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Mammal Phylogeny

**Mesozoic Differentiation, Multituberculates, Monotremes,
Early Therians, and Marsupials**

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Phylogenetic Systematics and the Early History of Mammals

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Overview

Numerous recent authors have used phylogenetic systematics to study mammalian evolution. As a result, there have been many fundamental changes in our view of early mammalian history compared with the view of a decade ago. However, even phylogenetic analyses have produced conflicting interpretations of this history. On closer inspection, many of the conflicts may simply reflect the different samples of taxa and characters that have been brought to bear on this issue. In a series of computer parsimony analyses, different rates of evolution in the dentition, skull, and postcranium were responsible for different tree topologies that resulted when different, restricted character samples were analyzed. When sampling artifact is removed and all available character data analyzed, a highly corroborated, stable phylogeny remains, which is largely consistent with the temporal distributions of taxa recorded in the fossil record. Several patterns dominate this phylogeny. Most transformations in the head involved elaborate repackaging of an expanded brain and special sense organs, remodeling of the masticatory system, and accelerated evolution of a highly complex dentition. Postcranial evolution involved differentiation of the vertebral column and remodeling of the limbs and girdles, associated with parasagittal gait. Another pattern involved evolutionary miniaturization similar in detail to historical patterns in other miniaturized tetrapod lineages, suggesting the existence of developmental constraints common to all tetrapods. Although some of these patterns have long been recognized, others have become evi-

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dent only as the effects of rate and sampling in phylogenetic analyses have become more fully understood.

Introduction

The contemporary phylogenetic perspective on early mammalian history has obvious, deep foundations in earlier research, but it is nevertheless significantly different from the dominant view of a decade ago. Phylogenetic analyses have changed our measures of the most fundamental properties of Mammalia, including its definition, diagnosis, membership, the relationships among its members, and its distribution in time and space. Below, I first review some of the conceptual transformations that have arisen under phylogenetic systematics, and I then devote the bulk of this report to summarizing what now appear to be the most strongly corroborated and stable relationships in early mammalian history.

Identifying which aspects of early mammalian phylogeny are "stable" and which are not is far from a categorical process. The details of cynodont phylogeny have long been the subject of debate, particularly the relationships among the extinct taxa most closely related to mammals and among the basal mammals themselves. Numerous phylogenetic analyses have recently pursued this problem (e.g., Crompton and Sun, 1985; Crompton and Luo, this volume, chapter 4; Gauthier et al., 1988, 1989; Kemp, 1982, 1983; Hopson and Barghusen, 1986; Novacek, 1986, 1989, 1990; Novacek and Wyss, 1986; Rowe, 1986, 1988; Rowe and Simmons, unpublished; Sues, 1985; Wible, 1987, 1990, 1990; Wible et al., 1990; Wible and Hopson, this volume chapter 5). Although general agreement on a number of points has emerged, there remain conflicting views on other aspects of relationship, on diagnoses for groups whose memberships are not disputed, and on interpretations of individual characters.

Resolution of these conflicts is complicated by the fact that published analyses have all used different samples of taxa and characters. Phylogenetic methods have themselves varied considerably among studies, further complicating the issue, but I focus only on the problem of sampling. To better understand sampling effects, several series of computer-assisted parsimony analyses have been designed to measure how different assemblages of taxa and characters affect the global tree topology (Donoghue et al., 1989; Gauthier et al., 1988, 1989; Rowe, 1988; Rowe and Simmons, unpublished). All of these studies, and particularly that by Rowe and Simmons (unpublished), endeavored to bring together a large and, more important, diverse osteological data base that sampled all parts of the skeleton and dentition, in a wide range of extant and extinct taxa. By selectively adding and deleting different subsets of taxa and characters in a large data matrix, these tests helped to identify the points in early mammalian phylogeny that were most consistently resolved and were relatively immune to change as the analytic sample was changed.

At the same time, the tests identified taxa whose positions were more sensitive to sampling variations and placed constraints on their range of possible positions.

This approach to measuring phylogenetic pattern has arrived at new assessments of phylogenetic pattern in early mammalian history, while also providing strong corroboration of many points made in older literature. Not surprisingly, the new phylogenetic patterns suggest that previously unrecognized processes may have played key roles in shaping early mammalian history.

Issues in Early Mammalian History

MAMMALIAN MONOPHYLY. Prior to the advent of phylogenetic systematics, the focus of study on early mammals was to elucidate the reptile-to-mammal transition (e.g., Aulie, 1974; Crompton and Jenkins, 1973; Olson, 1959, 1962; Simpson, 1959, 1960, 1961). With a rich sequence of fossils extending from the Carboniferous to the Recent, the origin of mammals was taken as the premier example of an evolutionary transition from one Linnean class to another. Evolutionary grades played a central role in discussion of this event. Influential generalizations about issues ranging from macroevolution to natural selection to convergence were derived from study of this lineage and were later extrapolated to other metazoan lineages. The major debates waged in the literature involved whether Mammalia was polyphyletic, and which character or character assemblage most meaningfully marked a boundary between reptilian and mammalian grades (e.g., Hopson and Crompton, 1969; Olson, 1959, 1962; Reed, 1960; Simpson, 1959, 1960, 1961, 1971; Van Valen, 1960). The influence of environment via natural selection was virtually the only mechanism invoked to describe morphological patterns discovered in this history. It was argued that similar environmental demands led to the convergent evolution of "mammalian" characters in many different lineages. Implicit in many discussions is the thought that convergence was so prevalent that the true genealogy could never be known with any precision.

Phylogenetic systematics has turned our attention from many of these issues. The discovery of monophyletic taxa replaced definition of grades as the central issue in understanding early mammalian history. There has been no doubt for a century that extant mammalian species share a unique common ancestor at some point in history, and that Mammalia is monophyletic in the strict meaning of the term (e.g., Haeckel, 1897; Rowe, 1988). Whereas Simpson (1971, p. 192) and most others dismissed mammalian common ancestry as "trivial" (but see Reed, 1960), phylogenetic systematics has reorganized our analyses with this as a pivotal point (Fig. 10.1). This attitude reflects a shift in our conceptual view of Mammalia, and of taxa generally. Previous views saw taxa as classes defined by characters, while

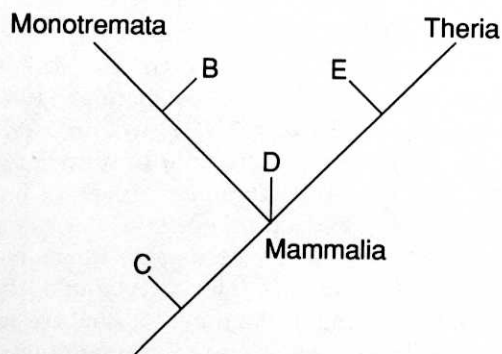


FIGURE 10.1. Potential relationships between fossils and the extant sister lineages whose common ancestor defines Mammalia. Any fossil that is not itself a monotreme or therian can have only four possible positions. It can be closest to therians, closest to monotremes, or lie outside of Mammalia. Taxa in position D are of unresolved position within Mammalia (Rowe, 1988).

contemporary phylogenetics views taxa as individuals defined by common ancestry (e.g., de Queiroz, 1988; de Queiroz and Gauthier, 1990; Gauthier, 1986; Ghiselin, 1984; Hull, 1976; Rowe, 1987, 1988). Current phylogenetic debate focuses on the content and diagnosis of Mammalia, on the relationships among its members and extinct relatives, and on interpreting the new pattern of character hierarchy and genealogy.

