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DEFINITION, DIAGNOSIS, AND ORIGIN OF MAMMALIA

TIMOTHY ROWE
Department of Geological Sciences, University of Texas, Austin, Texas 78713-7909

ABSTRACT—Mammalia is defined by its ancestry as the taxon originating with the most recent common ancestor of extant Monotremata and Theria. To diagnose Mammalia as so defined, 176 character transformations in the skull and postcranial skeleton, distributed among Placentalia, Marsupialia, Multituberculata, Monotremata, Morganucodontidae, Tritylodontidae, and *Exaeretodon,* were polarized, scored, and subjected to PAUP. Only one most parsimonious tree was identified (BL = 190, CI = 0.926): (*Exaeretodon* (Tritylodontidae (Morganucodontidae (Monotremata (Multituberculata (Marsupialia, Placentalia))))))).

Thirty-seven osteological synapomorphies diagnose Mammalia. Triassic and Early Jurassic taxa commonly referred to as mammals, including Morganucodontidae, Kuehneotheriidae, and Haramiyidae, were found to lie outside of Mammalia. These fossils document that the mammalian lineage had diverged from other known synapsid lineages by the Norian (Late Triassic). However, the earliest evidence that Monotremata and Theria had diverged from their most recent common ancestor, and thus the earliest evidence of Mammalia itself, is of Bathonian (Middle Jurassic) age. Many of the diagnostic attributes of Mammalia are associated with either the sensory organs housed in the skull, the masticatory system, or the craniovertebral and atlas–axis articulations. Modification of each of these regions has long been tied to the origin of mammals. However, other synapomorphies are identified which suggest that additional factors must be sought to fully understand the origin of Mammalia.

INTRODUCTION

Since 1758, when Linnaeus coined the name Mammalia and was the first to include cetaceans and chiropterans among its members, there has been little question that Mammalia is a natural group of some sort, with basically the extant membership we now recognize (Gill, 1902; Gregory, 1910). Under the theory of evolution this concept was formalized by recognizing mammals as each other's closest living relatives, and the 'naturalness' that Linnaeus recognized and described typologically is now understood as common ancestry.

Among living organisms there is no difficulty in deciding whether a specimen is or is not a mammal, and I am unaware of any case of mistaken identity of a Recent mammal in the last 200 years. There can be little doubt that extant mammals share a unique common ancestor and that Mammalia is monophyletic. As Haeckel wrote:

> The various characteristics in which all 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. . . . 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; capitalization original).

Mammalia is one of the most thoroughly studied segments of Life. In the century since Darwin's theory led to its recognition as a genealogical entity, one might expect general accordance to have been achieved in our understanding of its more fundamental evolutionary properties. Nevertheless, significant disagreement exists on its diagnostic attributes, membership, relationship to extinct Synapsida, classification, distribution in time and space, rate-related properties, and others. These conflicts have arisen primarily through the consideration of fossils. For example, the boundary distinguishing Mammalia from its closest extinct relatives is generally held to be indistinct because of the fragmentary preservation of early mammalian fossils. This in turn has led to dispute on whether or not certain fossils are mammals, and subsequent debate on second-order properties of Mammalia such as its distribution in time. One cannot doubt that incompleteness of the fossil record has appreciably constrained the availability of data. But when the methods used to frame and study questions about early mammalian history are themselves examined, it is evident that conflicting methodology has also been an important source of difficulty. One manifestation of this problem is that no single character can be found in common to all of the osteological diagnoses of Mammalia published in the last 30 years (Table 1). Kirsch (1984:21) described the situation:

> It is a considerable irony that an operational osteological diagnosis remains elusive for Mammalia, a

> group with one of the best fossil records. . . . the consistent osteological features of living mammals—the single lower jaw bone and complex middle ear—appeared gradually and repetitively both within Mammalia and collateral lineages; in short the osteological criteria define a *grade,* not a monophyletic clade.

As this quotation suggests, the dispute on diagnostic attributes is itself primarily a consequence of underlying disagreement (or indecision) on what will be referred to as the conceptual definition of Mammalia. A wide variety of conceptual definitions of Mammalia can be found in the literature, reflecting the more important controversy on our conceptual view of taxa generally. Are taxa grades, clades, nominal classes, individuals, some combination of these, or some other entity altogether? Without a consistent conceptual definition of Mammalia (or any other taxon) it is not surprising to see a lack of uniformity in the measurement of its diagnostic attributes. Moreover, because the definition and diagnosis of Mammalia logically precede the measurement of other properties, such as its distribution in time and space or rate-related properties of Mammalia as a whole, the conflicts in these systematic problems may be felt at other levels of investigation.

The distinction between definition and diagnosis is discussed below. A definition of Mammalia based on its ancestry is recommended as most consistent with the goals of phylogenetic analysis. Character data bearing on the relationship among the highest systematic categories of Mammalia and its closest extinct relatives are then analyzed phylogenetically (Appendices I–III) to provide an osteological diagnosis of Mammalia based on this definition. A series of outgroups is identified to establish the polarity of transformation of diagnostic characters (Figs. 1–3). Thirty-seven mammalian synapomorphies are identified by the analysis, and the rationale for their assignment to Mammalia are briefly summarized below. The implications of this view of definition and diagnosis of Mammalia are then briefly explored.

DATA AND METHODS OF ANALYSIS

Data discussed below are based on cited literature and my examination of specimens in the following museums: Museum of Paleontology, University of California, Berkeley; Museum of Northern Arizona; National Museum of Natural History; American Museum of Natural History; Museum of Comparative Zoology, Harvard University; Vertebrate Paleontology Laboratory, Balcones Research Center, University of Texas; British Museum (Natural History); Zaklad Paleobiologii, Polish Academy of Science; Paleontological Institute, Academy of Sciences of USSR; South African Museum; and Bernard Price Institute for Paleontological Research, University of the Witwatersrand.

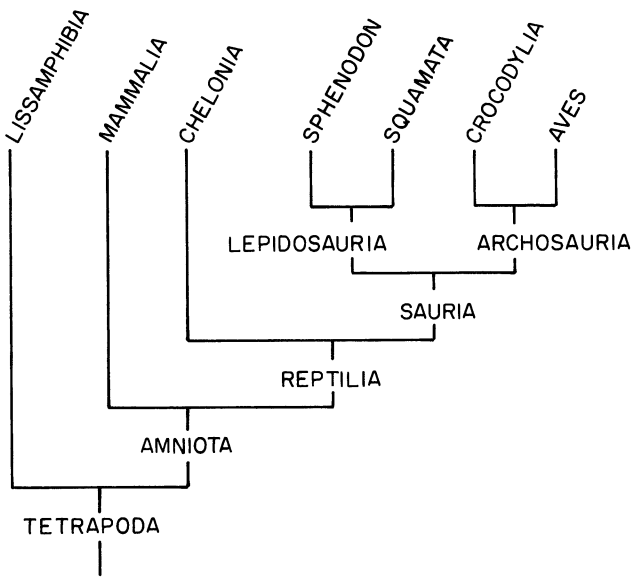

FIGURE 1. Tetrapod phylogeny depicting the relationship of Mammalia to other extant tetrapods. Character data for this hypothesis are discussed in Gauthier et al. (1988a).

Principal literature sources for the taxa discussed below are as follows. *Exaeretodon:* Bonaparte (1962, 1963, 1966), Hopson (1984). Tritylodontidae: Clark and Hopson (1985), Gow (1986a), Grine et al. (1979), Grine and Vrba (1980), Hopson (1964), Kuhne (1956), Sues (1983, 1985, 1986, pers. comm.). Morganucodontidae: Clemens (1979a), Crompton (1974), Crompton and Jenkins (1979), Crompton and Sun (1985), Gow (1985, 1986b), Jenkins and Crompton (1979), Jenkins and Parrington (1976), Kermack et al. (1973, 1981), Krusat (1980). Monotremata: Archer et al. (1979), Gregory (1947), Griffiths (1978), Kuhn (1971), Lester and Archer (1986), Lester and Boyde (1986), Presley (1980, 1981, 1984). Multituberculata: Clemens and Kielan-Jaworowska (1979), Hahn (1977, 1978a, b), Kielan-Jaworowska (1971), Kielan-Jaworowska et al. (1984, 1986), Krause and Jenkins (1983). Theria: Clemens (1979b), Marshall (1979), Novacek and Wyss (1986a), Maier (1987). General references: deBeer (1937), Gauthier et al. (1988a, b), Gregory (1910), Hopson and Barghusen (1986), Kemp (1982, 1983), McKenna (1987), Romer (1956), Rowe (1986a).

The analysis described below was carried out in the context of more general phylogenetic analyses of the higher systematic categories of Synapsida (Rowe, 1986a) and Amniota (Gauthier et al., 1988a, b). These studies helped to identify the taxa that have the most direct bearing on diagnosing Mammalia osteologically. Several factors were evaluated in identifying the most informative taxa for analysis, including the higher systematic category relationship within Mammalia, identification of its most proximate outgroups, and completeness of fossils in both the ingroup and outgroups (see below). The principal terminal taxa chosen for

TABLE 1. Previous diagnoses (referred to as "definitions" by most authors) of Mammalia. This list includes the original diagnosis by Linnaeus and osteological diagnoses published in the last thirty years.

Linnaeus, 1758 (quoted from Gregory, 1910:28):

"Mammals have a heart with two auricles and two ventricles, with hot red blood; that the lungs breathe rhythmically; that the jaws are slung as in other vertebrates, but 'covered,' i.e., with flesh, as opposed to the 'naked' jaws of birds; that the penis is intromittent; that the females are viviparous, and secrete and give milk; that the means of perception are the tongue, nose, eyes, ears, and the sense of touch; that the integument is provided with hairs, which are sparse in tropical and still fewer in aquatic mammals; that the body is supported on four feet, save in the aquatic forms, in which the hind limbs are said to be coalesced into a tail (the only erroneous idea in the whole definition)."

Kermack and Mussett, 1958

1) Dentary–squamosal joint.

Simpson, 1959

1) Single bone in lower jaw, articulating directly with squamosal.
2) Three auditory ossicles.

Reed, 1960

A. Non-skeletal characters:
1) Endothermy.
2) Complete double circulation, with higher arterial pressure in non-pulmonary portion.
3) Retention of 4th left aortic arch as functional arch of aorta.
4) Enucleated, round erythrocytes (secondarily oval in Camelidae).
5) Loss of renal portal system.
6) Possession of diaphragm.
7) Combination of integumental characters: hair, sebaceous glands, sweat glands.
8) Possession of mammary glands, functional in females.
9) Nitrogenous wastes excreted as urea instead of uric acid.
10) Possession of specialized facial dermal muscles.

B. Skeletal characters:
1) Articular–quadrate joint not a suspensorium.
2) Dentary–squamosal joint present.
3) Three middle ear ossicles present.
4) Mandible consists of one bone only, the dentary.
5) Secondary (false palate) present.
6) Double occipital condyle instead of but one.
7) Mammalian-type atlas–axis complex.
8) Cusps present on cheek teeth.
9) Lumbar ribs lacking.
10) Mammalian-type ethmoturbinals present.

Van Valen, 1960

1) Care for young.
2) Intelligence (i.e., ability to learn).
3) Activity, "perhaps the most important."

Simpson, 1960

1) Dentary–squamosal joint.

TABLE 1. (*Continued*)

MacIntyre, 1967

Amniote craniate Chordata with:
1) Three middle ear ossicles (malleus, incus, and stapes) not in contact with dentary in adults.
2) Cochlea of inner ear with at least one full coil.
3) Mesozoic fossils also with tribosphenic or pretribosphenic cheek teeth.
4) Recent species also viviparous, with nipples; separate anal and urogenital openings; heart with two ventricles, left aortic arch dominant. Usually endothermic, hairy, or both; scapula with supraspinous fossa.

Hopson and Crompton, 1969

Amniote vertebrates with:
1) Articulation between dentary and squamosal.
2) Postcanine teeth in which primary cusps (paracone and protoconid of the standard nomenclature) are primitively flanked by anterior and posterior accessory cusps, which may lie on straight line with primary cusps or may be set off from them at an angle to longitudinal axis of jaw so that the three cusps form a triangle.
3) Limited pattern of tooth replacement with postcanines divided into premolars and molars (or approaching this condition), except in secondarily specialized cases in which premolars are not replaced.

Crompton, 1974

1) Transverse jaw movements.
2) Tooth replacement limited to deciduous and permanent teeth.
3) Division of postcanine row into premolars and molars with relative positions of upper and lower molars fixed.

Crompton and Jenkins, 1979 (informal diagnosis)

1) Jaw joint formed in part by dentary and squamosal.
2) Postcanine teeth differentiated into premolars and molars.
3) During occlusion, buccal surface of lower molars shears against lingual surface of uppers, forming a consistent pattern of wear facets.
4) Jaw movement during occlusion guided in dorsomedial direction by structure of molars.
5) Cavum epiptericum partially floored below trigeminal and geniculate ganglia.
6) Well-developed fenestra rotunda present lateral to jugular foramen.
7) Cochlear region of inner ear large relative to skull size compared with that of cynodonts.
8) All known Triassic mammals were small.
9) Presence of anticlinal vertebra and major structural differences between thoracic and lumbar vertebrae.
10) Atlanto–axial joint possesses a large protuberant dens.
11) Pelvis with narrow, rod-like ilium directed anterodorsally, large obturator foramen, and reduced pubis.

