimum age of Mammalia in the Early Cretaceous (MacIntyre, 1967; Benton, 1990) or the Upper Jurassic (Gauthier et al. 1988b; Rowe, 1988, in press), whereas other suggestions would extend its minimum age to various times during the Triassic (Hopson, 1987, 1991; Lucas and Hunt, 1990; Lillegraven and Krusat, 1991; Miao, 1991). Still other definitions would extend the oldest record of Mammalia back into the Permian (Reed, 1960; Van Valen, 1960) or well into the Carboniferous (Ax, 1987; Loconte, 1990).

As a result of recent phylogenetic analyses (Kemp, 1982, 1983; Gauthier et al. 1988b, 1989; Rowe, 1988; Wible, 1991; Crompton and Luo, in press; see also Kemp, 1988; Miao, 1991), even antagonists in this particular debate now agree on many aspects of the relationship of Mammalia within Cynodontia (Fig. 2) and agree that all known Carboniferous, Permian, Triassic, and Early Jurassic fossils arose prior to the last common ancestor linking extant monotremes and therians (=Mammalia). The earliest fossils with apomorphies that arose within crown clade Mammalia, thus providing unambiguous evidence for the minimum age of that taxon (e.g., Gauthier et al., 1988b; Rowe, 1988; Norell and Novacek, 1992), are from the Late Jurassic (Bathonian) Stonesfield Slate of England (e.g., Owen, 1871; Aulie, 1974; Desmond, 1984; Rowe, 1988). Linnaeus coined the name in 1758 for the extant mammals then known, building on John Ray's (1693) earlier category Vivipera. Sir Richard Owen (1871) identified the Stonesfield Slate fos-

sils as the oldest mammals more than a century ago. And the clade stemming from the last common ancestor those fossils shared with Theria and Monotremata has been known by no other name than Mammalia ever since (e.g., Huxley, 1880; Haeckel, 1897; Gill, 1902; Gregory, 1910; Desmond, 1984; Rowe, 1988; de Queiroz and Gauthier, 1992). There may be divergent ideas about what the name Mammalia means: is it a character or set of characters, a group of taxa, or an ancestor and all its descendants? Nonetheless, its universal usage by comparative biologists (de Queiroz and Gauthier, 1992), except for some paleontologists, has long been for the crown clade Mammalia, viz., the last common ancestor of Monotremata and Theria, and all of its descendants (Rowe, 1988).

All uses of Mammalia listed in Figure 1 apply to clades (except those of Owen [1871], Simpson [1959], and Miao [1991]), and they are clearly phylogenetic in that sense. But because paleontologists have applied the name to very different entities, there must be some criterion other than descent itself, such as an assortment of organismal traits or a particular combination of taxa, upon which that "tradition" rests. The history of the problem reveals that the prime factor in the dispute over inclusiveness of Mammalia within Synapsida stems from divergent views on which (preservable) character(s) ought to be regarded as essential to membership in that taxon (e.g., Simpson, 1959; Gow, 1985; Miao, 1991). A dense fossil record is sometimes thought to defy precise definition of names, which are held to reflect arbitrary divisions of an evolutionary continuum (e.g., Olson, 1959; Simpson, 1959; Hopson, 1987). As far as characters are concerned, that may be the case. There will always be subjectivity and ambiguity in identification and delimitation of the essential mammalian features. This debate extends across more than 50 years of literature, and yet no single character is common to all proposals (Rowe, 1988). The choice of a particular character (or set of characters) has been justified recently in terms of its purported biological significance (Lucas, 1990, 1992; Lucas and Hunt, 1990), the "profoundness of the apo-

morphy" (Gow, 1985:559), its correlation with "other important changes in the skull" (Hopson, 1987:17), or simply because it is "time-honoured" and "highly practical" (Miao, 1991:589). Oddly enough, some paleontologists regard the emphasis on preservable characters as a virtue of their definitions rather than a deficiency in their data (e.g., Miao, 1991).