INCOMPLETENESS. Incompleteness of the fossil record has been, and continues to be, a major obstacle in interpreting early mammalian history. Most Mesozoic taxa relevant to this history lie within the smallest order of vertebrate size magnitudes (McMahon and Bonner, 1983). Few specimens have survived the rigors of transport, burial, and diagenesis, and their tiny size renders them very difficult to find in the field. Most that have been recovered consist of only the hardest and most resilient parts of the skeleton, and even today most Mesozoic taxa are known only from dentitions. Understandably, this led to a strong analytic bias toward dental data, with the aim of developing a taxonomy that might apply to the majority of taxa. The resulting framework was handicapped, however, in that researchers were largely unable to fit nondental data into it. Another major shortcoming of the older framework is that it treated homoplasy as an inductively recognized phenomenon. When character data from the skull or postcranial skeleton conflicted with the distributions of dental data, the dental characters were necessarily taken as evidence of relationship, while the skeletal characters were generally dismissed as convergent.

Contemporary methods choose among competing phylogenetic hypotheses based on their information content as well as on parsimony (e.g., Kluge, 1989). Consequently, researchers have recently endeavored to

bring more diverse character data into their analyses, to test previous views. As a result, several hundred skeletal characters and a large body of new dental evidence have come to bear on early mammalian systematics (e.g., Novacek, 1986, 1989, 1990; Novacek and Wyss, 1986; Rowe, 1988; Rowe and Simmons, MS; Gauthier et al., 1988; Wible, 1987, 1990, 1991). This has had a very positive effect, but the shift to character-rich analyses has come at the cost of taxon richness, as most researchers have opted to omit fragmentary fossils from consideration. Although there is both theoretical and empirical justification for this (Rowe, 1988; Rowe and Simmons, in press), it is also clear that even highly incomplete taxa can preserve data of critical importance to tree topology (Gauthier et al., 1988; Donoghue et al., 1989). These and other results (Rowe and Simmons, in press) point to the sampling methods used to construct a matrix as a significant source of artifact and discrepancy between analyses.

Ironically, as more complete fossils and more encompassing analytic procedures have emerged, new sources of missing data have been discovered inherent in the data themselves. Evolution itself leads to the loss of data through the transformation and divergence of form (e.g., Doyle and Donoghue, 1987; Gauthier et al., 1988; Donoghue et al., 1989). In a real sense, characters can become extinct within a lineage, resulting in the loss of potentially critical historic information. For example, one cannot score the presence of a single versus a divided caniniform tooth root in taxa that have lost the caniniform teeth. Unlike nonpreservation, this type of information loss has a complex temporal component in that its extent is related to both the temporal scope of the problem and the evolutionary rates of the character systems analyzed.

RATES OF EVOLUTION AND MISSING DATA. The degree to which data are lost as a result of divergence can be viewed as a complex function of time. Data loss is potentially most severe in analyses that span broad temporal intervals and seek to reconstruct ancient branching patterns, and which sample small, rapidly evolving sets of characters. It is noteworthy that while nonpreservation is usually a problem only with fossils, divergence can affect both extinct and extant taxa. Moreover, by virtue of having survived to the recent, extant taxa may be especially prone to data lost through this process. The effects of divergence are such that analyses of extant taxa alone can produce mistaken estimates of character polarities, distributions, and tree topologies (Doyle and Donoghue, 1987; Donoghue et al., 1989; Gauthier et al., 1988).

Variation in evolutionary rates of different characters and character systems is the primary cause of "mosaic evolution," which has long been acknowledged as a problem in discerning phylogenetic patterns. However,

only recently have efforts been directed at understanding its effects in any particular phylogenetic analysis. Minimizing the adverse effects of mosaic evolution involves discovering data that transform at an average rate appropriate to resolving the problem at hand. Characters or systems evolving too slowly may have recorded nothing of the history of interest, while systems evolving too rapidly may become too transformed to preserve any useful information.

Rates of character evolution cannot be determined *a priori*, but methods are emerging to base measurements on a data matrix and the most parsimonious phylogeny found within it when all data are considered. One technique compares average homoplasy levels for different subsets of characters within a single matrix, using a single tree topology. Higher than average homoplasy levels in one region, for example, the dentition, reflect more rapid transformation rates for that region than for the other regions sampled in the matrix. The homoplasy retention index (Farris, 1989a, 1989b) is a convenient measure for comparing average homoplasy levels of different character subsets (Cloutier, 1991; Rowe and Simmons, unpublished). Rowe and Simmons (unpublished) compared homoplasy levels in the dentition, the skull exclusive of the dentition, and the postcranium. Homoplasy was found in all three regions, but it was not distributed equally in each. The skull and postcranium recorded similar levels, whereas the dentition recorded minimally a 30% higher homoplasy level. The enormous diversity of mammalian dental morphology reflects a rapid rate of evolution expressed over a 140-million-year history.

Additional tests showed that, predictably, the phylogenetic resolving power of the dentition was strongest over relatively short segments of the tree. Dental characters by themselves resolved few relationships, and omitting them altogether had little effect on the tree topology found with all data. However, this is not to say that the dentition was uninformative, or even that it was uninformative for older events. Dental characters were diagnostic at most levels on the phylogeny described below, but without the signal provided by the more slowly evolving cranium and postcranium, the distributions of most dental characters remained equivocal (Rowe and Simmons, unpublished).

PHYLOGENETIC RESOLUTION AND STABILITY. Although it may be obvious that no taxon or character is relevant to phylogenetic analyses at all levels, methods to identify the most informative sample of taxa and characters for any given problem have been less than clear. A step in this direction was recently taken by the design of series of tests to analyze some of the effects of sampling in understanding early mammalian history (Rowe and Simmons, unpublished). The tests focused on the relationship between completeness, measured from a data

matrix, and phylogenetic resolution, the degree to which taxa are arrayed in a strictly dichotomous branching pattern (Mickey and Platnick, 1989). The interactive capabilities of PAUP (Swofford, 1989) and Hennig 86 (Farris, 1986) were used to study a matrix of 151 characters for 24 of the major groups of mammals and their closest extinct relatives. By systematically adding and deleting taxa according to their degrees of completeness, it was possible to examine the relationships among some of the different kinds of information recorded in the matrix and to evaluate the relevant contributions of different taxa and character subsets to the final tree topology.

The tests found a general correspondence between taxon completeness and phylogenetic resolution. However, it was also clear that the two are not strictly coupled and that incomplete taxa offered potentially critical information to resolving phylogenetic questions. Nevertheless, ten relatively incomplete taxa remained unresolved in this analysis, in that each could be placed in several equally parsimonious phylogenetic positions and removing them had no effect on relationships among the other taxa. There was also a cumulative effect of incompleteness, which led to an exponential decrease in resolution as more and more incomplete taxa were added to the matrix. Hence, simply including all available taxa may not produce as unambiguously informative results as analyzing a select sample of available taxa. Selection is not an *a priori* process and can be made only with tests such as these.

Despite lability in the positions of some taxa, the tests consistently found a stable topology among fourteen other taxa (Fig. 10.2). This topology remained unchanged when different samples of taxa were added or removed from the analysis. Only when large sets of character data were deleted did resolution diminish.