TABLE 1. (*Continued*)

Fakui and Guihai, 1933:40-41

"Mandible consisting of only a singular dentary and the accessory jaw bones having turned into the components of a middle ear."

Kermack and Kermack, 1984

1) Squamosal–dentary joint.
2) Chain of three auditory ossicles.

Crompton and Sun, 1985

1) Dentary condyle articulating with squamosal glenoid.
2) Anterior lamina forming side wall to cavum epiptericum and surrounding V3 and possibly V2.
3) Floor to cavum epiptericum below primary exit of seventh nerve.
4) Prootic canal.
5) Double-rooted molars aligned longitudinally.
6) Loss of alternate tooth replacement of postcanine teeth.
7) Prominent medial ridge and groove on dentary for support of postdentary bones.

Gow, 1985

1) Small size.
2) Definitive growth.
3) Presence of promontorium.
4) Diphyodonty.

Hopson and Barghusen, 1986

1) Dentary with well-developed articular condyle contacting well-developed glenoid cavity on squamosal.
2) Postcanine teeth differentiated into premolars, which undergo single replacement, and molars, which are not replaced.
3) Postcanine teeth with divided roots (convergently derived in Tritylodontidae).
4) Molar teeth with well-developed shear surfaces that form a consistent pattern of wear facets (convergently derived in Tritylodontidae).
5) Quadrate with elongate stapedial process, the crus longus of the mammalian incus.

Clemens and Lillegraven, 1986:66 (provisional diagnosis)

Synapsids characterized by evolution of a dentary–squamosal articulation between lower jaw and skull.

analysis were *Exaeretodon,* Tritylodontidae, Morganucodontidae, Monotremata, Multituberculata, Marsupialia, and Placentalia. Data bearing on the monophyly of these taxa are summarized elsewhere (Rowe, 1986a, and references therein).

Characters from the entire skeleton were considered and all apomorphic conditions shared by two or more of the terminal taxa were analyzed (Appendix I). The data matrix includes all of the applicable characters that were used in cladistic analyses of roughly this same segment of Synapsida by Hopson and Barghusen (1986), Kemp (1982, 1983), McKenna (1987), Novacek and Wyss (1986a), and Rowe (1986a). One hundred seventy-six character transformations distributed among 140 binary and 18 multistate characters were scored on a taxon–character matrix (Appendix III) and subjected to the Branch and Bound algorithm of Swofford's (1984) mainframe computer software PAUP. Only one most parsimonious tree was identified (Fig. 3), with a Branch Length (BL) of 190 steps and a Consistency Index (CI) of 0.926. Autapomorphies of the terminal taxa are ignored in this analysis, and only characters varying in two or more of the terminal taxa were used to calculate CI. Ingroup variation was noted while scoring the matrix, but because only one state can be entered into PAUP, only the presumed primitive state for each taxon was entered, based on ingroup hypotheses discussed by Rowe (1986a). This limitation in PAUP yields a tree that is more parsimonious than it would be if the variation within terminal taxa for these same characters were also considered in calculating tree length. Although this result is undesirable, it appears justifiable in that the goal of the analysis was the relationship among, rather than within, the terminal taxa.

All multistate characters were entered as unordered data, so that state 0 could give rise to state 1 and then to state 2, or state 2 could be transitional to state 1, or both states 1 and 2 could arise independently from state 0. In doing so, any state in the transformation series can evolve from any other without adding extra steps to the tree length. All missing data were entered into PAUP simply as '9' although two types of missing data are distinguished in Appendix III. Nonpreservation is listed as '?' and characters that are nonapplicable are listed as 'N' (e.g., homodont vs. heterodont dentition cannot be scored for taxa lacking teeth). Following the suggestion of Maddison et al. (1984), at least two outgroups were used to determine polarity of character transformation for all characters scored.

A series of separate runs of the data matrix for the principal taxa was made using PAUP. In the early runs, an effort was made to score as separate characters all anatomical variants, despite current views that some might be manifestations of a single transformation. For example, suspension of the ectotympanic (angular), malleus (articular), os goniale (prearticular), and ossiculum accessorium mallei (surangular) from the skull were initially treated as separate characters. However, because functional integration of these characters is generally acknowledged, most students consider the transformations of these bones as a single character. Because an initial PAUP run confirmed their concordant distributions, in subsequent runs the transformations of these four bones were treated as a single character. In this way I attempted to avoid biasing the resulting tree with split or inflated characters, while also avoiding a priori decisions about character interdependence.

The choice of extinct taxa was limited by their completeness (Table 2). Numerous relevant fossil taxa are known from relatively complete specimens, but a considerable diversity of others is represented by mere

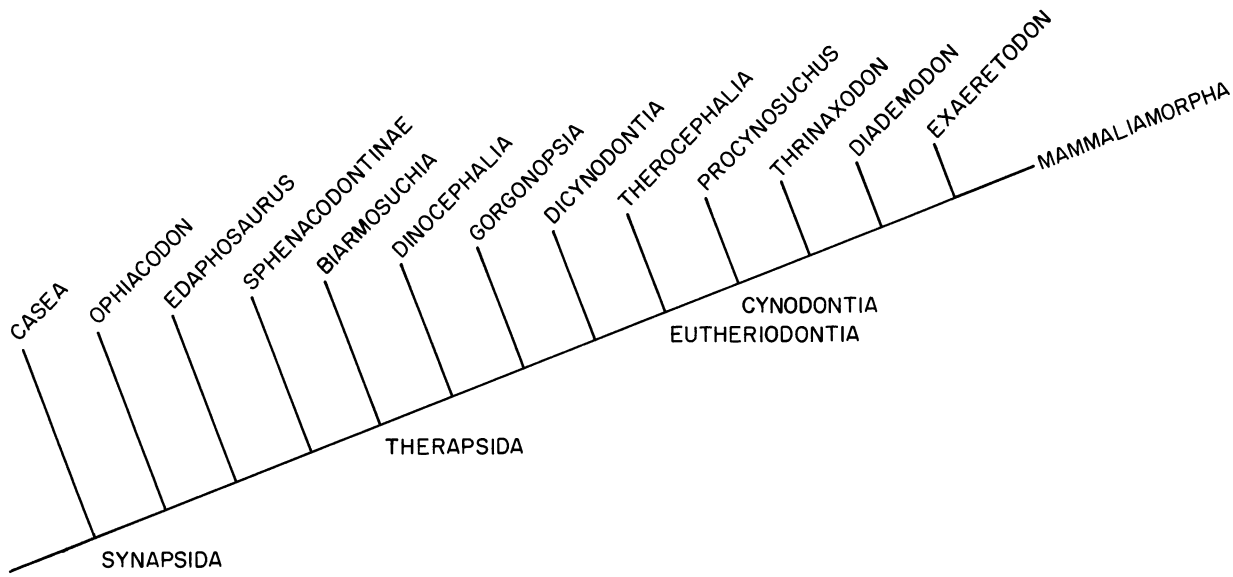

FIGURE 2. Phylogeny of higher systematic categories of Synapsida. This hypothesis depicts the consecutive outgroups used to determine ancestral states for the terminal taxa in this analysis. Character data for this hypothesis are discussed in Rowe (1986a) and Gauthier et al. (1988a).

fragments. In order to identify the most stable elements of relationship among all of the named taxa, the analysis focused on only the most complete. Completeness was measured using the total number of characters in the data matrix (Appendices I, III), and all characters scored '?' or 'N' were considered to be missing data. Only extinct taxa that lie within or exceed the range of completeness of extant taxa (88–96%) are considered at length below. It is significant that missing data are not exclusively a problem with fossils. A number of characters were scored 'N' in extant monotremes, marsupials, and placentals because they have diverged too far from the ancestral state to be assessed without assuming a priori some hypothesis of relationship (Gauthier et al., 1988a).

A number of fossils that have figured prominently

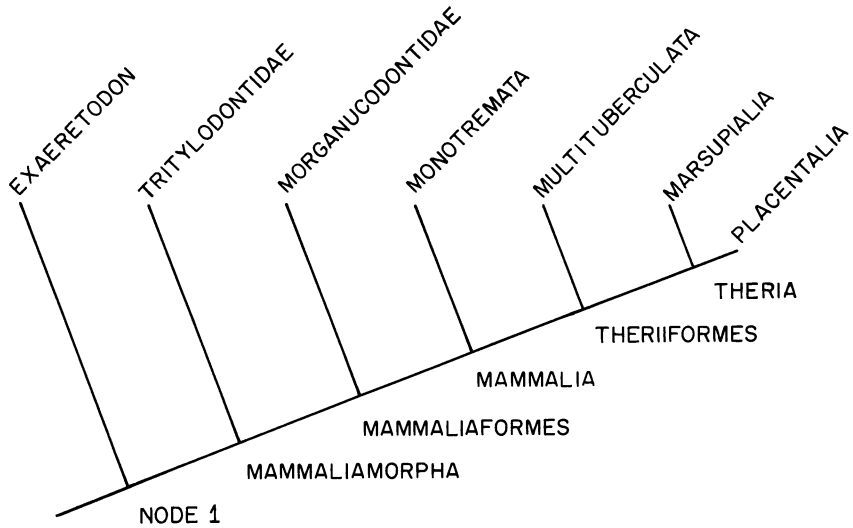

FIGURE 3. Phylogeny of terminal taxa that were the subject of this analysis (see Data and Methods of Analysis), based on PAUP analysis of 176 character transformations (Appendices I–III). Tree length = 190 steps. Branch-length ranges: Node I (Unnamed Taxon) = 10 to 15 steps; Mammaliamorpha = 56 to 62 steps; Mammaliaformes = 16 to 25 steps; Mammalia = 32 to 43 steps; Theriiformes = 18 to 25 steps; Theria = 15 to 22 steps. Consistency index (CI) for this tree is 0.926; all apomorphies were stripped from the matrix before calculating CI.

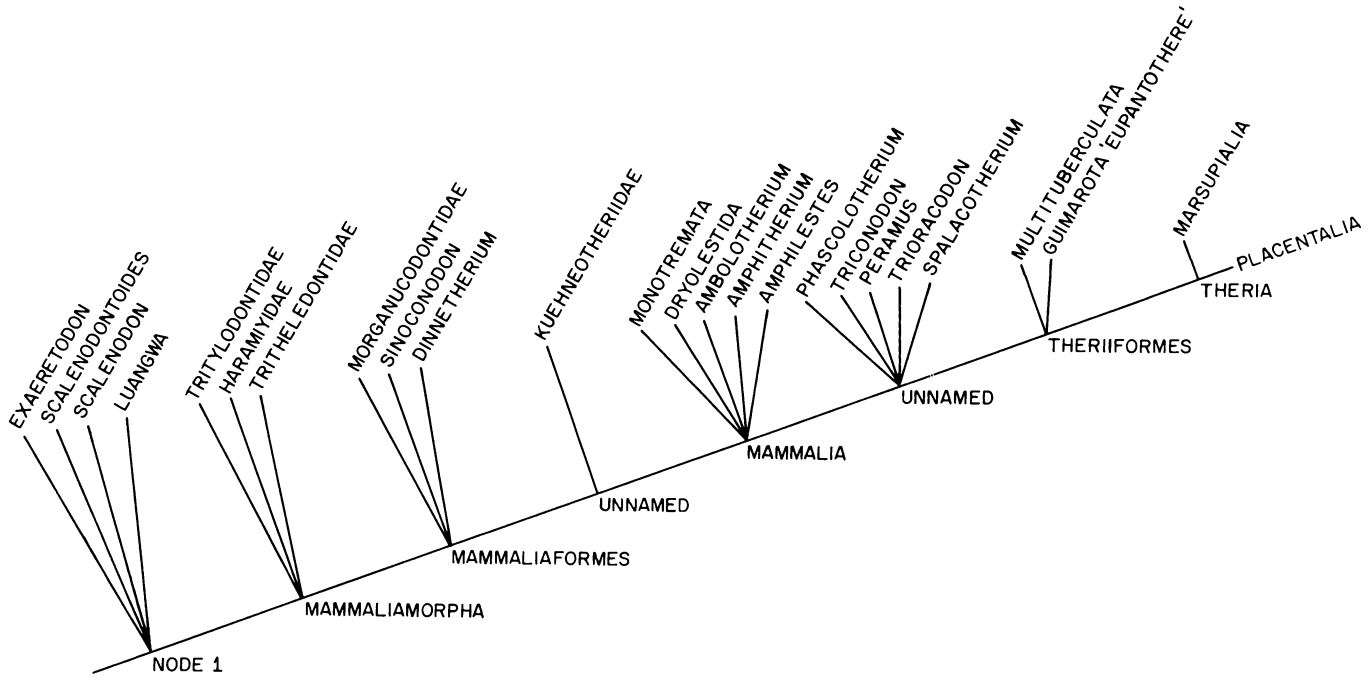

FIGURE 4. Manually estimated positions of incomplete Mesozoic fossil taxa, based on characters in Appendix I and their distributions among taxa 88% or more complete (see Fig. 3).

in previous discussions of the origin of mammals were omitted from the data matrix because they fell outside of the completeness range of living taxa. Most are based on isolated jaw fragments and dentitions. Their exclusion resulted in loss of the considerable information reflected in the known diversity of dental form. However, virtually none of the currently known skeletal diversity is found only in taxa based on deficient specimens. Only a small portion of the total available data appears to have been sacrified to identifying the most stable elements of relationship. It is unlikely, moreover, that the deficient taxa are sufficiently informative to overturn a hypothesis based on complete taxa. For example, it is unlikely that an isolated jaw might lead us to believe that placentals are more closely related to monotremes than to marsupials.