A definition expressed in terms of characters would be especially unstable when intermediate states remain to be discovered, as is likely in much-favored definitions based on morphologically distinctive, functionally integrated character complexes. The dentary-squamosal jaw articulation, a classic example, was once commonly cited as the definitive mammalian character complex (e.g., Simpson, 1959, 1960, 1961). However, as more complete fossils of the near outgroups of Mammalia were discovered (Crompton, 1958; Kuhne, 1958; Romer, 1969), the distinctiveness of the mammalian craniomandibular joint was found simply to reflect the lack of knowledge of intermediate morphologies, and the meaning of the name Mammalia became controversial (e.g., Barghusen and Hopson, 1970; Simpson, 1971). That kind of instability does not pose the same problem when the names of monophyletic taxa are defined by ancestry, any more than the inclusion of fossils in phylogenetic analyses makes recognition of monophyletic taxa any less objective (Gauthier et al., 1988a, 1988b, 1989; Donoghue et al., 1989; Kluge, 1990). Because therians and monotremes must share some ancestor in a phylogenetic system, the meaning of the name Mammalia, at least in terms of its ancestry, will always be the same, even if its known contents and its diagnosis continue to change (de Queiroz and Gauthier, 1992).

In the Linnaean tradition, as character concepts change, so can the meaning of names, at least in terms of what those names connote about contents and diagnosis and, most importantly, ancestry (Rowe, 1988; de Queiroz and Gauthier, 1992). Moreover, the meanings of character-based definitions are inherently unstable because the distributions of characters and the diagnoses of taxa will inevitably change as new taxa are

discovered and as new bodies of data are incorporated into phylogenetic analyses. The principle of total evidence (Kluge, 1989) insures this continual change, as current phylogenetic hypotheses are tested in progressively more inclusive analyses. With ancestry-based definitions, however, the known contents and diagnosis may change, but the meaning of that name in terms of a specified clade would be both stable and unambiguous. Because therians and monotremes must share some common ancestor in a phylogenetic system, the meaning of the name Mammalia, at least with respect to that ancestor, whether it could be identified as such or not, will always be the same (Rowe, 1987, 1988; de Queiroz and Gauthier, 1992).

Current debate over the name Mammalia highlights the fact that many paleontologists continue to operate in a system influenced in fundamental ways by a pre-Darwinian world view. The cost to their taxonomy is instability in both the usage and meaning of names, ambiguous conveyance of information on ancestry, and conflicting, imprecise measures of the secondary properties arising through the process of descent. More in keeping with the Darwinian Revolution is a phylogenetic taxonomy based explicitly on common ancestry, which more stably and informatively serves systematists by communicating unambiguously the results of phylogenetic analyses. Even when the three living species of monotremes become extinct (the ultimate fate of species), the name Mammalia will remain attached to the taxon stemming from their last common ancestor with therians (see discussion of priority by de Queiroz and Gauthier, 1992). That definition defines the name Mammalia precisely, unequivocally, and stably, preserving its most general and informative usage for those working within a system whose central tenet is evolution.

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## Statistical Significance of the Matrix Correlation Coefficient for Comparing Independent Phylogenetic Trees

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Ultrametric trees or dendrograms (=phenograms of some authors; Sneath and Sokal, 1973) have received much attention in phylogenetics and are used to portray the relationships among members of a given taxonomic group in the presence of constant evolutionary rates, corresponding to a molecular clock hypothesis (Blanken et al., 1982). However, additive trees or cladograms provide a better representation of phylogenetic distances in the presence of unequal evolutionary rates among lineages (Tateno et al., 1982). Numerous algorithms permit derivation of ultrametric or additive trees from distance matrices or directly from character matrices (Felsenstein, 1982; Gordon, 1987; Swofford and Olsen, 1990; Penny et al., 1992). With these methods arose the problems of efficiency (Milligan, 1981). Which algorithm is the best? What is a good phylogenetic tree? How should the efficiency of a particular method be measured?

The next logical step after characterization of the various methods is to compare the stability of the constructed phylogenetic trees under different reconstruction techniques (Sokal et al., 1992). Consensus

tree methods (Day, 1986, and references therein) and consensus indices (Rohlf, 1982) were derived to measure the similarity between phylogenies or to produce a compromise solution reflecting the common agreement of several trees. More recently, procedures have been proposed to compare trees statistically (Page, 1988; Lapointe and Legendre, 1990, 1992), and significance tables have been published for many consensus indices (Shao and Rohlf, 1983; Shao and Sokal, 1986). The present paper proposes tables of critical values of the cross-product matrix correlation coefficient (Rohlf, 1982), designed to allow statistical comparison of trees while taking into account the metric information embedded in the branches of a phylogeny.

### TREE PROPERTIES

The relationships among the objects of a set  $W = \{1, 2, \dots, n\}$  that represents a given taxonomic group can be portrayed in a matrix  $\mathbf{D}$  of pairwise distances. Such a matrix of metric distances must satisfy four minimal conditions (cf. Sneath and Sokal, 1973):