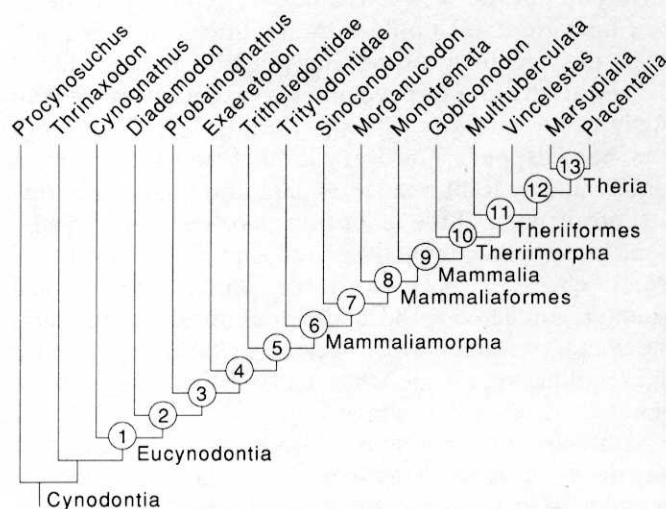


FIGURE 10.2. Eucynodont phylogeny (see text).

This effect was most marked when the dentition was analyzed alone, and at only a few nodes did resolution diminish when either the cranial or postcranial data set was deleted. Even during the rapid drop in resolution that accompanied the cumulative addition of incomplete taxa, the topology in Figure 10.2 was found in all of the equally parsimonious trees. Because it consistently summarizes the largest and most diverse osteological data sample yet analyzed, and includes the taxa most relevant to understanding early mammalian history, I take the phylogeny depicted in Figure 10.2 to be the preferred hypothesis for now. This phylogeny supports many aspects of earlier work, although it also differs from all previously published studies at least in detail.

Eucynodont Phylogeny and the Early History of Mammals

The diagnoses discussed below are based on the recent analysis by Rowe and Simmons (unpublished). Character distributions were measured using the DELTRANS option of PAUP for all character data and the sixteen taxa depicted in Figure 10.2. Readers are referred to Rowe and Simmons (unpublished) for details of methodology and for a complete listing of all character distributions and taxon diagnoses.

Geological dates for the taxa in this phylogeny are from Harland et al. (1990). As noted in that work, the time span over which the phylogenetic events of interest occurred is one of the most poorly constrained of the entire Phanerozoic. Very few radiometric dates have been obtained; only three are known for the entire Jurassic, and linear interpolations provided all of the Jurassic dates cited below. All dates have an error margin of between 10 and 30 million years, roughly 7% to 20% of the total time involved, and considerable future improvement in the numbers listed below can be expected. In addition to this imprecision, superpositional relationships are unresolved for several clusters of taxa. What is known of the temporal distribution of these taxa is consistent with the sequence of branching in this phylogeny. Temporal resolution is sufficiently poor, however, that it would be consistent with a range of other phylogenetic hypotheses as well.

NODE 1: EUCYNODONTIA. Eucynodontia offers a convenient place to begin discussion, because it is one of the most stable and widely recognized monophyletic groups within Cynodontia, and there is abundant support for using the cynodonts *Thrinaxodon* (Fourie, 1974; Jenkins, 1971) and *Procynosuchus* (Kemp, 1979, 1980) as consecutively more distant outgroups, to polarize characters transforming among eucynodonts (Gauthier et al., 1988; Hopson and Barghusen, 1986; Kemp, 1982; Rowe, 1986, 1988; Wible, unpublished). Eucynodontia is

the taxon stemming from the last common ancestor that mammals share with *Cynognathus*.

Eucynodontia is diagnosed by characters of the skull and dentition. The attachment of eucynodont cheek-teeth was transformed from the ancestral cynodont pattern of ankylosis with the jaws (e.g., Crompton, 1963) to a new attachment via greatly elongated tooth roots that are anchored by a periodontal ligament. There was also a major reduction in the rate of cheektooth replacement and the initiation of bilateral occlusion, though only irregular wear facets were produced in early members of this group. Ligamentous attachment, the so-called thecodont gomphosis, offers a degree of mobility of each tooth within its socket that is critical to the development and maintenance of precise, complex occlusal patterns (e.g., Johnson, 1983; Noble, 1969; Ten Cate, 1969). Slowing of tooth replacement was also crucial to maintaining occlusion. These diagnostic apomorphies of Eucynodontia mark the beginning of an acceleration in dental evolutionary rates and the onset of occlusal complexity that is so characteristic of mammals among extant gnathostomes. Additional diagnostic characters of eucynodonts include participation of the surangular in the craniomandibular joint, reduction of the quadrate ramus of the pterygoid, and the absence of incisiform teeth in the maxilla anterior to the caniniform.

The fossil record of eucynodonts begins near the end of the Scythian Stage of the Early Triassic, which extended from 245 ± 10 to 241 ± 10 million years ago (Harland et al., 1990). The oldest eucynodonts are *Cynognathus* and the more derived eucynodont, *Diademodon*, which occur together in *Cynognathus* Zone sediments of the South African Karoo (Anderson and Cruickshank, 1978; Kitching, 1977), and which provide a minimum age for Eucynodontia. Because the phylogeny (Fig. 10.2) indicates that *Diademodon* originated later than *Cynognathus*, it would seem that the earliest parts of eucynodont history occurred in unrecorded, pre-*Cynognathus* Zone times. Future fossil discoveries and increased biostratigraphic resolution are likely to push eucynodont history back toward the beginning of the Early Triassic, although just how far back the lower time limit might extend is more difficult to constrain. *Cynognathus* has not been recovered from rocks younger than Early Triassic, but its sister lineage, represented here at Node 2, has survived to produce more than 4,000 extant species and a diversity of extinct species.

NODE 2: (UNNAMED). This unnamed taxon comprises the last common ancestor that mammals share with *Diademodon* and all its descendants. *Diademodon* was long classified as a "gomphodont" cynodont, a group united on resemblances in the dentition that have been taken as evidence of a herbivorous diet. The gompho-

donts were thought to represent an evolutionary radiation of herbivorous cynodonts that diverged early in the Triassic from a persistently predatory lineage from which mammals ultimately descended (e.g., Crompton, 1972; Hopson, 1969; Hopson and Barghusen, 1986). However, analyses of a broader sample of data, including characters from the skull and postcranium as well as the dentition, argue that the gomphodonts form a paraphyletic assemblage, because some gomphodonts, in particular *Exaeretodon* and tritylodontids, are more closely related to mammals than to *Diademodon* (see below). In this light, it appears that either the diets of cynodonts are more evolutionarily labile than has been believed and herbivory has evolved several times, or previous interpretations of diet in these taxa are mistaken.

Node 2 is diagnosed by additional transformation of the dentition. Members of this group have cheekteeth with consistent, regular sets of wear facets, which indicate consistent occlusal patterns. Some members of this group, such as *Sinoconodon* and a number of extant species, lack occlusion because the teeth are either greatly simplified or are absent altogether. Nevertheless, all of these taxa retain other features derived within this group that identify them as members of Node 2 and that indicate the absence of occlusion and wear facets to be reversals to a pre-eucynodont state, rather than retained plesiomorphies. This node is also diagnosed by contact between the palatal processes of the premaxillae, which meet behind the incisive foramen (later reversed in *Exaeretodon*).

Like Eucynodontia, the first fossil record of Node 2 appears in the early Triassic (Scythian) *Cynognathus* Zone of the South African Karoo. Unlike its sister taxon (Node 3), *Diademodon* did not survive the end of the early Triassic.