To test this expectation, a sample of deficient taxa was scored for the characters in Appendix I, added to the matrix, and run on PAUP. It included Tritheledontidae, *Sinoconodon, Dinnetherium,* Kuehneotheriidae, and Haramiyidae (Table 2). The addition of these taxa raised the number of equally parsimonious trees to 25, in contrast to the single tree found for the relatively complete taxa (Fig. 3). However, it did not change the relationship among complete taxa; differences among the 25 trees were solely in the placement of the deficient taxa. Because of the importance given many incomplete taxa in previous discussions, their phylogenetic positions are estimated in Figure 4, based on this test and an earlier preliminary analysis (Rowe, 1986a). A more thorough discussion of this problem will be presented elsewhere.

Two additional data runs were made using PAUP to examine a recent claim by Hopson (1987:18A) that "In a phylogeny [of synapsids] based primarily on cranial and dental synapomorphies, one will find a great deal of convergent evolution in the postcranial skeleton; the opposite will be the case in a phylogeny based primarily on postcranial synapomorphies." The first run was limited to the 91 cranial characters scored in Appendix I, and the second included only the 67 postcranial characters. Contrary to Hopson's expectation,

TABLE 2. Completeness of taxa discussed in this analysis, measured as a percentage of the total number of characters scored for all taxa (Appendix I).

Taxon	% Complete
Exaeretodon	99
Tritylodontidae	99
Morganucodontidae	97
Marsupialia	96
Placentalia	95
Multituberculata	90
Monotremata	88
Tritheledontidae	49
Sinoconodon	37
Dinnetherium	11
Kuehneotheriidae	10
Haramiyidae	2

both data sets yield the same tree as the combined cranial and postcranial data set (Fig. 3). The CI for cranial data is 0.908 (BL = 109) and for the postcranium is 0.951 (BL = 81). There is consistently a very good fit between each data set (cranial, postcranial, and combined) and the one tree (Fig. 3).

The diagnoses discussed below are post hoc descriptions of the outcome of the PAUP analysis. That is, when describing the level of synapomorphy of characters, I am not prejudging the characters but am instead simply reporting the results of the finished analysis of characters described in Appendix I. A complete listing of character assignments is presented in Appendix II.

DEFINITION AND DIAGNOSIS

It has become evident that different taxonomic operations have been confused under the term 'definition' (Ghiselin, 1969, 1984; Rowe, 1987), and that it is systematically useful to distinguish between them. One operation entails the development of a conceptual view of Mammalia and revolves around philosophical problems such as whether Mammalia is a clade, a grade, an individual, a class of objects, or some other entity. It explores more strictly theoretical questions about how we perceive nature and is not primarily dependent on character data, though such data are obviously important to it in many ways. This is definition. In the other operation, the question is asked: which attributes may be useful in identifying Mammalia? Argument revolves around tangible data that in the present study are osteological characters. This is diagnosis. Development of a method for diagnosis follows logically from the particular taxon definition that is chosen.

Definition

In conventional logic a definition states the attributes both necessary and sufficient for categorization of an entity; the thing must have the attribute(s) if it is to be properly called a member of the category. In taxonomy since before Linnaeus, taxa have been defined by their characters. This tradition has persisted in virtually all treatments of Mammalia, which is commonly 'defined' by the presence of a dentary–squamosal craniomandibular joint or three middle ear ossicles (Table 1). However, Ghiselin (1969, 1984) has argued that in the phylogenetic system definitions of taxa can be made only in terms of genealogy. Taxa cannot be defined in terms of characters, as they were under typological pre-evolutionary paradigms, because the defining characters in effect would be forbidden to evolve. For example, if Tetrapoda were defined on the basis of four pentadactyl limbs, snakes, by definition, would not be tetrapods. Ancestry, however, is an organismal property that is fundamental to all evolving entities and that cannot itself transform. In the phylogenetic system, ancestry is the only criterion that is both necessary and sufficient for taxon membership and therefore provides the only means of properly defining taxa (Rowe, 1987). In a phylogenetic context, Tetrapoda is more appropriately defined by its most recent common ancestor (viz., the immediate ancestor of extant Lissamphibia and Amniota) and comprises that ancestor and all its descendants. In the phylogenetic system, despite their lack of limbs snakes are tetrapods because their ancestors were tetrapods. As Gauthier argued, "Ancestry rather than overall similarity must be the basis for a phylogenetic system" (Gauthier, 1986:8).

Following this suggestion, Mammalia may be defined as comprising the most recent common ancestor of living Monotremata (Ornithorhynchidae and Tachyglossidae) and Theria (Marsupialia and Placentalia), and all of its descendants. Thus, if an organism is born to a mammal it is by definition a member of Mammalia, regardless of whether it has hair, mammary glands, or any other character commonly associated with mammals. This definition also follows the suggestion of Patterson and Rosen (1977) and Gauthier (1984; Gauthier et al., 1988c), that widely used names such as Mammalia be restricted to all taxa stemming from the most recent common ancestor of at least two extant lineages, in this case Monotremata and Theria. Such a definition is likely to promote taxonomic precision and stability because discovery or reevaluation of fossils probably will not alter the hypothesis that monotremes and therians are each others' closest living relatives. The apparent stability of this hypothesis is a reflection of the enormous amount and diversity of character data pertaining to the close relationship of monotremes and therians among living taxa. In addition, by stating its definition in terms of the two principle divisions of Mammalia, one can design simple three-taxon tests of potentially diagnostic attributes (see below).

The definition proposed here is consistent in many respects with historic conceptions of Mammalia and preserves important aspects of the conventional usage of the term. Linnaeus, working under a pre-evolutionary paradigm, coined the name for living species. To recast his concept in an evolutionary mold requires only that their most recent common ancestor and all of its descendants also be included. Such a view is implicit in its current usage by the majority of evolutionary paleontologists and neontologists (but see Van Valen, 1960; Reed, 1960; MacIntyre, 1967).

Kemp (1983; see also Kuhne, 1958; Patterson, 1981) discussed a relationship that was found to be most strongly corroborated by this analysis, which is that Morganucodontidae and Tritylodontidae are consecutive outgroups to the taxon defined by the most recent common ancestor of Monotremata and Theria (Fig. 3). Kemp chose to include Morganucodontidae within Mammalia, as has traditionally been done by paleontologists, rather than restricting the name to the node from which Monotremata and Theria branch. Other

authors have also argued for the inclusion of extinct outgroups under the name Mammalia. Van Valen (1960) suggested that all therapsids be referred to as mammals, and Reed (1960) would include sphenacodontines as well. However, these suggestions are mutually incompatible and have little merit for phylogenetic studies in that all are based on typological arguments which contend that these outgroups possess some 'essential' mammalian character. Most importantly, it seems clear that any discussion of the origin of Mammalia should revolve around elucidation of the attributes present in the most recent common ancestor of living species instead of a more inclusive taxon.

The semantic issue of which node on the cladogram should be assigned the name 'Mammalia' is significant, and care must be taken that it not be confused with the entirely distinct question of the phylogenetic relationship among the terminal taxa that are the subject of this analysis. Assignment of the name 'Mammalia' (or any other nomenclature) is important because it reflects our view of the structure of the world and may profoundly affect our communications about that structure (see Rowe, 1986a, b, 1987). However, it has no bearing on the ample character evidence arguing, for example, that Monotremata and Theria are more closely related to each other than to Morganucodontidae. One might be tempted to argue that the definition suggested here simply 'defines' morganucodontids and kuehneotheriids out of Mammalia, and that the diagnosis of Mammalia presented below is little more than a semantic exercise. But the divergence of Monotremata and Theria from their most recent common ancestor is an historic phenomenon that cannot be changed by semantic manipulation, and it is this phenomenon that is of central interest to any study of Mammalia as a whole.

Diagnosis

A diagnosis has been often viewed as a statement of characters that might be useful in distinguishing one taxon from others, but explicit identification of the level of generality of these characters traditionally has not been required. Relatively little historical information can be gleaned from such diagnoses, however, because probably the most significant historical information lies in the relationship between the character and the level at which it appeared. Only characters that can be polarized and assigned to a particular level of generality (i.e., synapomorphies) are germane to phylogenetic inquiry. In the phylogenetic system, therefore, a taxon diagnosis is a statement of its hypothesized synapomorphies. These are not 'defining' characters, because they may continue to evolve following their first appearance in the ancestor of the taxon. Using the definition that Mammalia comprises the immediate ancestor of Monotremata and Theria and all taxa stemming therefrom, its diagnosis can be most simply framed as a three-taxon problem in which Monotremata and Theria are compared to the closest outgroups of Mammalia (see below).

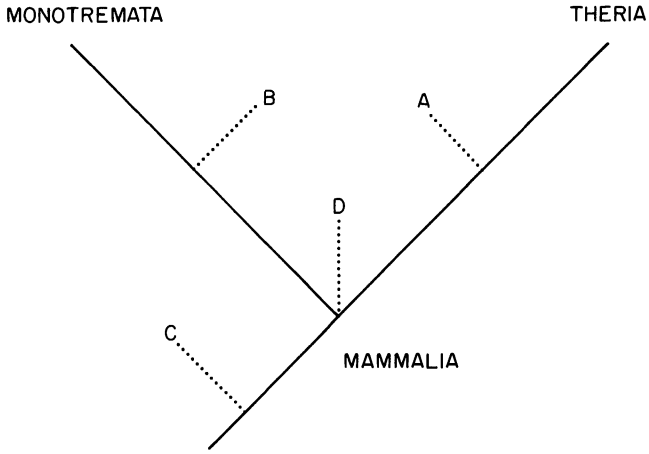

FIGURE 5. Potential relationships of fossils to the principal mammalian taxa. Any fossil that is not itself a member of either Monotremata or Theria can have one of only four potential relationships. It can be most closely related to Theria (**A**), most closely related to Monotremata (**B**), not a member of Mammalia (**C**), or a member of Mammalia sedis mutabilis (**D**) (see Analysis of Fossils).

ANALYSIS OF FOSSILS

A consequence of the definition employed in this study is that any fossil that is not itself a member of either Theria or Monotremata can have only four possible relationships within this hypothesis (Fig. 5A–D). It can be most closely related to Theria (Fig. 5A), most closely related to Monotremata (Fig. 5B), not a member of Mammalia as defined herein (Fig. 5C), or placed in an unresolved position within Mammalia (Fig. 5D).

Mammalian fossils that lie in positions 5A and 5B potentially provide critical information to diagnosing Mammalia, because any taxa in these positions will be relatively more plesiomorphic than extant Monotremata and Theria, and their inclusion in the analysis will thus aid in detecting homoplasy within Mammalia. Most of the taxa found to occupy these positions were only poorly informative in this regard, however, because the fossils upon which they are based are less than about 15% complete (Table 2). Multituberculata is a notable exception, being 90% complete, and was scored for the present analysis.

Taxa assigned to position 5C are outgroups of Mammalia. Characters preserved in at least the two most proximate outgroups (Maddison et al., 1984) were assumed to reflect the primitive states from which mammalian synapomorphies arose.

Two classes of taxa may be assigned to an unresolved position within Mammalia (Fig. 5D). The actual, most recent common ancestor of Mammalia would occupy this position on the cladogram, although it must be

appreciated that identification of potential ancestral status is decided secondarily, on the basis of what a specimen lacks (Patterson and Rosen, 1977). That is, the ancestor of Mammalia would have all of the mammalian synapomorphies, but its ancestral position could only be recognized by its lack of all apomorphies evolved in its descendants. No such taxon was identified in this study.

The other class in position 5D is composed of taxa based on deficient specimens that preserve some of the synapomorphies of Mammalia but do not preserve any apomorphies of a mammalian subgroup. A number of these taxa were encountered in this study. They are assigned here to Mammalia sedis mutabilis (Wiley, 1981). Although it remains possible that one of the sedis mutabilis taxa is in fact the ancestor of Mammalia, little can be gained from such speculation because so few data can be brought to bear on the issue. Moreover, because they do not permit evaluation of all identified mammalian synapomorphies, it remains possible that discovery of more complete specimens will result in their assignment to a position outside of Mammalia, though closer to it than any of the outgroups analyzed below. Fossil taxa assigned to Mammalia sedis mutabilis (Fig. 5D) therefore do not provide an adequate basis upon which to measure properties of Mammalia as a whole. In contrast, fossils in positions 5A and 5B do provide evidence that monotremes and therians had diverged from their common ancestor. Estimates of the minimum age, ancestral distribution, and so forth for Mammalia can thus be based on the earliest fossil(s) that preserves characters which are demonstrably derived within Mammalia (Hennig, 1981).