NODE 3: (UNNAMED). This unnamed taxon comprises the last common ancestor mammals share with *Probainognathus* and all taxa stemming from it. *Probainognathus* was widely regarded as being close to the direct ancestry of mammals and representing a morphotype from which mammals descended (Allin, 1986; Romer, 1969, 1970; Hopson and Kitching, 1972; Crompton and Jenkins, 1973, 1979). However, other cynodonts now appear to be more closely related to mammals than is *Probainognathus*, notably *Exaeretodon* (Gauthier et al., 1988; Rowe, 1986, 1988) and tritylodontids (Kemp, 1982, 1988a, 1988b; Rowe, 1986, 1988; Wible, 1991; Wible and Hopson, this volume, chapter 5; Gauthier et al., 1988). The latter taxa were considered only distant relatives of mammals because their highly apomorphic dentitions seemed to demand a long expanse of independent evolution (e.g., Crompton, 1972; Hopson, 1969). However, when viewed in light of all available data, the dentitions of *Exaeretodon* and tritylodontids

appear to be the result of a rapid rate rather than a distant time of divergence. Although their dentitions offer little unambiguous information on higher-level relationships of these taxa, the more slowly evolving skulls and postcrania bear a host of unequivocal, unique resemblances to mammals that are not found in *Probainognathus* (see below).

Most of the characters diagnosing Node 3 manifest increased rates of development of the bones surrounding the brain. The parietals, which primitively remained paired throughout life and formed the borders of the pineal foramen, became fused, completely closing off the pineal foramen in adults. The pineal body itself is retained in most mammals, suggesting that this transformation reflects more an increase in the rate of parietal growth than any qualitative change in the underlying structure of the brain (Roth et al., 1986). In addition, the prootic and opisthotic bones fuse to form the petrosal, reflecting a similar developmental acceleration. In the postcranium, proximal expansions of the ribs known as costal plates, which extended over both the thoracic and lumbar vertebrae in eucynodonts ancestrally (Jenkins, 1971), were lost from the thoracics, and only the short lumbar ribs retained any vestige of these structures (Romer, 1970).

The oldest member of Node 3 is *Probainognathus*. It is known from the Chanares Formation of Argentina (Romer, 1970), which was deposited during the Ladinian Stage of the Middle Triassic, roughly between 239 ± 8 and 235 ± 5 million years ago (Harland et al., 1990). *Probainognathus* did not survive the end of the Triassic, unlike its sister taxon (Node 4).

NODE 4: (UNNAMED). This unnamed taxon comprises the last common ancestor that mammals share with *Exaeretodon* and all of its descendants (Rowe, 1986, 1988). The group is diagnosed by a number of characters in the vicinity of the braincase, the dentition, and the postcranium. A partial floor developed beneath the cavum epipterygium, below the presumed position of the ganglion of the facial nerve, though the cavum remained open beneath the trigeminal ganglion (Bonaparte, 1966). The prootic was elaborated with the appearance of the novel posterolateral flange, beneath which reappeared a long quadrate ramus of the pterygoid, a structure that had been reduced in eucynodonts ancestrally (Node 1). On the mandible, the retroarticular process became elongated and strongly recurved, forming the structure referred to in mammals as the manubrium mallei and continuing an ancient trend involving remodeling of the acoustic system. In the dentition, there was a reduction to only three incisiform teeth in the premaxilla. Other dental modifications may have occurred in the ancestor of this group, but the dentitions in *Exaeretodon* and currently known basal members of its sister taxon (Node 5) are too divergently

specialized to permit unequivocal interpretation of ancestral morphology.

In the postcranium, costal plates were completely lost from the ribs. In the pelvis, the iliac blade was reduced in size by a deep emargination of its dorsal edge and an overall reduction in the posterior iliac spine. In retrospect, these changes may mark a step toward parasagittal locomotion and the eventual coupling of breathing tides and locomotor cycles that facilitated the eventual increase in metabolic scope and level characteristic of modern mammals (Bramble, 1989; Bramble and Jenkins, 1989). It is doubtful, however, that those physiological modifications were more than incipient at this stage.

Exaeretodon is the oldest member of Node 4, occurring in the Santa Maria Formation of Brazil (Barbarena, 1974, cited in Hopson, 1984), which was probably deposited late in the Ladinian Stage of the Middle Triassic, roughly between 239 ± 8 and 235 ± 5 million years ago (Harland et al., 1990). *Exaeretodon* extends into the Late Triassic Ischigualasto sediments of Argentina (Bonaparte, 1966; Hopson, 1984), which are somewhere between 235 ± 5 and 223 ± 10 million years old (Harland et al., 1990).

NODE 5: (UNNAMED). This group comprises the last common ancestor mammals share with tritheledontids and all of its descendants. This is one of the most distinctive and strongly diagnosed taxa within Cynodontia. Virtually all parts of the skeleton were remodeled in association with a dramatic reduction in body size. The early members of this group lie within the smallest order of vertebrate size magnitudes and exhibit many of the classic structural features induced by evolutionary miniaturization that have been documented in various teleost (Fink, 1981; Roberts, 1981), lissamphibian (Alberch and Alberch, 1981; Hanken, 1983, 1984; Wake, 1966), and squamate (Rieppel, 1984) lineages. The origin of this taxon marked the beginning of a long history—extending from the beginning of the Jurassic into the Paleocene and encompassing nearly 140 million years—that was carried out in tiny animals (Rowe, 1989).

Cranial reorganization in Node 5 involved inflation of the nasopharyngeal cavity, remodeling of the orbit, further enclosure of the brain, and further modification of the acoustic and masticatory systems. The nasal chamber expanded to such a degree that the choana was displaced backwards from its ancestral position in front of the orbit to a new position entirely behind the orbit. The roof of the choana was also modified as the pterygopalatine ridges became reoriented and separated by a series of parallel troughs. These probably mark the positions of the auditory tubes, indicating establishment of the intricate connection between the nasopharynx and middle ear cavity that is characteristic of extant

mammals (Barghusen, 1986). At the same time, the orbit developed an extensive medial wall formed by a descending flange from the frontal and an ascending flange from the palatine. The borders of the orbit also changed as the prefrontal and postfrontal bones were lost, leaving the orbit confluent with the temporal fenestra. Elsewhere in the skull, the quadrate rami of the pterygoid and epipterygoid joined the prootic to form a very broadly reflected posterolateral flange. Further closure of the braincase occurred with the development of a medial wall separating the internal acoustic meatus from the cavum cranii, and a bony separation between the fenestra rotunda and the jugular canal.

The auditory and masticatory systems remained intricately coupled, and any changes in one system were probably felt to some degree in the function of the other system. The postdentary bones became reduced to a thin rod of bones lying within a deep Meckelian sulcus, signaling greater auditory sensitivity to high frequencies, and the surangular was withdrawn from the craniomandibular joint. At the front of the jaws the dentaries, which develop from separate anlage in all gnathostomes (e.g., de Beer, 1937), remained separate throughout ontogeny, instead of fusing to form an osseous symphysis as was the case in eucynodonts ancestrally. Without a fused symphysis, some capacity for longitudinal rotation of each mandible was present, though this potential was limited by the persistence of large coronoid bones and transverse processes of the pterygoids.