RESULTS

Heated controversy has recently surrounded the relationship of Mammalia to living and extinct tetrapods. Gardiner (1982) and Løvtrup (1985) argued that mammals and birds are each other's closest living relatives, and that extinct synapsids, long believed to include the proximate ancestors of mammals, played no role in mammalian phylogeny. However, Gauthier et al. (1988a, b) dispelled this notion after reexamining all of the data presented by Gardiner and Løvtrup, as well as extensive additional data summaries in Gauthier (1984) and Rowe (1986a) and elsewhere in the published literature. In a parsimony analysis of 274 characters from extant and extinct amniotes, only one most parsimonious tree was found by PAUP (Fig. 1), in which Mammalia is the sister taxon of all other amniotes (see also Gaffney, 1979, 1980). Moreover, from fossil data it is clear that Mammalia lies deeply internested within Synapsida (Figs. 2, 3), as has been thought for nearly a century. Data bearing on the relationships among the higher systematic categories of extinct Synapsida have been discussed at length elsewhere (e.g., Kemp, 1982, 1983; Brinkman and Eberth, 1983; Hopson and Barghusen, 1986; Reisz, 1986; Rowe, 1986a; Gauthier et al., 1988a). In this section only data pertaining to the most proximate outgroups of Mammalia and higher-level relationships within the group (Fig. 3) are discussed. All characters are referred to below according to their numbered order in Appendix I.

Node I. (Unnamed Taxon)

The most inclusive taxon identified in this study is an unnamed group comprising the most recent common ancestor of *Exaeretodon* and Mammaliamorpha (new taxon, see below), and all taxa stemming from it (Figs. 2, 3). This taxon is diagnosed by ten unequivocal synapomorphies and possibly by an additional five equivocal characters (i.e., branch length range = 10–15).

Unequivocal synapomorphies are: 8) closed pineal foramen, 9) fused parietals in adults, 10) parietal expanded onto the anterior face of the occipital plate (state 1), 15) maxilla participates in the anterior border of the subtemporal fenestra, 32) ectopterygoid co-ossified with pterygoid in adults, 48) posterolateral flange of prootic, 49) cavum epiptericum at least partially floored by prootic in adults (state 1), 80) upper tooth row closely approaches pterygoid transverse flange, 109) thoracic ribs without rhomboidal expansions of proximal shafts, and 111) short interclavicle.

Three multistate characters diagnose this group, but ambiguity exists in which of their various states is diagnostic. These are: 116) procoracoid excluded from the glenoid either narrowly (state 1, with state 2 diagnostic of Mammaliamorpha) or widely (state 2, in which case state 1 would be diagnostic of *Exaeretodon*); 128) ulnar olecranon forming a simple process (state 1, with state 2 diagnostic of Mammaliamorpha) or a tall process that grasps the humerus in a notch (state 2, in which case state 1 would be diagnostic of *Exaeretodon*); 130) iliac blade reduced, being either emarginated from above (state 1) or with a flat dorsal margin (state 2).

Two additional equivocal characters might be diagnostic but are subject to other, equally parsimonious interpretations: 13) horizontal ventral maxilla margin; and 42) internal carotid artery perforates basisphenoid. In both cases, the derived state could diagnose this taxon, being subsequently lost in tritylodontids, or it could have arisen independently in *Exaeretodon* and Mammaliaformes.

Mammaliamorpha, New Taxon

Mammaliamorpha is the sister taxon of *Exaeretodon*. It comprises the last common ancestor of Tritylodontidae and Mammalia, and all its descendants. Mammaliamorpha is diagnosed by 56 unequivocal synapomorphies and equivocally by six additional characters (i.e., branch length range = 56–62).

Unequivocal synapomorphies are: 2) premaxillary extranasal process contacts nasal to exclude maxilla from narial border, 4) prefrontal absent, 6) frontal with

an orbital process that meets the palatine, 7) postorbital absent, 19) quadrate–paroccipital process contact, 20) quadrate with dorsomedial flange and crus longus, 24) occipital condyles lie far posterior to the fenestra vestibuli, 31) palatine with dorsal orbital process, 34) pterygoids widely separated by highly vaulted choana, 35) lateral fossa on pterygoid, 37) epipterygoid quadrate ramus extends below the basioccipital, 38) quadrate rami of pterygoid and epipterygoid form lateral flange joining the posterolateral flange of the petrosal, 39) epipterygoid contacts ventral and posterior edge of frontal, 44) parasphenoid–pterygoids form three postchoanal parallel ridges separated by deep troughs, 45) basicranium with sigmoidal bend, 51) prootic and opisthotic fused in adults (=petrosal), 53) internal acoustic meatus walled medially, 55) paroccipital hyoid muscle pit, 56) paroccipital process bifurcate distally, 57) paroccipital process directed laterally (state 1), 58) solid mastoid process (state 1), 68) dentaries not fused in symphysis, 74) postdentary bones reduced to a thin rod lying deep within the Meckelian sulcus, 75) surangular does not participate in the craniomandibular joint, 76) articular with elongate retroarticular process, 81) three upper incisors, 86) postcanine teeth with well developed shear surfaces and consistent wear patterns, 88) postcanine tooth roots completely divided, 89) postcanine roots divided by transverse plane, 94) atlas neural arch foreshortened, 95) atlas postzygapophysis absent, 98) axis centrum depressed, 99) prominent dens, 100) neural canal diameter in cervical greater than in thoracic vertebrae, 102) posterior thoracic neural spines strongly inclined, 105) posterior caudal vertebrae elongated, 108) vertebral centra platycoelous, 112) sternum segmented (=sternebrae), 115) acromion process well developed (state 1), 119) glenoid open ventrally, 120) humeral head subspherical and slightly inflected (state 1) 124) epicondylar foramen not enclosed, 131) iliac blade triangular in cross-section, 132) posterior iliac spine reduced to a small nub, 133) acetabulum lies behind sacrum, 134) cotyloid notch directed dorsally, 137) pubis lies ventral and posterior to acetabulum, 138) ischiadic spine short and blunt, 139) obturator foramen diameter greater than acetabulum, 140) epipubic bones, 141) femoral head subspherical and slightly inflected dorsally (state 1), 143) greater trochanter separated from articular surface by a deep notch, 144) lesser trochanter forms tubercle on medial side of femoral shaft (state 1), 150) astragalar foramen and canal, 151) astragalus with distinct articular head for cuboid, and 152) tuber calcis square and protuberant (state 1).

One additional multistate character is diagnostic of Mammaliamorpha, but its diagnostic state is equivocal: 40) parasphenoid alae expanded and either ventrolaterally flared (state 1, in which case ontogenetic fusion to petrosal diagnoses Mammaliaformes), or fused to petrosal (state 2, with parasphenoid flared ventrolaterally diagnostic of Tritylodontidae).

Three characters might be diagnostic at this level, but given present data it is equally possible that they are diagnostic of node 1 (*Exaeretodon* + Mammaliamorpha). As described above, these are: 116) procoracoid widely excluded from glenoid (state 2), 128) tall olecranon that grasps humerus in notch (state 2), and 130) ilium with flat dorsal margin (state 2).

The Farris optimization option of PAUP also assigned to this node character 83) caniniform tooth with double roots. However, because it is scored as missing data (N) in tritylodontids, which lack a caniniform, it is here considered diagnostic of the less inclusive taxon Mammaliaformes (new taxon, see below), which is the minimum level at which its distribution can be confirmed empirically.

One other character was equivocally assigned to this level: 82) caniniform tooth absent. Its assignment to this level by PAUP is surely an artifact of having excluded incomplete fossil taxa. Many partially preserved Triassic and Jurassic taxa possess a caniniform tooth. Absence of a caniniform tooth is probably a state independently evolved in Tritylodontidae, Monotremata, and Multituberculata, although this convergence cannot be demonstrated by the matrix summarized here (see Data and Methods of Analysis).

Mammaliaformes, New Taxon

Mammaliaformes is the sister taxon of Tritylodontidae within Mammaliamorpha. It comprises the last common ancestor of Morganucodontidae and Mammalia and all its descendants. Mammaliaformes is diagnosed by 16 unequivocal synapomorphies, and up to nine equivocal characters (i.e., branch length range = 16–25 steps).

Unequivocal synapomorphies include: 10) parietal expanded over hindbrain (state 1 to 2), 16) zygoma slender along its entire length, 21) interparietal absent as separate adult element (but may be present in early ontogeny), 30) secondary palate extends to end of upper tooth row, 41) parasphenoid widely separates pterygoids, 46) basicranium between fenestrae vestibuli wider than choana, 49) cavum epiptericum completely floored in late ontogeny, 50) prootic canal, 52) petrosal promontorium, 60) fenestra rotundum separate from jugular foramen, 66) dentary with well-developed squamosal contact, 87) postcanine teeth differentiated into premolariforms and molariforms, 91) prismatic enamel, 103) one or more anticlinal lumbar neural spines, 104) lumbar centrum faces inclined, 125) humerus ulnar condyle as large as radial capitulum.

Three of the equivocal characters (92, 97, 155) are not actually preserved in Morganucodontidae and are here assigned to the less inclusive level of Mammalia, the minimum level at which their distributions can be confirmed by observation. Characters 13) horizontal ventral maxilla, and 42) internal carotid artery pierces basisphenoid, may have originated convergently at this level and in *Exaeretodon*, or they may have originated at Node I and reversed in Tritylodontidae (see Node I). Character 40) parasphenoid alae fusing in early ontogeony to the otic capsule (state 2), probably is diagnostic of Mammaliaformes because it appears functionally associated with the promontorium.

Nevertheless, given available data it might be diagnostic of Mammaliamorpha, with flared alae (state 1) diagnostic of Tritylodontidae. Three additional characters appear ambiguous on this matrix, but their ambiguity is probably an artifact of excluding deficient taxa and further complicated by the highly derived dentitions of Tritylodontidae, Monotremata, and Multituberculata. These are: 79) triangular mandibular movement during mastication, 83) caniniform tooth with double roots, and 84) unilateral postcanine occlusion.

Relationships within Mammalia

Before discussing the diagnosis of Mammalia, its ingroup relationships require brief clarification. Marsupialia and Placentalia have long been grouped together in Theria, which is defined here as comprising the most recent common ancestor of extant marsupials and placentals, and all taxa stemming therefrom. The monophyly of Theria is widely recognized and a large body of diverse character data support this view (e.g., Huxley, 1880; Gregory, 1910; Huber, 1930; Edgeworth, 1935; deBeer, 1937; Romer and Parsons, 1977; Clemens, 1979b; Marshall, 1979; Novacek and Wyss, 1986a; Rowe, 1986a). Analysis of the data in Appendix I identified 15 unequivocal synapomorphies and as many as seven additional ambiguous synapomorphies (see Appendix II). Because this relationship was not the principal focus of the present study, character data bearing on the diagnosis of Theria are not detailed here. It should be noted that several taxa traditionally placed in Theria (e.g., Kuehneotheriidae) are not therians (or even mammals) following this analysis.

The positon of Multituberculata has been controversial. Although there has been general agreement that multituberculates are mammals, there has been only great uncertainty on their relationships within Mammalia. For some time, Multituberculata was allied with Monotremata in 'Prototheria' (e.g., Hopson, 1970; Kermack and Kielan-Jaworowska, 1971; Kermack and Kermack, 1984). More recently, however, interpretation of the characters diagnosing the group has been questioned (e.g., Griffiths, 1978; Presley, 1981; Kemp, 1983; Clemens, 1986; Kielan-Jaworowska et al., 1986) and many workers have now rejected Prototheria, although the position of Multituberculata has remained uncertain. The present analysis supports the view that Prototheria is paraphyletic. Eighteen unequivocal synapomorphies were found that are shared by Multituberculata and Theria (Appendix II), and seven ambiguous characters might also be diagnostic at this level. The name Theriiformes has been proposed for the taxon defined by the last common ancestor of Multituberculata and Theria (Rowe, 1986a). The diagnosis of Theriiformes has been discussed in greater detail elsewhere (Rowe and Greenwald, 1987; MS).

Mammalia Linnaeus, 1758

In diagnosing Mammalia, PAUP recognized a branch-length range of 32–43 steps. Of the 11 characters PAUP treated in some way equivocal, five (92, 97, 153, 155, 158) can be resolved as mammalian synapomorphies based on additional data that are discussed below. Thirty-seven characters are therefore described here as diagnostic of Mammalia; ambiguity in the six remaining characters is then briefly described.

1) Premaxilla Internasal Process Absent—The internasal (=prenasal, ascending) process was present in Tetrapoda ancestrally, and although rarely preserved in fossils it is now known to persist in *Exaeretodon,* Tritylodontidae (Sues, 1986), and Morganucodontidae (Rowe, 1986a). The internasal process is absent in adult Monotremata, Multituberculata, and Theria, rendering the external nares confluent in postnatal ontogeny.

11) Squamosal Suspensorial Notches Absent—In Cynodontia ancestrally, two notches cut the ventral edge of the squamosal to receive processes from the quadrate and quadratojugal. The notches persist in *Exaeretodon,* Tritylodontidae, and Morganucodontidae. In adult Monotremata, Multituberculata, and Theria the suspensorial notches are absent.