The postcranial skeleton of tritheledontids has not been described in detail, apart from a brief overview by Broom (1932). However, thanks to the generosity of A. W. Crompton and J. A. Hopson, I was able to score postcranial material that they are currently studying. As they point out (personal communication), the preserved portions of the tritheledontid postcranium are virtually identical to those of tritylodontids and morganucodontids. In the vertebral column, differentiation of the cervical region was marked by great foreshortening of both the centra and neural arches, indicating a highly mobile neck. Thoracic and lumbar regions also show strong differentiation, and the sacrum was reduced from a massive structure to one that comprised only two or at most three vertebrae. The iliac blade was correspondingly reduced, and the acetabulum was rotated backwards to a new position entirely posterior to the sacrum. It is at this point in history that the rod-like iliac blade with triangular cross section, characteristic of most extant mammals, appeared. All of these changes suggest that sagittal axial flexion-extension in a roughly sagittal plane was a major component in locomotion in the members of Node 5.

The limbs were also modified, especially at their proximal articulations. The glenoid became widely open ventrally as the coracoid was reduced and shifted for-

ward, permitting a great degree of freedom at the shoulder. The femur also took on a highly characteristic form, with a strongly differentiated subspherical head flanked laterally and medially by sharply differentiated greater and lesser trochanters. As with the shoulder, this probably enhanced stability of the hip joint over an increased range of excursion. Taken as a whole, these modifications suggest that in Node 5 a great step was taken toward the coupling of locomotion cycles and breathing tides, and perhaps also elevation in metabolic scope, as is characteristic of extant mammals (Bramble, 1989; Bramble and Jenkins, 1989).

Tritheledontidae is diagnosed by a distinctly modified dentition, in which there were both unique crown morphology and a reversal to the pre-eucynodont mode of cheektooth attachment via ankylosis to the jaws (e.g., Gow, 1980; Hopson and Barghusen, 1986). Occlusal facets were still produced, but the relationship between upper and lower teeth was less intricate and regular than in Eucynodontia ancestrally. In light of the large body of data from the skull and postcranium placing tritheledontids within Node 5, there is little doubt that these dental characters are reversals rather than plesiomorphy. Despite its seemingly primitive aspect, the tritheledontid dentition continues to reflect the rapid rate of dental evolution among eucynodonts.

Node 5 is first recorded in rocks that were long considered Late Triassic but that now appear to be Early Jurassic in age (e.g., Olsen and Galton, 1984), between 208 ± 8 and 203 ± 7 million years old. Tritheledontids appear more or less simultaneously with morganucodontids, tritylodontids, and *Sinoconodon*. The geologically "simultaneous" appearance of these taxa is another instance in which resolution of the fossil record lags behind that of the fossils themselves, whose preserved characters support fully resolved, stable relationships among all of these taxa. Prior to the Early Jurassic records of these taxa, there is a gap in the eucynodont fossil record that extends to the base of the Carnian, and which could be anywhere from 10 to 40 million years long. However, even with the outside estimate of 40 million years, the stratigraphic gap alone is unable to account for the number of characters diagnosing this node under an assumption of uniform evolutionary rate during eucynodont phylogeny (Rowe, 1989). There appears to have been a true burst in evolutionary rates that occurred along the stem of Node 5. It is probably no coincidence that this increase in rate is correlated with miniaturization.

NODE 6: MAMMALIAMORPHA. Mammalianomorpha comprises the last common ancestor that mammals share with Tritylodontidae and all its descendants (Rowe, 1986, 1988). Mammalianomorpha is diagnosed by characters of the cranium, dentition, and postcranium. A degree of uncertainty exists in the distributions of some

postcranial characters listed here because the tritheledontid postcranium is as yet poorly known. This leaves open the possibility that some characters described below are more widely distributed than described here. Nevertheless, there is strong, unequivocal support for monophyly of Mammalianomorpha, and it is clear that none of these character states occurs outside of Node 5. Moreover, this degree of uncertainty was insufficient to compromise phylogenetic resolution among the taxa depicted in Figure 10.2 in any of the tests aimed at understanding sampling effects (Rowe and Simmons, unpublished).

The medial wall of the mammalianomorph orbit is even more extensive than was the case in Node 5 ancestrally, with the orbitosphenoid joining the previous contributions by the frontal and palatine. Even with this addition, however, the primitive orbital fissure was not yet completely closed. At the rear of the skull, the prootic posterolateral flange became perforated by cranial vessels. In addition, the paroccipital process was elaborately modified, bifurcating distally to form separate quadrate and mastoid processes that are separated ventrally by a deep fossa, which is often interpreted (probably erroneously) to have provided origin to a hyoid muscle. The quadrate process developed direct articulation with the quadrate, whereas in eucynodonts ancestrally the two bones were separated by an intervening slip of the squamosal.

The dentition underwent further profound modification with the development of multiple roots and a consequent escalation in complexity of crown morphology and occlusal relationships. Crown diversity in the cheekteeth is so great and so widely divergent among the taxa within Mammalianomorpha, especially tritylodontids, that little can be said of precise crown structure in mammalianomorphs ancestrally. Root morphology is also variable, with three or more roots developing on the cheekteeth in a number of taxa. Some authors have argued that division of the roots is non-homologous in basal mammalianomorphs because root morphology differs among these taxa (Sues, 1985; Hopson and Barghusen, 1986). However, in light of the other data supporting mammalianomorph monophyly, it would appear that there were divided roots in the cheekteeth of mammalianomorphs ancestrally. Like crown structure, mammalianomorph root morphology diversified at a rapid rate from a common ancestral form with divided roots.

In the postcranium, the atlas-axis complex became more flexible with loss of the atlas postzygapophysis and flattening of its centrum. At the same time, a stout dens formed as a neomorphic outgrowth from the axis centrum, contributing strength and stability to the joint (Jenkins, 1969, 1971). At the opposite end of the vertebral column, the distal caudal centra became elongated with greatly reduced neural and haemal arches. Associated with vertebral differentiation was the seg-

mentation of the sternum, to produce sternbrae. The sternum originated developmentally and functionally as a part of the shoulder girdle. However, in mammaliaforms it appears to have become functionally linked to the vertebral column as well, by facilitating the parasagittal flexion-extension of the vertebral column. The appearance of epipubic bones, which lay embedded in the abdominal musculature, may also be linked to parasagittal locomotion, although a host of other functions have been suggested.

Tritylodontids include large animals, such as *Kayentatherium* (Sues, 1986a), as well as very small forms such as *Oligokyphus* (Kuhne, 1956). The highly derived dentition of tritylodontids offers both strong corroboration of the group's monophyly and evidence pertaining to their phylogeny. Recent phylogenies (Clark and Hopson, 1985; Sues, 1986b) indicate that tritylodontids arose from a small ancestor, and that size increase within the group was secondary.

Mammaliaforms first appear in the Early Jurassic, between 208 ± 8 and 203 ± 7 million years ago (see above, Node 5). Tritylodontids have a record that extends to into the Middle and perhaps the Late Jurassic (e.g., Clark and Hopson, 1985).

NODE 7: (UNNAMED). This unnamed taxon comprises the last common ancestor that mammals share with *Sinoconodon* and all its descendants. The diagnosis of this taxon consists solely of features of the skull, which may simply reflect that the postcranium of *Sinoconodon* is virtually unknown. The diagnosis of this group is more extensively detailed by Crompton and Luo (this volume, chapter 4). Information used to score character states for *Sinoconodon* (Rowe and Simmons, unpublished) was generously provided by Z. Luo and A. W. Crompton (personal communication), supplementing previous literature (Crompton and Sun, 1985; Patterson and Olson, 1961).

The medial wall of the orbit became completely closed by further expansion of the orbitosphenoid, which contributed to the orbital processes of the frontal and palatine. The hindbrain was expanded, causing the parietals to bulge outward into the temporal fenestrae and the basicranium to become wider than the choana. Correspondingly, the cavum epipterygium became completely enclosed beneath the trigeminal ganglion, and the petrosal promontorium also appeared.

On the dentary is a large condyle that articulates with a distinctive glenoid fossa on the squamosal (Crompton and Sun, 1985), although the quadrate and articular remained involved in the articulation and the postdentary bones remained attached to the mandible throughout life. The dentary-squamosal articulation is a widely discussed character. Under the character-based definitions of the Linnean System, many authors regarded it as the definitive structure dividing mammals from reptiles.

This engendered debate about whether Mammalia was mono- or polyphyletic because some authors asserted that the dentary condyle evolved convergently among the various Triassic and Jurassic taxa that possess it (e.g., Barghusen and Hopson, 1970). In light of the recent phylogenetic analyses summarized here and elsewhere, it is now evident that the dentary-squamosal articulation evolved only once, but that it is more widely distributed than previously believed. It is true that all mammals possess this articulation, but it now also appears true that not all taxa with a dentary-squamosal joint are mammals under a definition based on common ancestry.

The dentition of *Sinoconodon* is highly apomorphic in that the upper and lower cheekteeth did not occlude, and there was little or no replacement of them during ontogeny (Crompton and Luo, this volume, chapter 4). The position of the cheekteeth is also unique in that the rear end of the row extends onto the lower edge of the zygoma (Crompton and Sun, 1985; Crompton and Luo, this volume, chapter 4). This is yet another manifestation of the high rate of dental evolution in eucynodonts.

As with tritylodontids and tritheledontids, the earliest members of Node 7 first appear in the Early Jurassic (see above, Node 5).

NODE 8: MAMMALIAFORMES. Mammaliaformes comprises the last common ancestor shared by Mammalia and *Morganucodon* and all its descendants (Rowe, 1986, 1988). In older works (e.g., Hopson and Crompton, 1969), morganucodontids were considered to be among the oldest "true" mammals and were believed most closely related to monotremes among extant taxa. This was properly taken as an indication that Mammalia had both originated and split into its two major daughter lineages sometime before the Late Triassic. Implicit in this view was the idea that the origin of Mammalia corresponds to the appearance of the last common ancestor of monotremes and therians, and not a more distant ancestor. This view is formalized in the contemporary phylogenetic definition of Mammalia, which is based on the last common ancestor of living taxa. However, the strength of evidence now indicates that monotremes and therians are more closely related to each other than to morganucodontids (Kemp, 1983; Rowe, 1988; Gauthier et al., 1988; Wible, 1991). Under the phylogenetic definition, morganucodontids are not mammals, a conclusion hinging on their revised phylogeny. A number of authors continue to refer to morganucodontids and *Sinoconodon* as "mammals," evidently in an effort to preserve the traditionally recognized membership of Mammalia. However, this implicitly casts the definition of mammals in terms of characters and evolutionary grade, a perspective largely abandoned by the phylogenetic system (but see Szalay, this volume, chapter 9).

Mammaliaformes is diagnosed by characters of the skull and dentition. There was further modification of the orbital floor, in which the maxilla has come to participate (Luo, personal communication). There was also further modification of the dentition, in which the cheekteeth came to occlude in a unilateral pattern (Crompton and Jenkins, 1979; Crompton, 1989), although lateral excursion of the mandibles was still greatly constrained by the transverse process of the pterygoids and the persistence of a robust coronoid bone on the medial surface of the dentary. Mammaliaform cheekteeth are also differentiated into a pattern of relatively simple premolariform teeth in front, with more complex molariform teeth behind. Whether these dental groups also possessed the replacement patterns commonly associated with the terms "premolar" and "molar" is as yet unclear in most relevant extinct taxa.

Morganucodontids first appear together with *Sinocodon*, tritylodontids, and tritheledontids in the Early Jurassic (see above, Node 5).

NODE 9: MAMMALIA. Mammalia comprises the last common ancestor of monotremes and therians and all of its descendants (Rowe, 1986, 1987, 1988; Rowe and Simmons, unpublished; de Queiroz and Gauthier, 1990). In older literature, the mammalian boundary was ambiguous because no consensus could be reached on which character or character assemblage marked the most meaningful discontinuity between mammals and reptiles. This uncertainty is removed by a phylogenetic definition of Mammalia, whose common ancestry unequivocally sets it apart from all other taxa, living and extinct. The phylogenetic definition has also significantly altered our view of many basic properties of Mammalia, including its diagnosis, membership, and distribution in time. This is not merely a semantic transformation, because it reflects a revised genealogical hypothesis among the Mesozoic taxa that have long figured centrally in this debate, and it alters our measures of the most fundamental evolutionary properties of many of these taxa (Rowe, 1988).

Most of the skeletal characters diagnosing Mammalia, and which set the last common ancestor of monotremes and therians apart from morganucodontids, involve "repackaging" of an enlarged brain and special sense organs. In the snout, the prenasal process was lost in adults, rendering the external nares confluent. The nasal chamber expanded to such an extent posteriorly that its rearmost portion lies in a subcerebral position. An ossified cribriform plate appeared at the same time, fully separating the nasopharynx from the braincase. At the rear of the skull, the hindbrain became greatly inflated, resulting in profound remodeling of the skeletal structures in that region. The parietals bulged outward into the temporal fenestrae, and the paroccipital processes were rotated sharply downward as the brain

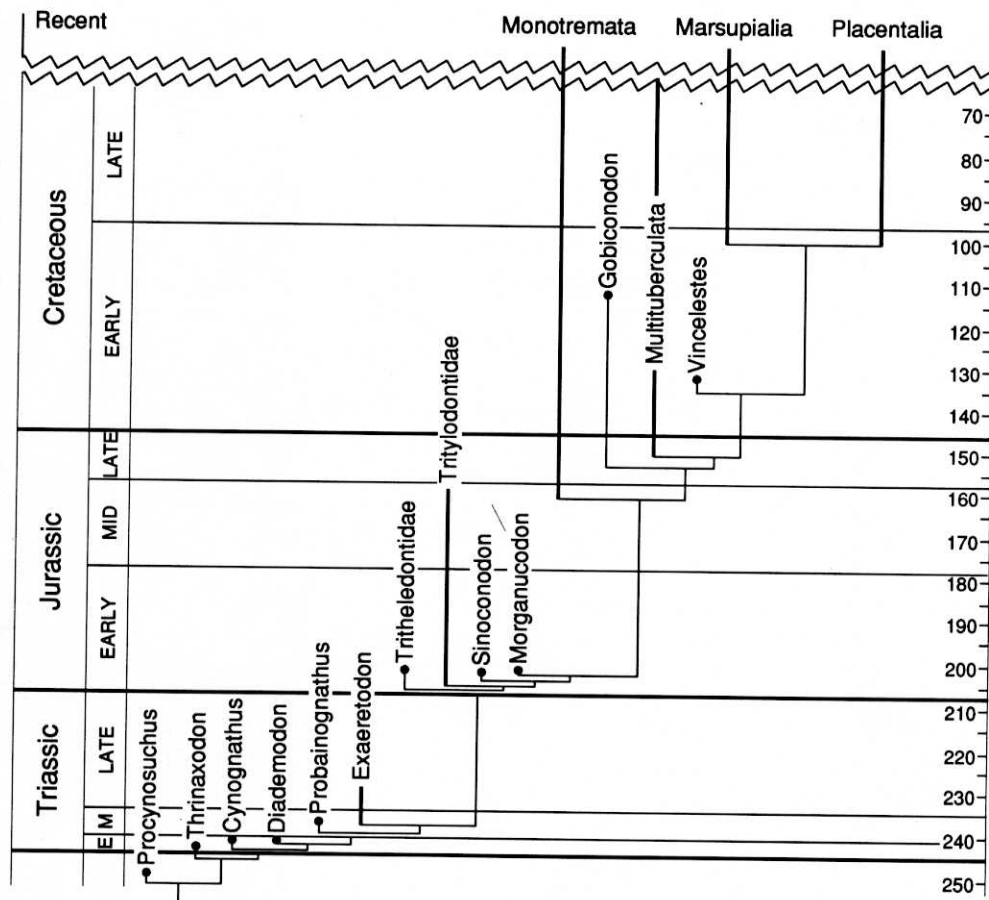
expanded outward over the region of the trigeminal ganglion and middle ear structures, from its ancestral position lying almost entirely between them. In addition, the occipital condyles were greatly expanded, coming to enclose the entire ventral two-thirds of the foramen magnum.