18) Quadratojugal Absent—The quadratojugal was present in Tetrapoda ancestrally and persists in *Exaeretodon* and Tritylodontidae. It is not preserved in currently known specimens of Morganucodontidae, but its presence is indicated by a facet on the quadrate (Krusat, 1980; Kermack et al., 1981). In contrast, in Monotremata, Theria, and Multituberculata the quadratojugal ossification is absent, although a ligamentous remnant may persist (Presley, pers. comm.).

22) Tabular Absent—As in Tetrapoda ancestrally, a tabular is retained in *Exaeretodon,* Tritylodontidae, and Morganucodontidae. Although previously reported in multituberculates (Kielan-Jaworowska, 1971), it is now known that the bone in question is pneumatic and a part of the mastoid, and that the tabular is absent (Kielan-Jaworowska et al., 1986). It is also absent in Monotremata and Theria. A tabular has been reported in some therians (e.g., deBeer, 1937), but as the element in question is a cartilage bone derived from the tectum posterior, it is now generally agreed that it is not a true tabular (Presley, 1980), which in other tetrapods is a membrane bone.

25) Occipital Condyles Expanded—In Cynodontia ancestrally, the occipital condyle is a paired structure in which each exoccipital forms a distinct condyle that lies beside the lower third or quarter of the foramen magnum, protrudes behind it, and faces almost directly backwards. This condition persists with little modification in *Exaeretodon,* Tritylodontidae, and Morganucodontidae. However, in Monotremata, Multituberculata, and Theria the occipital condyles have expanded upwards and laterally, coming to lie far apart from one another, and to enclose the entire ventral two-thirds of the foramen magnum. As a result, the condyles together traverse a much wider arc of abduction, and the area of their articular surface is greatly increased over the condition in the outgroups.

26) Ethmoid and Maxillary Turbinals Ossified—In Amniota ancestrally there may have been a primary

concha projecting from the lateral wall of the nasal capsule into the cavum nasi proprium (Gauthier et al., 1988a), but it did not ossify to form sphenethmoid turbinals such as those that occur in Mammalia. One might debate the presence of cartilaginous turbinals in some nonmammalian members of Synapsida, but there is little doubt that ossified turbinals were absent in *Exaeretodon,* Tritylodontidae, and Morganucodontidae (Rowe, 1986a). Howeover, in Monotremata and Theria turbinals ossify to form bony extensions of the maxilla and sphenethmoid into the nasal cavity. Whether turbinals were present in Multituberculata is not known at present.

27) Internasal Septum Ossified—The internasal septum remained unossified in *Exaeretodon,* Tritylodontidae, and Morganucodontidae, as in Tetrapoda ancestrally. In Monotremata, Multituberculata (Kielan-Jaworowska et al., 1986), and Theria the internasal septum is ossified.

28) Cribriform Plate—In Amniota ancestrally, and in all nonmammalian synapids including *Exaeretodon,* Tritylodontidae, and Morganucodontidae, the floor of the braincase beneath the olfactory bulbs is not ossified. However, in Monotremata, Multituberculata (Kielan-Jaworowska et al., 1986), and Theria the ethmoid ossifies beneath the olfactory bulb to form the cribriform plate, which is perforated by the terminal branches of the olfactory nerve as they pass from the cranial cavity to the olfactory epithelium.

33) Pterygoid Transverse Process Vestigal—In Amniota ancestrally, the transverse process of the pterygoid (=lateral pterygoid flange) was massive and extended laterally to terminate very close against the coronoid bone on the inner surface of the mandible. Although the 'robustness' of the process became somewhat diminished within Cynodontia, a strong process persists in *Exaeretodon,* Tritylodontidae, and Morganucodontidae. In contrast, in Monotremata, Theria, and Multituberculata the transverse process is reduced to a vestigial structure, the hamulus pterygoidei (Sues, 1986). The pterygoids are also widely separated from the mandible and the pterygoideus musculature has come to lie between the two.

47) Hindbrain Overlies Fenestrae Vestibuli—The hindbrain is comparatively narrow and lies entirely between the fenestrae vestibuli in *Exaeretodon,* Tritylodontidae, and Morganucodontidae, as in Tetrapoda ancestrally. In Monotremata, Multituberculata, and Theria the hindbrain is greatly expanded and overlies the fenestrae vestibuli.

54) Tegmen Tympani—In Amniota ancestrally, and persisting in *Exaeretodon,* Tritylodontidae, and Morganucodontidae the tegmen tympani and an enclosed cavum supracochleare are absent. Instead, the petrosal (prootic + opisthotic) participated directly in the side wall of the braincase, separating the cranial cavity from the middle ear and the cavum supracochleare was continuous with the cavum epiptericum. However, in Monotremata, Multituberculata, and Theria the tegmen tympani forms a thin plate of bone that is spread over the cochlear capsule, forming a new side wall of the cranial cavity, and dividing the cavum epiptericum by enclosing the cavum supracochleare beneath it. The geniculate ganglion of the facial nerve is enclosed within the latter cavum. Within Mammalia the cavum supracochleare may gain communication with the tympanic cavity and tympanic antrum of the mastoid, in which case it is the tegmen tympani instead of the petrosal that separates the middle ear cavity from the cranial cavity.

57) Paroccipital Process Directed Ventrally—In Cynodontia ancestrally, the paroccipital process was an undivided structure that slopes ventrolaterally, a condition that persists in *Exaeretodon.* In Tritylodontidae and Morganucodontidae the distal end of the paroccipital process is divided to form separate quadrate and mastoid processes, and is oriented nearly horizontally (state 1). In contrast, in adult Monotremata, Multituberculata, and in Theria ancestrally, the bifurcate paroccipital process is directed ventrally in a near-vertical orientation (state 2). This analysis supports the view that the mammalian condition evolved from that represented in tritylodontids and morganucodontids (state 1).

58) Pneumatic Mastoid Process—In Amniota ancestrally, the paroccipital process is a densely ossified structure, a condition that persists in *Exaeretodon,* Tritylodontidae, and Morganucodontidae. However, only in Monotremata, Multituberculata (Kielan-Jaworowska et al., 1986), and Theria does it inflate ventrally and posteriorly to form a protuberant, pneumatic structure that contacts the ectotympanic.

61, 62) Stapes Small and Imperforate—The stapes underwent a number of transformations in synapsid history (Novacek and Wyss, 1986b). In *Exaeretodon,* Tritylodontidae, and Morganucodontidae it remained relatively large and is perforated by the stapedial foramen. In Monotremata, Multituberculata (Miao and Lillegraven, 1986), Marsupialia, and Placentalia ancestrally, the stapes is a minute bone that is not perforated in adults. A stapedial foramen persists through ontogeny in many adult therians (Novacek and Wyss, 1986b), but based on the distribution of the foramen outside of Theria, it is simplest to conclude that this is a reversal arising within therians. Despite the persistence of the foramen in these adults, the stapes remains a tiny bone, indicating that its size and perforation are not completely linked.

63) Styloid Process—In Amniota ancestrally, Reichert's cartilage is ossified to form the stylohyal (ceratohyal) which persisted as a separate element in the hyoid skeleton (deBeer, 1937; Romer, 1956). This condition occurs in extant nonmammalian tetrapods and persists in Tritylodontidae (Sues, 1986). The hyoid apparatus is only rarely preserved in fossils and has not been recovered in *Exaeretodon* or Morganucodontidae, but it is nevertheless clear that in these taxa the stylohyal remained a discrete element and was not fused to the skull. In contrast, in Monotremata, Multituberculata (Kielan-Jaworowska et al., 1986), and

Theria the stylohyal fuses early in ontogeny to the otic capsule, joining the rear part of the distal end of the paroccipital process, to form the styloid process.

64) Hyoid Arch-Petrosal Bridge—As described by Presley (1980), the hyoid arch remained a separate element in nonmammalian synapids, a condition that persisted in *Exaeretodon,* Tritylodontidae, and Morganucodontidae (see above). However, in embryos of monotremes and marsupials a dorsal process of the hyoid cartilage is incurved distal to its attachment to the crista parotica (i.e., the styloid attachment) and makes a second attachment to the petrosal, posteroventral to the fenestra vestibuli. In adult monotremes this bridge co-ossifies with the petrosal to form the anterior margin of the foramen stylomastoideum definitivum, whereas in marsupials ossification spreads into the ventral part of the bridge to form the processus tympanicum petrosi, a possible homolog of the placental caudal entotympanic. The bridge fails to contact the petrosal in most placentals. In Multituberculata, a small ridge of bone on the petrosal behind the fenestra vestibuli may be the adult derivative of the bridge (Kielan-Jaworowska, pers. comm.), but its fate remains uncertain in this extinct group because only relatively late adult stages can be observed.

65) Craniomandibular Joint Positioned Anterior to Fenestra Vestibuli—The craniomandibular joint is positioned near the rear of the skull, at the level of the fenestra vestibuli, in Cynodontia ancestrally, and persists in this position in *Exaeretodon,* Tritylodontidae, and Morganucodontidae. In contrast, in Tachyglossidae, Theria, and Multituberculata the craniomandibular joint lies well anterior to the fenestra vestibuli. In adult *Ornithorhynchus* the glenoid is elongated and lies lateral to the fenestra, and it has been contended that this is the ancestral state for Mammalia (Gregory, 1910; deBeer, 1937). However, Edgeworth (1935) described that the glenoid begins ontogeny anterior to the fenestra, in the position maintained throughout life in other mammals, and only later elongates in an ontogenetic transformation unique to *Ornithorhynchus.*

67) Craniomandibular Joint Formed Exclusively by Squamosal and Dentary—In Tetrapoda ancestrally, the quadrate and articular participated in the craniomandibular joint (CMJ), a condition persisting in *Exaeretodon,* Tritylodontidae, and Morganucodontidae. In *Exaeretodon,* Tritylodontidae, and other nonmammalian cynodonts (see Kemp, 1983; Hopson and Barghusen, 1986) the surangular maintains its primitive participation in the CMJ. In morganucodontids the dentary replaces the surangular in the CMJ, but the quadrate–articular joint persisted throughout ontogeny in all of these taxa. In contrast, in adult Monotremata, Multituberculata, and Theria the quadrate–articular articulation is no longer part of the adult CMJ, which is instead formed *exclusively* by the dentary and squamosal. Within Theria, additional bones such as the alisphenoid may also participate in the CMJ, but such conditions presumably were derived from the ancestral mammalian condition in which only the dentary and squamosal were involved.

69) Meckelian Sulcus Enclosed—The Meckelian sulcus is a prominent trough on the medial surface of the ramus and condylar process of the dentary that is present in a number of cynodonts, including *Exaeretodon,* Tritylodontidae, and Morganucodontidae. It holds the postdentary elements, which together form a thin bar that lies almost entirely within the sulcus. In Monotremata, Multituberculata, and Theria the postdentary bones are detached from the mandible, becoming suspended from the skull in adults, and the Meckelian sulcus is enclosed by the dentary, forming a posterior extension of the Meckelian canal.

72) Coronoid Bone Vestigial—In *Exaeretodon,* Tritylodontidae, and Morganucodontidae a large coronoid bone is present in the mandible. Although the coronoid is absent in extant monotremes and therians, N. Greenwald (pers. comm.) has pointed out what appears to be a vestigial remnant in the extinct ornithorhynchid *Obdurodon* (Archer et al., 1979). Similar remnants of the coronoid have been reported by Hahn (1977) in primitive multituberculates, and by Krebs (1971, 1987) in Dryolestida and 'pantotheres' (see Prothero, 1981, on the paraphyly of pantotheres). Members of the latter two taxa are assigned to Mammalia sedis mutabilis and Theriiformes sedis mutabilis, respectively (Fig. 4; Rowe, 1986a). It appears that the coronoid became greatly reduced in Mammalia ancestrally, and that its complete loss occurred independently at least three times, within monotremes, multituberculates, and the lineage that includes Theria.

73) Splenial Vestigial or Absent—The splenial is present in *Exaeretodon,* Tritylodontidae, and Morganucodontidae. It is absent in Monotremata, Multituberculata, and Theria, but a vestigial splenial has been identified in Dryolestida (Krebs, 1971). The splenial was unequivocally reduced in Mammalia ancestrally, but whether it was entirely absent cannot be determined unambiguously until the current assignment of Dryolestida to Mammalia sedis mutabilis is resolved.

77) Malleus (Articular), Os Goniale (Prearticular), Ossiculum Accessorium Mallei (Surangular), and Ectotympanic (Angular) Suspended from Skull—In Tetrapoda ancestrally, and persisting in *Exaeretodon,* Tritylodontidae, and Morganucodontidae, the stapes and quadrate were suspended from the skull, but the articular, prearticular, surangular, and angular were attached throughout ontogeny to the mandible. In contrast, in Monotremata, Theria, and Multituberculata (Miao and Lillegraven, 1986) all of these bones are suspended from the cranium. Their migration from the mandible to suspension beneath the cranium is well known in mammalian ontogeny (e.g., deBeer, 1937). It has often been contended that this evolved convergently in monotremes, therians, and possibly in some extinct mammals such as Multituberculata, and that it should not, therefore, be properly regarded as a synapomorphy of Mammalia as defined in this study.