The visceral arch skeleton was also affected by inflation of the hindbrain. The middle ear ossicles, which derive from the first arch, shifted, in the most famous transformation of this entire history, from their primitive attachment throughout ontogeny to the mandible, to a new position suspended beneath the adult cranium. As a result, the quadrate (now the incus) and articular (now the malleus) were removed from the craniomandibular joint, which in adult mammals is built entirely from the dentary and squamosal, with occasional secondary contributions from other bones such as the alisphenoid. The second visceral arch was also affected. The stapes was reduced and the stapedia foramen, retained in adult morganucodontids, tritylodontids, and most mammalian embryos, was lost in adult mammals. Lateral to the stapes, Reichert's cartilage became attached to the cranium but, unlike the ear ossicles, its proximal end coossified with the cranium to form the adult styloid process, while its more distal corpus became detached and continued its primitive role in the hyoid apparatus. Technically a visceral arch derivative, the transverse process of the pterygoid became reduced from a massive structure that fit closely between the coronoid bones of the mandible to a vestigial structure, the pterygoid hamulus. The modifications of the middle ear probably signal greater auditory sensitivity to high frequencies. Taken collectively, these visceral arch modifications all contributed far greater ranges of lateral movement and longitudinal rotation of the mandibles than ever before.

In the postcranium, modification of the occiput was complemented by the atlas, whose formerly separate parts fused to form a solid ring. In addition, the cervical ribs became fused to their vertebrae, enclosing the foramina transversaria, and perhaps also contributing strength and stability to the craniocervical mobility. Elsewhere in the postcranium, the limbs and girdles developed secondary ossification centers or epiphyses. In many areas these are related to the more intricate and precise sculpting of the joints, for example, in the styloid processes of the radius, tibia, and fibula. Secondary ossifications are also involved in the fibular flabellum, patella, and sesamoid bones in the flexor musculature of the hands and feet. At least a small degree of opposition of the hallux to the other toes was possible in mammals ancestrally, though the degree of movement is left ambiguous by the highly modified feet on monotremes (see Szalay, this volume, chapter 9).

Because Mammalia is defined on the basis of the common ancestor of two extant lineages, it is also possi-

FIGURE 10.3. Cynodont phylogeny superimposed on a Mesozoic time scale, based on Harland et al. (1990). Scale is in millions of years before present. Extinct taxa known from only very limited stratigraphic ranges are represented by small circles; taxa with extended ranges are depicted with heavy line. The range for monotremes is inferred from the fossil record of its sister taxon.



ble to provide a “soft” diagnosis. As detailed elsewhere (Gauthier et al., 1988, Appendix B; Gauthier et al. 1989), extensive remodeling of “soft” tissues affected the nervous system, circulatory system, pulmonary system, digestive system, excretory system, endocrine system, and the integument and modified a number of developmental and metabolic pathways. Behavioral modifications have also been documented. Although we will probably never know the exact levels within Synapsida at which these modifications arose, these characters nevertheless distinguish mammals among extant tetrapods (Gauthier et al., 1988, 1989) and can be postulated to have been present in, if not apomorphic of, the ancestral mammal.

A long gap in the stratigraphic record separates the oldest mammal fossils from morganucodontids, the sistergroup of mammals. The oldest fossil possessing character states derived within Mammalia is *Phascolotherium bucklandi*, a member of Theriimorpha (Rowe, 1988). It is known from the Middle Jurassic (Bathonian) Stonesfield Slate of England, which is between 166 ± 8 and 161 ± 8 million years old (Harland et al., 1990). This estimate of the minimum age of Mammalia represents a reduction by nearly one-fourth over pre-

vious estimates, which treated morganucodontids as the earliest mammals.

The large number of osteological characters diagnosing Mammalia may reflect a jump in evolutionary rates, as was the case with the origin of Node 5 (above). However, with the wide margin of dating error and a major gap in the mid-Jurassic fossil record (Fig. 10.3), it remains possible that this number merely reflects average evolutionary rates during the Jurassic, and that stratigraphic incompleteness accounts for their accumulation at this node.

NODE 10: THERIIMORPHA. Theriimorpha is the only taxon discussed here that I prefer to diagnose using a stem-based definition (de Queiroz and Gauthier, 1990). The monophylies of theria and Mammalia are both firmly established; hence there is little doubt that a monophyletic taxon exists that includes therians and all extinct taxa closer to therians than to monotremes. Despite this certainty on monophyly of Theriimorpha, its diagnosis is among the weakest of any on the tree, and relationships among the basal theriimorphs are sufficiently unresolved that stable node-based definitions are not yet practical. This weakness is due in part to

the high incompleteness of virtually all Mesozoic fossils representing the group, as well as to the lack of a fossil record and the highly apomorphic nature of monotremes, the sister taxon of Theriimorpha. Doubtless, as the Jurassic through Early Cretaceous segment of theriimorph history is more completely understood, the diagnoses of Theriimorpha and a number of subsequent nodes will be revised.

The basal theriimorph represented in Figure 10.2 is *Gobiconodon*, which is the most complete of the theriimorphs that consistently fell outside of Theriiformes in the analyses summarized above. There are many other taxa that cluster unresolved in this position, such as *Trioracodon ferox*, *Triconodon mordax*, *Phascolotherium bucklandi*, and the unnamed "eupantothere" briefly described by Krebs (1987). In one of the many equally parsimonious trees, *Gobiconodon* and *Triconodon* are sister taxa in what would constitute a monophyletic Triconodonta, based on tooth crown morphology. However, there are numerous other possible relationships among basal theriimorphs, and stable resolution of their relationships will probably be gained only with the discovery of more complete specimens.

The diagnosis of Theriimorpha includes the inflected angle, or pterygoideus shelf, of the dentary. In addition, the external acoustic meatus became redirected to occupy a characteristic position behind the craniomandibular joint. Both characters are equivocal because of the highly apomorphic state of monotremes. In the shoulder girdle, the coracoid was reduced, as indicated in *Gobiconodon* by a reduced articular facet on the scapula.