However, the assertions of convergence are based on the now falsified hypothesis that Morganucodontidae is a member of the paraphyletic taxon Prototheria and that Kuehneotheriidae is a member of Theria (Kemp, 1983). When all of the data pertaining to mammalian phylogeny are considered, it is simplest to view suspension of the postdentary bones as a homologous transformation in Monotremata, Multituberculata, and Theria, and that it is properly a synapomorphy of Mammalia.

78) Ectotympanic Horizontal and Suspended from Cranium—The reflected lamina of the angular is attached to the mandible and defines a more or less vertical plane in *Exaeretodon,* Tritylodontidae, and Morganucodontidae. In Mammalia it becomes suspended from the cranium and is renamed the ectotympanic (see Character 77). In Monotremata and Multituberculata (Miao and Lillegraven, 1986) the ectotympanic is roughly horizontal throughout adult ontogeny (state 1), whereas in marsupials and therians it begins ontogeny horizontally but then rotates to varying degrees to secondarily achieve a roughly vertical orientation (state 2; deBeer, 1937). Hence, horizontal orientation of the ectotympanic is ancestral for Mammalia.

92) Proatlas Ossification Absent—In Tetrapoda ancestrally, the two halves of the proatlas arch ossified as separate structures. The proatlas ossification persists in *Exaeretodon* and Tritylodontidae. This region of the neck is unknown in Morganucodontidae and Multituberculata. In adult Monotremata and Theria the proatlas arch is absent as a separate structure, although embryonic rudiments remain recognizable (Jenkins, 1969, 1971; Presley, 1980). Loss of the proatlas arch might diagnose Mammaliaformes, but pending further knowledge of Morganucodontidae it is provisionally assigned to Mammalia, the minimum level at which observation confirms it as diagnostic.

93) Atlas Intercentrum and Neural Arches Fused—In Tetrapoda ancestrally, the right and left atlas arches and intercentrum remained separate throughout ontogeny, as they do in *Exaeretodon,* Tritylodontidae, and Morganucodontidae. The atlas of Multituberculata is not known. In Monotremata and Theria the atlas neural arches fuse together dorsally, and their pedicles fuse to the atlas intercentrum ventrally to create a single osseous atlantal ring.

96) Atlas Rib Absent—In Amniota ancestrally, a separate atlantal rib articulated in a synovial joint with the atlas intercentrum and neural arch. The atlas rib persists in *Exaeretodon,* Tritylodontidae, and Morganucodontidae. Multituberculata is not known in this respect. In Monotremata and Theria the atlas rib does not differentiate, and although its rudiment continues to project laterally from the atlas, there is no joint or movable articulation.

97) Axis Prezygapophysis Absent—A prezygapophysis is present on the axis neural arch in Amniota ancestrally and it persists in *Exaeretodon* and Tritylodontidae. This region is unknown in Morganucodontidae. In Monotremata, Multituberculata (Kielan-Jaworowska, pers. comm.), and Theria the axial prezygapophysis is absent. Although possibly diagnostic of Mammaliaformes, pending further knowledge of Morganucodontidae, this character is provisionally assigned to Mammalia.

101) Postaxial Cervical Ribs Fused to Vertebrae—In Tetrapoda ancestrally, all of the presacral ribs articulated in movable (presumably synovial) joints with their corresponding vertebrae. The cervical ribs remain movable in *Exaeretodon,* Tritylodontidae, and Morganucodontidae. In contrast, in Monotremata, Multituberculata (Kielan-Jaworowska, pers. comm.), and Theria both the capitulum and tuberculum of the cervical ribs are fused with their corresponding vertebrae, enclosing the foramina transversaria in a solid bony ring.

129, 147, 148) Styloid Processes on Distal Ends of Radius, Tibia, and Fibula—The styloid processes are absent from nonmammalian synapsids, including *Exaeretodon,* Tritylodontidae, and Morganucodontidae, in which the ends of these bones are uniformly convex. However, in Monotremata, Multituberculata, and Theria ancestrally, each of these bones has a prominent finger-like projection, the styloid process. It is likely that development of syloid processes on the radius, tibia, and fibula is a manifestation of a single developmental process that is associated with secondary ossifications, because all of these features appear at the same level. But because there are no experimental data to support such a contention, and the developmental processes behind secondary ossifications are not yet understood, I tentatively score the styloid process as a separate character for each bone.

145) Patella and Patellar Facet on Femur—The patella and its facet on the distal end of the femur were absent in Tetrapoda ancestrally, as is the case in *Exaeretodon,* Tritylodontidae, and Morganucodontidae. In contrast, in Monotremata, Multituberculata, and Theria, the patella forms a sesamoid within the tendon of insertion of the M. quadriceps femoris, and a prominent patellar facet occurs on the femur.

153) Entocuneiform-Hallucial Articulation Saddle-shaped (state 1 or 2)—In nonmammalian synapsids, the articulation between the entocuneiform and metatarsal I is hemicylindrical, largely constraining metatarsal excursion about a horizontal axis, as is the case in metatarsals II–IV and between phalanges. Tritylodontidae is not known in this respect, but the primitive entocuneiform–metatarsal articulation can be observed in *Exaeretodon* and *Megazostrodon.* In contrast, this articulation is saddle-shaped, permitting excursion about vertical and horizontal axes in Monotremata, Multituberculata, and Theria ancestrally. In the latter two taxa, this feature is much more prominently developed than in monotremes, permitting a comparatively wider range of hallucial abduction–adduction (state 2) than in Monotremata (state 1). With such a

distribution, PAUP treated this character as equivocal. It is equally parsimonious to conclude that the primitive state was present in Mammalia ancestrally, or that state 1 was present and transitional to state 2, or that state 2 was present with state 1 diagnosing Monotremata. However, insofar as some degree of offset articulation is present in both monotremes and theriiforms, I regard this character as diagnostic of Mammalia, although which of its derived states is diagnostic remains equivocal.

155) Sclerotic Ossicles Absent—Sclerotic ossicles were present in Tetrapoda ancestrally, and although very delicate, they have been preserved in a number of fossil synapsids including Tritylodontidae (Rowe, 1986a). They are not preserved in currently known specimens of *Exaeretodon,* Morganucodontidae, or Multituberculata, but they are unequivocally absent in Monotremata and Theria. Although possibly diagnostic of Mammaliaformes, pending further fossil discoveries I regard loss of the sclerotic ossicles as diagnostic of Mammalia, the minimum level at which observation confirms it as diagnostic.

156) Secondary Ossifications on Long Bones and Girdles—Secondary ossifications were absent in Tetrapoda ancestrally, as is the case in *Exaeretodon,* Tritylodontidae, and Morganucodontidae. In Monotremata, Multituberculata, and Theria secondary ossifications can be observed in subadults on the ends of the long bones and on the dorsal edges of the ilium and scapula. Within Theria, secondary ossifications are present on many other bones as well, including the vertebral centra, metapodials, and phalanges.

158) Flexor Sesamoids (state 1 or 2)—Flexor sesamoids, which lie in the tendons of insertion of the manual and pedal flexor musculature, are absent in Tetrapoda ancestrally, as is the case in *Exaeretodon* and Morganucodontidae. Tritylodontidae is not known in this respect. These are delicate structures and one might argue that absence is indistinguishable from nonpreservation. However, they are preserved in small multituberculate specimens (e.g., pes of *Kryptobaatar dashzevegi;* Kielan-Jaworowska, pers. comm.) and in numerous therian fossils. They are also present in extant monotremes and therians. Well preserved, articulated hands and feet are known for *Exaeretodon* (Bonaparte, 1963), an articulated pes is known for the morganucodontid *Megazostrodon rudnerae* (Jenkins and Parrington, 1976), and well-preserved hands and feet are preserved in a number of nonmammalian cynodonts; none preserve sesamoids. Flexor sesamoids are treated here as diagnostic of Mammalia. Single sesamoids are present in Monotremata, whereas paired sesamoids are present in multituberculates and therians; it is unclear whether single or paired sesamoids were present in Mammalia ancestrally.

Six additional characters (17, 82, 135, 146, 149, 152) were identified by PAUP as potential synapomorphies of Mammalia, but with equally parsimonious explanations also available. Two of these, 149) tibio–astragalar joint formed between two condyles and two sulci, and 152) elongate, square tuber calcis (state 2), were assigned as potential mammalian synapomorphies by Farris optimization. However, because they are scored as missing data (N) in Monotremata, I treat them as apomorphic of Theriiformes, the minimal level at which observation confirms their distribution. In a similar way, the laterally directed external auditory meatus (17) is scored as missing data (N) for Monotremata and Multituberculata, and I prefer to assign it to Theria, the minimum level at which its distribution can be confirmed. The parafibular flabellum (146) might have evolved in Mammalia ancestrally and subsequently been lost in Theria, or it may have evolved independently in monotremes and multituberculates. Closure of the acetabular cotyloid notch (135), might also diagnose Mammalia and have reversed in Multituberculata, but under this hypothesis it is equally parsimonious to hypothesize that closure evolved independently in monotremes and therians.

The potential assignment of the remaining equivocal character, loss of the caniniform tooth (82), to Mammalia is almost certainly an artifact of excluding deficient fossil taxa. A caniniform tooth is widely distributed in Synapsida, including most therian groups and many fossil mammaliamorph taxa not considered in this report. It seems more likely that caniniform loss occurred convergently in Tritylodontidae, Monotremata, and Multituberculata, than in Mammalia ancestrally with the caniniform reappearing within the group numerous times. However, until the deficient taxa can be scored and brought into this more general framework, some ambiguity will continue to surround interpretation of this character.

ORIGIN OF MAMMALIA

Under a definition based on common ancestry, the membership of Mammalia is somewhat different than has been recognized by most recent students of mammalian history. Morganucodontidae, Kuehneotheriidae, *Dinnetherium, Sinoconodon,* Haramiyidae, and a number of other extinct taxa commonly viewed as the earliest mammals can no longer be considered mammals in a strict sense. This is not to say that their significance is in any way diminished, only that they are informative at a more general level than previously understood.

Morganucodontidae and Kuehneotheriidae were previously viewed as the earliest representatives of the lineages including extant Monotremata and Theria, respectively (e.g., Hopson and Crompton, 1969; Fraser et al., 1985). As such, their first appearance (Norian, Late Triassic) was properly taken as the minimum age of Mammalia. However, it is now evident that while these fossils document that the mammalian lineage had diverged from other known synapsid lineages by the Norian, their appearance predates the minimum age, of Mammalia itself. The oldest fossil preserving char-

acters derived within Mammalia is *Phascolotherium bucklandi,* from the Bathonian (Middle Jurassic; Clemens et al., 1979) Stonesfield Slate of England.[1] It shares two derived characters with Multituberculata and Theria ancestrally: loss of the angular process of the dentary (70) and an incipient pterygoideus shelf ("inflected angle") developed on the medial surface of the dentary below the entrance to the Meckelian canal (71). The angle is present in the outgroups of Mammalia considered above and in Monotremata ancestrally.[2] The pterygoideus shelf is absent in Monotremata and the outgroups of Mammalia, and although developed more strongly in multituberculates and therians ancestrally, it is here viewed homologous with the structure preserved in *Phascolotherium.*

These characters are our earliest evidence of Mammalia, tenuous though they may seem. A far more extensive assemblage of characters derived within Mammalia can be observed in a diversity of Late Jurassic fossils. No character data were found that support the conventional view, that monotremes and therians diverged from their common ancestor in the Triassic. Mammalia may be as much as 40 million years younger than previously estimated. Consequently, natural historians interested in rate-related properties for Mammalia as a whole must revise by 18% all rate estimates developed under the conventional view. This also alters the context in which the origin of Mammalia and divergence of monotremes and therians are thought to have occurred. Under the conventional view, these events would be studied in the setting of Pangaea, during a time of relative crustal stability, whereas it now appears that they occurred during a period of intense global tectonic activity.

[1]Two other taxa from Stonesfield, *Amphilestes broderipii* and *Amphitherium prevostii,* require comment. Both are known only from isolated teeth and dentaries. The dentaries preserve the enclosed Meckelian canal (Character 69), a mammalian synapomorphy. On this basis they may be assigned to Mammalia sedis mutabilis, but because they preserve no characters currently recognized as derived within Mammalia, they offer little help in estimating its age.

[2]The angular process has a complex history, evidently being lost and reppearing a number of times within Mammalia. Monotremata is difficult to assess because the dentaries of the echidna and platypus are uniquely modified. However, what appears to be a small angular process is present in the adult echidna, and on this basis I consider the angle to have been present in Monotremata ancestrally. Although labeled a 'pseudangular' process in *Dinnetherium* (Jenkins et al., 1983), I agree with Sues (1986) in recognizing the structure in question as the true angle. The angular process is reportedly absent in an edentulous dentary attributed to *Kuehneotherium* (e.g., Prothero, 1981). Even granting this identification, in light of the data summarized above, loss of the angle is most parsimoniously interpreted as having occurred convergently in *Kuehneotherium.* Loss of the angle in *Phascolotherium* is considered to reflect recent common ancestry with Multituberculata and Theria.

This diagnosis has associated a large assemblage of characters with the origin of Mammalia, most of which are new in this context. On cursory inspection, however, many appear related to familiar explanations. For example, it has long been thought that the origin of mammals involved remodeling of the accoustic and masticatory systems (e.g., Allin, 1975; Crompton and Parker, 1978), modification of the nasopharynx (e.g., Bennett and Ruben, 1986), and increase in stability and mobility of the craniovertebral joint (e.g., Jenkins, 1969, 1971). Most of the diagnostic characters might be intuitively grouped under one or more of these headings (see below). This suggests that the number of characters listed independently above might eventually be reduced as constraining functional or developmental relationships among them are demonstrated. But until a relationship is indeed established, it is best to list the characters separately, to make clear the pattern of stucture to be illuminated by such explanations. Moreover, these characters vary independently within Mammalia, as other studies have shown. The new data offer means of testing and potentially enriching conventional understanding of the evolution of these functional complexes.

Associated with the ear are: loss of the squamosal suspensorial notches (11), loss of the quadratojugal (18), expansion of the hindbrain over the fenestrae vestibuli (47), the tegmen tympani and its enclosure of the cavum supracochleare (54), ventral orientation of the paroccipital process (57), the pneumatic mastoid process (58), reduction of the stapes (61), loss of the stapedial foramen (62), attachment of the styloid process to the cranium (63), the hyoid arch–petrosal bridge (64), the craniomandibular joint positioned anterior to the fenestra vestibuli (65) and formed exclusively by the dentary and squamosal in adults (67), suspension of the middle ear ossicles from the skull (77), and the horizontal ectotympanic (78).

Characters localized to the nasopharynx, evidently associated primarily with respiration and perhaps also with metabolic levels and olfaction, include loss of the internasal process of the premaxilla (1), ossification of the maxillary and ethmoid turbinals (26), the ossified internasal septum (27), and the ossified cribriform plate (28).

Characters associated with the masticatory system include loss of the squamosal suspensorial notches (11) and quadratojugal (18), reduced pterygoid transverse processes (33), the styloid process (63), the position (65) and composition (67) of the craniomandibular joint, enclosure of the Meckelian sulcus (69), reduction or loss of the coronoid bone (72) and splenial (73), and suspension of the middle ear ossicles from the cranium (77). As has long been recognized, some of these are also associated with the ear.

Associated with the craniovertebral joint are expanded occipital condyles (25), loss of the proatlas ossification (92), fusion of the atlas intercentrum and arches (93), loss of the atlas rib (96), loss of the axis

prezygapophysis (97), fusion of the postaxial cervical ribs to their vertebrae (101), and possibly also loss of the tabular (22), and ventral orientation of the paroccipital process (57).

This diagnosis identified a number of additional characters that appeared in the ancestor of Mammalia, but which are not obviously associated with the more familiar explanations. These include the styloid processes of the radius (129), tibia (147), and fibula (148); the presence of the patella (145), the modified entocuneiform–hallucial articulation (153), loss of the sclerotic ossicles (155), the presence of secondary ossifications (156), and the presence of flexor sesamoids (158). It would appear that further factors must be sought if our explanations and understanding of the origin of Mammalia are to be complete.

CONCLUSIONS

The boundary between Mammalia and its closest extinct relatives is quite distinct. Previous obscurity of this boundary appears in large degree a result of confusing taxon definition with diagnosis, and preserving such pre-evolutionary typological methods as defining taxa on the basis of 'essential' characters. It should come as little surprise that such methods, which predate the theory of evolution by centuries (e.g., Stevens, 1984), fail to yield a clear understanding of mammalian phylogeny. A definition of Mammalia based on ancestry describes its most fundamental evolutionary property and unequivocally sets Mammalia apart from all other taxa, whether extant or extinct. The improved resolution afforded by such a definition has provided means of corroborating and enriching many long-held views of the origin of mammals. However, it has also suggested significant revision in traditional measurements of such evolutionary properties of Mammalia as its diagnosis, membership, distribution in time and space, and others.

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APPENDIX I

The hypothesis of relationship discussed above (Fig. 3) is based on this summary of 176 transformations distributed among 158 characters for the eight principal taxa that were the subject of this analysis. The ancestral state for each character is scored 0, bsaed on outgroup comparison among the taxa depicted in Figure 2. Derived states are scored 1 and 2. The asterisk denotes multistate characters, which were all entered as unordered data. The distribution of these characters among the eight terminal taxa were entered into PAUP (Swofford, 1984) and subjected to the Branch and Bound algorithm. The outcome of this analysis is described in the text and summarized in Appendix II. The matrix of character states scored for each taxon that was entered into PAUP is presented in Appendix III (see Data and Methods of Analysis).

Cranium

1) *Premaxilla*—With (0) or without (1) internasal (=ascending, prenasal) process in postnatal ontogeny.
2) *Premaxilla*—Extranasal process separate from (0) or meeting (1) nasal to exclude maxilla from nares.
3) *Septomaxilla*—Present (0) or absent (1).
4) *Prefrontal*—Present (0) or absent (1).
5) *Frontal*—Frontals over forebrain narrow (0) or widely expanded to broadly separate orbits (1).
6) *Frontal*—Confined to skull roof with flat ventral surface (0) or with a process that meets the ascending process of the palatine in the medial orbital wall (1).
7) *Postorbital*—Present (0) or absent (1).
8) *Pineal foramen*—Present (0) or absent (1).
9) *Parietals*—Separate (0) or fused (1) in adults.
*10) *Parietal*—Largely confined to intertemporal girder (0), expanded onto occipital face (1), or bowed outwards to laterally displace the temporal fenestra (2).
11) *Squamosal*—Quadrate and quadratojugal notches on base of squamosal descending flange present (0) or absent (1) in adults.
12) *Squamosal*—Cranial moiety confined to zygomatic root (0) or contributing broadly to the cranial wall (1).
13) *Maxilla*—Ventral margin bowed ventrally (0) or horizontal (1).
14) *Maxilla*—Orbit open ventrally (0) or floored by maxilla (1).
15) *Maxilla*—Excluded from (0) or participates in (1) border of subtemporal fenestra.
16) *Zygomatic arch*—Robust (0) or slender (1).
17) *External auditory meatus*—On posterior (0) or ventrolateral (1) surface of zygoma.
18) *Quadratojugal*—Present (0) or absent (1).
19) *Quadrate-paroccipital contact*—Absent (0) or present (1).
20) *Quadrate*—Dorsomedial flange and crus longus absent (0) or present (1).
21) *Interparietal* (=postparietal)—Present (0) or absent (1) as discrete adult element (may be present embryonically in either state).
22) *Tabular*—Present (0) or absent (1).

23) *Posttemporal fenestra*—Present (0) or absent (1) in adults.
24) *Occipital condyles*—Positioned level with (0) or far posterior (1) to rear border of fenestra vestibuli.
25) *Occipital condyles*—Enclose ventral one-third (0) or two-thirds (1) of foramen magnum.
26) *Ethmoid and maxillary turbinals*—Unossified (0) or ossified (1).
27) *Internasal septum*—Unossified (0) or ossified (1).
28) *Cribriform plate*—Absent (0) or present (1).
29) *Pneumatic sinuses*—Absent (0) or present (1) in the frontal, ethmoid, and sphenoid.
*30) *Osseous secondary palate*—Ends anterior to (0), level with (1), or posterior to (2) posterior end of upper tooth row.
31) *Palatine*—Orbital process absent (0) or present (1) and contributing to median orbital wall.
32) *Ectopterygoid*—Separate (0) or absent (1) as separate adult element.
33) *Pterygoid transverse flange*—Well developed (0) or vestigial (=pterygoid hamulus) (1).
34) *Choanal vault*—Shallow with closely positioned pterygoids (0) or highly vaulted and pterygoids widely separated (1).
35) *Pterygoid*—Convex (0) or excavated by fossa (1) behind transverse process.
36) *Prootic anterior lamina*—Present (0) or absent (1).
37) *Epipterygoid quadrate ramus*—Level with basioccipital (0) or expanded ventrally below basioccipital (1).
38) *Epipterygoid and pterygoid quadrate rami*—Directed posteriorly (0) or forming lateral flange (1) that joins prootic posterolateral flange.
39) *Frontal–epipterygoid contact*—Epipterygoid contacts frontal ventrally (0) or ventrally and posteriorly (1).
*40) *Parasphenoid alae*—Small (0), widely flared ventrolaterally (1), or fused to auditory capsule (2).
41) *Parabasisphenoid*—Narrow (0) or laterally expanded (1) to widely separate pterygoids.
42) *Internal carotid artery*—Enters cavum cranii through cavum epiptericum (0) or perforates basisphenoid (1).
43) *Pila antotica*—Ossified (0) or not (1).
44) *Basicranium*—Ventral ridge system absent (0) or median parabasisphenoid ridge separated by shallow troughs from closely appressed parasagittal pterygoid ridges (1).
45) *Basicranium*—Ventral basicranial surface flat (0) or with sigmoidal bend (1).
46) *Basicranium*—Basicranium between fenestrae vestibuli narrower (0) or wider than (1) choana.
47) *Hindbrain*—Lies entirely between (0) or expanded laterally to overlie (1) fenestrae vestibuli.
48) *Prootic posterolateral flange*—Absent (0) or present (1).
*49) *Cavum epiptericum*—Open ventrally below exit of facial nerve (0) or enclosed ventrally by a partial (1) or complete (2) prootic floor in late ontogeny.
50) *Prootic canal*—Absent (0) or present (1).
51) *Prootic and opisthotic*—Separate (0) or fused at early ontogenetic stage (1) to form petrosal (=periotic).
52) *Petrosal promontorium*—Absent (0) or present (1).
53) *Internal auditory meatus*—Open (0) or walled (1).
54) *Tegmen tympani*—Absent (0) or present (1).
55) *Paroccipital process "hyoid muscle" pit*—Absent (0) or present (1).
56) *Paroccipital process*—Undivided (0) or bifurcated (1) distally to form separate mastoid and quadrate processes.
*57) *Paroccipital process*—Directed ventrolaterally (0), laterally (1), or sharply downturned (2).
*58) *Mastoid process*—Absent (0), densely ossified (1), or pneumatic (2).
*59) *Cochlea*—Short and uncoiled (0), elongate and partly (less than 360°) coiled (1), or elongate and coiled at least 360° (2).
60) *Fenestra rotundum*—Confluent with (0) or separated from jugular foraman (1).
61) *Stapes*—Large (0) or very small (1) relative to skull length.
62) *Stapes*—Perforated by stapedial foramen (0) or imperforate (1) in adults.
63) *Stylohyal*—Separate (0) or attached (1) to cranium in adults.
64) *Hyoid–petrosal bridge*—Absent (0) or present (1).
65) *Craniomandibular joint*—Positioned level with (0) or anterior to (1) fenestra vestibuli.
66) *Dentary*—Does not contact squamosal (0) or has well developed squamosal contact (1).
67) *Craniomandibular joint*—Quadrate and articular participate in joint (0), or joint formed exclusively by dentary and squamosal (1) in adult.
68) *Dentaries*—United in fused symphysis (0) or unfused (1).
69) *Dentary*—Meckelian sulcus forms medial groove (0) or enclosed canal (1) in adults.
70) *Dentary*—Angular process present (0) or absent (1).
71) *Dentary*—Pterygoideus shelf absent (0) or present (1).
72) *Coronoid*—Large (0) or vestigial to absent (1).
73) *Splenial*—Large (0) or vestigial to absent (1).
74) *Postdentary bones*—Broadly exposed behind dentary (0) or reduced to narrow rod lying in Meckelian sulcus (1).
75) *Surangular*—Participates (0) or does not participate (1) in craniomandibular joint.
76) *Articular*—Retroarticular process short (0) or elongate (1) (=manubrium mallei).
77) *Articular (malleus), prearticular (os goniale), surangular (ossiculum accessorium mallei), angular (ectotympanic)*—Attached to mandible (0) or suspended from cranium (1) in adults.
*78) *Ectotympanic*—Oriented horizontally (0), inclined throughout ontogeny (1), or horizontal in early and vertical in late ontogeny (2).
79) *Mandible*—Based on wear facets, mandibular movement during mastication predominantly orthal (0) or with medial component (1).

Dentition

80) *Upper tooth row*—Widely separated from (0) or nearly reaching (1) level of front of pterygoid transverse flange.
81) *Upper incisors*—Four or more upper incisors (0) or three upper incisors (1) present.
82) *Caniniform*—Caniniform maxillary tooth present (0) or absent (1).
83) *Caniniform*—Single (0) or double (1) roots.
84) *Postcanines*—Bilateral (0) or unilateral (1) postcanine occlusion in adults.
85) *Upper postcanine teeth*—External cingulum absent (0) or present (1).
86) *Postcanine teeth*—With irregular occlusal pattern (0)

or with well-developed shear surfaces and consistent wear pattern (1).

87) *Postcanine teeth*—Homodont (0) or differentiated (1) into premolariforms and molariforms.
88) *Postcanine tooth roots*—Undivided (0) or completely divided (1) roots.
89) *Postcanine tooth roots*—Plane of root division (or incipient division) anteroposterior (0) or transverse (1).
90) *Molariform teeth*—Principle cusps oriented in row(s) (0) or in reverse triangle pattern (1).
91) *Enamel*—Nonprismatic (0) or prismatic (1).

Axial Skeleton

92) *Proatlas neural arch*—Present (0) or absent (1).
93) *Atlas neural arches and intercentrum*—Separate (0) or fused (1) to form ring-like structure.
94) *Atlas neural arch*—Elongate (0) or shortened (1) anteroposteriorly.
95) *Atlas postzygapophysis*—Present (0) or absent (1).
96) *Atlas rib*—Present (0) or absent (1).
97) *Axis*—Prezygapophysis present (0) or absent (1).
98) *Axis*—Centrum cylindrical (0) or depressed (1).
99) *Dens* (=odontoid process)—Absent or vestigal (0) or strongly developed (1).
100) *Cervical neural canals*—Diameter equal to (0) or much greater than (1) in thoracic vertebrae.
101) *Postaxial cervical ribs*—Separate (0) or fused (1) to vertebrate.
102) *Posterior thoracic vertebrae*—Neural spines vertical (0) or strongly inclined (1).
103) *Lumbar neural spines*—All vertical (0) or one or more anticlinal (1).
104) *Lumbar intervertebral articulations*—Centrum articular facets perpendicular to notochordal axis (0) or inclined (1).
105) *Posterior caudal vertebrae*—Undifferentiated (0) or differentiated (1) with elongate distal centra bearing reduced neural and haemal arches.
106) *Tail*—Shorter (0) or longer (1) than presacral vertebral column.
107) *Vertebral anapophyses*—Absent (0) or present (1).
108) *Vertebral centra*—Shallowly amphicoelous (0) or platycoelous (1).
109) *Thoracic ribs*—Proximal shafts with (0) or without (1) rhomboidal proximal expansions.

Pectoral Girdle and Forelimb

110) *Interclavicle*—Present (0) or absent (1).
111) *Interclavicle*—Elongate anteroposteriorly (0) or shortened (1) such that it is roughly as long as wide.
112) *Sternum*—Unsegmented (0) or segmented (1) to form sternebrae.
113) *Clavicle*—Articulates with interclavicle (0) or manubrium sternae (1).
114) *Supraspinous fossa*—Absent (0) or present (1).
*115) *Acromion process*—Weakly developed and oriented anteriorly (0); strongly developed, everted laterally, and inclined downwards to level of glenoid (1); or strongly inflected, points posteriorly, and extends far ventral to roof of glenoid (2).
*116) *Procoracoid*—Participates in (0), is narrowly excluded (1), or is widely excluded from glenoid (2).
117) *Procoracoid*—Large and in contact wih sternum (0) or reduced to a tiny splint that does not contact sternum (1) in adults.
118) *Coracoid*—Large and in contact with sternum (0) or reduced to a tiny bone lying at front of glenoid that does not contact sternum (1) in adults.
119) *Glenoid*—Deep crescent-shaped notch with posteriorly directed scapular facet (0) or broadly open with scapular facet directed ventrolaterally (1).
*120) *Humeral head*—Slightly expanded (0), sub-spherical and somehwat inflected dorsally (1), or spherical and strongly inflected dorsally (2).
121) *Humerus*—Greater and lesser tubercles form pronounced crests (0) or low ridges (1).
122) *Humerus*—Spinatus muscle insertions undifferentiated (0) or separate infraspinatus and supraspinatus insertions on humeral lesser tubercle (1).
123) *Humerus*—Bicipital groove absent (0) or present (1).
124) *Humerus*—Ectepicondylar foramen present (0) or absent (1) in adults.
125) *Humerus*—Ulnar condyle smaller than (0) or approximately as large as (1) radial capitulum.
126) *Humerus*—Ulnar condyle bulbous (0) or forming trochlea (1).
127) *Humerus*—Entepi- and ectepicondyles robust (0) or weakly developed (1).
*128) *Ulna*—Olecranon process absent (0) or forming simple process (1) or extending well above articular surface and grasping humerus in notch (2).
129) *Radius*—Styloid process absent (0) or present (1).

Pelvic Girdle and Hind Limb

*130) *Ilium*—High, arched (convex upward) dorsal margin above acetabulum (0); emarginated (concave upward) dorsal margin (1); or low, flat dorsal margin (2).
131) *Ilium*—Lateral surface flat (0) or divided into dorsal and ventral moieties by longitudinal ridge (1) giving it triangular shape in coronal section.
132) *Ilium*—Posterior iliac spine robust and extends beyond acetabulum (0) or reduced to small nub that lies entirely anterior to acetabulum (1).
133) *Acetabulum*—Lies beneath (0) or behind (1) sacrum.
134) *Acetabulum*—Cotyloid notch directed posteriorly (0) or dorsally (1).
135) *Acetabulum*—Cotyloid notch open (0) or closed (1).
136) *Acetabulum*—Articular surface smoothly hemispherical (0) or forming an inverted U (1).
137) *Pubis*—Extends anterior to (0) or lies entirely ventral and posterior to acetabulum (1).
138) *Ischium*—Posterior spine elongate (0) or short and blunt (1).
139) *Obturator foramen*—Diameter less than (0) or greater than (1) that of acetabulum.
140) *Epipubic bones*—Absent (0) or present (1).
141) *Femur*—Head rounded and predominantly in plane of shaft (0), subspherical and inflected dorsally (1), or spherical and inflected medially (2).
142) *Femur*—Head confluent with shaft (0) or set apart on constricted neck (1).
143) *Femur*—Greater trochanter confluent with femoral head (0) or separated from articular surface by deep incisure (1).
*144) *Femur*—Lesser trochanter forms low ridge on ventral surface of shaft (0), pronounced tubercle on medial

edge of shaft (1), or pronounced tubercle on ventral surface of shaft (2).

145) *Patella and patellar facet of femur*—Absent (0) or present (1).

146) *Fibula*—Parafibular flabellum absent (0) or present (1).

147) *Fibula*—Styloid process absent (0) or present (1).

148) *Tibia*—Styloid process absent (0) or present (1).

149) *Tibio–astragalar joint*—Simple (0) or formed by two asymmetrical condyles on tibia that articulate with two sulci on astragalus (1).

150) *Astragalus*—Sulcus between calcaneal facets open (0) or enclosed posteriorly to form astragalar canal and foramen (1).

151) *Calcaneum*—Distinct facet for articulation with cuboid absent (0) or present (1).

*152) *Tuber calcis*—Short, pointed tubercle (0); short, square tubercle (1); or square tubercle longer than wide (2).

*153) *Entocuneiform* (=distal tarsal I)—Distal end with hemicylindrical (0), or mildly (1) or strongly (2) saddle-shaped distal facet for articulation with metatarsal I.

154) *Metatarsal V*—Proximal tuberosity (=styloid process) absent (0) or present (1).

Miscellaneous Characters

155) *Sclerotic ossicles*—Present (0) or absent (1).

156) *Secondary ossifications*—Absent (0) or present (1) on long bones and girdles.

157) *Secondary ossifications*—Absent (0) or present (1) on thoracic vertebral centra.

*158) *Sesamoids*—Manual and pedal flexor sesamoids absent (0), present and unpaired (1), or paired (2).

APPENDIX II

The distributions of characters listed in Appendix I for the nodes and terminal taxa in Figure 3 are summarized below. Synapomorphies are recognized on the most parsimonious phylogeny (Fig. 3) at the level of generality at which observation confirms they are diagnostic. Unless otherwise noted, all transformations are from state 0 to 1. In listing multistate characters, the state applying to a node is placed in parentheses, e.g., 49(1) or 49(1 to 2). Reversals to ancestral states are preceded by a negative sign, e.g., −81. Characters are listed below at the levels assigned by the PAUP analysis except in cases where potential ambiguity is masked by Farris optimization, and where missing data leaves uncertain the level of generality. All equivocal characters or states are marked with an asterisk (*) and listed at every level at which they might have appeared. In the case of missing data, characters are listed where observation confirms their assignment and those one or more nodes to which the state-change might apply are listed in brackets.

Node I (UNNAMED): 8, 9, 10(1), 13*, 15, 32, 42*, 48, 49(1), 80, 109, 111, 116(1 or 2)*, 128(1 or 2)*, 130 (1 or 2)*.

Mammaliamorpha: 2, 4, 6, 7, 19, 20, 24, 31, 34, 35, 37, 38, 39, 40(1 or 2)*, 44, 45, 51, 53, 55, 56, 57(1), 58(1), 68, 74, 75, 76, 81, 82*, 83*, 86, 88, 89, 94, 95, 98, 99, 100, 102, 105, 108, 112, 115(1), 116(2)*, 119, 120(1), 124 , 128(2)*, 130(2)*, 131, 132, 133, 134, 137, 138, 139, 140, 141(1), 143, 144(1), 150, 151, 152(1).

Mammaliaformes: 10(1 to 2), 13*, 16, 21, 30(1), 40(2)*, 41, 42*, 46, 49(1 to 2), 50, 52, 60, 66, 79*, 83*, 84*, 87, 91 92*, 97*, 103, 104, 125, 155*.

Mammalia: 1, 11, 17*, 18, 22, 25, 26, 27, 28, 33, 47, 54, 57(1 to 2), 58(1 to 2), 61, 62, 63, 64, 65, 67, 69, 72, 73, 77, 78(1), 82*, 92[Mammaliaformes], 93, 96, 97 [Mammaliaformes], 101, 129, 135*, 145, 146*, 147, 148, 149*, 152*, 153(1 or 2)*, 155[Mammaliaformes], 156, 158(1 or 2)*.

Theriiformes: 3*, 5, 17*, 70*, 71, 106, 110, 113, 114, 115(1 to 2), 117, 118, 120(1 to 2), 121, 122, 123, 127, 141(1 to 2), 142, 144(1 to 2), 149[Mammalia], 152(1 to 2)[Mammalia], 153(2)[Mammalia], 154, 158(2)[Mammalia].

Theria: 3[Theriiformes], 12, 14, 17*, 23, 29, 36, 43, 59(0 to 2), 78(1 to 2), 79*, −81, −82*, 84*, 85, 90, 107, 126, 135*, 136, −146*, 157.

Exaeretodon: 13*, 42*, 116(1)*, 128(1)*, 130(1)*.

Tritylodontidae: −13*, 40(1)*, −42*, 82*.

Morganucodontidae: 79*, −82*, 84*, 85, 107.

Monotremata: 30(1 to 2), −39, 59(1), 82*, −105, 135*, 146*, 153(2 to 1)*, 158(2 to 1)*.

Multituberculata: 70*, −79*, 82*, 84*, −135*, 146*.

Marsupialia: 70*.

Placentalia: −70*.

APPENDIX III

This matrix lists the 158 characters distributed among the eight principal taxa that were analyzed using PAUP. Characters scored 0 denote the ancestral condition, and characters scored 1 or 2 denote derived conditions. Missing data are scored ? for unpreserved characters and N for states too derived to score without assuming some hypothesis of phylogeny (see Data and Methods of Analysis). The characters are listed by taxon in the order in which they appear in Appendix I. Under each taxon name, the first line lists characters 1–55, the second line lists characters 56–110, and the third line lists characters 111–158.

Outgroup

00000 00000 00000 00000 00000 00000 00000 00000 00000 00000 00000
00000 00000 00000 00000 00000 00000 00000 00000 00000 00000 00000
00000 00000 00000 00000 00000 00000 00000 00000 00000 000

Exaeretodon

00000 00111 00101 00000 00000 00000 01000 00000 01000 00110 00000
00000 00000 00000 00000 00001 00000 00000 00000 00000 00000 00010
10000 10000 00000 00101 00000 00000 00000 00000 0000? 000

Tritylodontidae

01010 11111 00001 00011 00010 00000 11011 01111 00011 00110 10101
11100 00000 00100 00011 10001 11N00 10110 00011 00111 01001 ?0110
11001 20011 00010 00202 11110 01111 10110 00001 11000 000

Morganucodontidae

01010 11112 00101 10011 10010 00001 11011 01112 11011 10121 11101
11101 00000 10100 00011 10011 10111 11110 1?011 0?111 01111 ?1110
11001 20011 00011 00202 11110 0111? 10110 00001 1100? 000

Monotremata

11010 11112 10101 1N111 11011 11102 1111N 01102 110NN 11121 11111
12211 11111 11110 011N1 111NN N1NN0 NN11N 11111 11111 11110 00110
N1001 20011 00011 0021N 111N1 01111 10111 111NN 1N101 101

Multituberculata

11?11 11112 10101 1N1?1 11011 ?1101 11111 011?2 1101N 11121 11111
12201 11111 11111 111N1 1110N 11N00 11110 1???? ?1111 11111 10111
N1112 N1112 11111 01212 11110 01111 21121 11111 12211 102

Marsupialia

11111 11112 11111 11111 11111 11111 11111 11112 1111N 11121 11111
12221 11111 11111 111N1 1121N 00111 11111 11111 11111 11111 11111
N1112 N1112 1111N 11212 111N1 11111 21121 01111 12211 112

Placentalia

11111 11112 11111 11111 11111 11111 11111 11112 1111N 11121 11111
12221 111N1 11110 111N1 1121N 00111 11111 11111 11111 11111 11111
N1112 N1112 1111N 11212 111N1 11111 21121 01111 12211 112