As described earlier (see Node 9, Mammalia) the oldest theriimorph is *Phascolotherium bucklandi*, which preserves the inflected angle, from the Middle Jurassic Stonesfield Slate (Rowe, 1988).

NODE 11: THERIIFORMES. Theriiformes comprises the last common ancestor therians share with multituberculates (*sensu* Simmons, this volume, chapter 11), and all its descendants. The position of Multituberculata has long been controversial, and no consensus can be found even in recent phylogenetic literature. However, the solution advocated here was stable in the face of the sampling tests described above and takes into account all available data (Rowe, 1988; Rowe and Simmons, unpublished; see also Sereno and McKenna, 1990).

Equivocation on the position of multituberculates appears in large part an artifact of sampling, which in the past was restricted to dental and cranial data. Although many authors have looked to the dentition for information on higher-level relationships, even the most primitive multituberculate teeth are so apomorphic that little unambiguous information relevant to the broad temporal scope of this problem remains. This dentition has been highly informative at the more restricted tem-

poral scope of relationships within the group, however (Greenwald, 1989; Simmons, this volume, chapter 11).

Relatively few cranial characters have been found to support any of the competing hypotheses of multituberculate relationships to other taxa, and homoplasy complicates the issue in every analysis. Multituberculates were long linked with morganucodontids and monotremes, based on resemblances of the braincase that subsequent studies have shown to be plesiomorphic (Presley, 1981; Kemp, 1983; Novacek and Wyss, 1986; Rowe, 1988). More recently, however, Wible (1991) analyzed selected subsets of the cranial and dental data used by Rowe (1988) and found what appeared to be new support for sister relationships between multituberculates and monotremes. Comparing these results is complicated because the two studies analyzed different sets of taxa and characters. The most inclusive analysis (Rowe and Simmons, unpublished) found that multituberculates and therians share communication of the post-temporal fenestra with an enclosed paracranial passage rather than with the temporal fossa, as it did in mammals ancestrally (Kielan-Jaworowska et al., 1986; Wible, 1990). In addition, the incus lies postertor to the malleus, and the ectotympanic lies on a plane inclined from the horizontal (Miao and Lillegraven, 1986).

Reference to the postcranium provides a great deal of additional corroboration of this relationship. It was recognized for many years that multituberculates and therians share striking postcranial resemblances (Gidley, 1909; Simpson and Elftman, 1928; Jenkins and McClearn, 1984), but most authors have asserted the similarities to be convergent because the dentitions of multituberculates and therians are so different. When all available data are considered, however, it now appears that the multituberculate dentition diverged at a rapid rate rather than at a distant in time, and that the postcranial similarities reflect common ancestry. The most marked similarities involve the shoulder girdle and humerus, the femur, and the ankle. In the shoulder, the procoracoid became lost as a discrete adult ossification and the acromion process became strongly down-turned, projecting to a level below the roof of the glenoid. The humeral head became spherical and strongly inflected dorsally, and the teres and deltopectoral crests became reduced to narrow tubercles separated by a narrow bicipital groove. The distal end was also modified with only weakly developed entepi- and ectepicondyles. The femoral head became spherical, inflected medially, and set apart from the shaft on a constricted neck. The lesser trochanter rotated from its former position medial to the shaft to a new position on the ventral surface of shaft, while the greater trochanter became elongated and massive. In the ankle, the calcaneal tuber was elongated to a length greater than its width. In the foot, the entocuneiform developed a strongly saddle-shaped articulation (*viz.*, fully oppos-

able hallux), and a styloid process developed on the proximal end of metatarsal V for the insertion of the peroneal musculature.

The oldest members of Multituberculata (*sensu* Simmons, this volume, chapter 11) are from the Kimmeridgian Guimarota deposits of Portugal, which are between 155 ± 8 and 152 ± 12 million years old. Many authors have included haramiyids, a poorly known taxon based entirely on isolated and highly derived teeth, within Multituberculata, extending the range of the group into the Triassic (Hahn, 1973; Sigogneau-Russell, 1989). However, haramiyids were the most phylogenetically labile taxa studied by Rowe and Simmons (unpublished). When analyzed with the taxa depicted in Figure 10.2, there were at least six other equally parsimonious positions for haramiyids besides the possibility that they are the sister taxon to multituberculates, and several thousand possible positions when all taxa were considered. This lability leaves little justification for using haramiyids to mark the minimum time of multituberculate origin. Moreover, the broad temporal separation between haramiyids and multituberculates speaks, albeit circumstantially, against the possibility of sister relationships between them.

NODE 12: (UNNAMED). This unnamed taxon comprises the most recent common ancestor of *Vincelestes* and Theria and all its descendants. *Vincelestes* is known from several nearly complete skulls and postcranial skeletons, but to date only a preliminary description of the skull (Bonaparte and Rougier, 1987) and details of the snout (Wible et al., 1990) have been published. Nevertheless, the conclusion that *Vincelestes* is the sister taxon of Theria has been reached by all who have treated it (Bonaparte and Rougier, 1987; Rowe and Simmons, unpublished; Wible et al., 1990); further testing of this conclusion will occur as Rougier completes his ongoing analysis of the postcranium. The skull in *Vincelestes* shares with therians a broad contact between the alisphenoid and frontal, and a cochlea that is elongated and coiled 360 degrees or more. Bonaparte and Rougier (1987) also described a small participation by the squamosal in the braincase.

Vincelestes is the earliest representative of Node 12. It was collected from the La Amarga Formation of Argentina, of Early Cretaceous (Hauterivian) age, roughly between 135 ± 8 and 132 ± 8 million years old (Harland et al., 1990).

NODE 13: THERIA. Theria comprises the most recent common ancestor shared by extant marsupials and placentals and all of its descendants (but see Cifelli, this volume, chapter 14, and Szalay, this volume, chapters 9 and 15, for a different concept of Theria) Because it is defined by two extant lineages, data from virtually every anatomical system diagnose Theria (e.g., Marshall,

1979; Lillegraven et al., 1987). Although the exact point within Theriimorpha at which most soft characters arose is uncertain, these characters are nevertheless apomorphic of therians, compared to other extant taxa, and we may infer the characters to have been present in extinct therians. There are a number of poorly known Mesozoic taxa, in particular deltatheridians and various other taxa commonly referred to as "therians of the metatherian-eutherian grade," that have not yet been analyzed phylogenetically. It is uncertain whether these taxa lie within Theria or only close to it, and their eventual inclusion into future phylogenetic analyses is likely to revise the following "hard" diagnosis.

Theria is diagnosed by modifications of both the cranium and postcranium. In the vicinity of the braincase, the anterior lamina of the prootic was lost, and the floor of the cavum epipterygium became enclosed predominantly by the alisphenoid. In addition, the pila antotica no longer formed an ossified adult structure, although atavistic remnants of the structure have been reported in rare Recent individuals (e.g., de Beer, 1937). The postcranium was marked by more subtle modifications. In the vertebral column, the inferior lamella appeared on the ventrum of the sixth cervical vertebra, and secondary ossifications developed on the faces of most or all presacral centra. Elsewhere in the postcranium, the acetabulum was remodeled by the development of an inverted, U-shaped articular tract for the femoral head.

Kuehneotherium was long viewed as the earliest therian (e.g., Hopson and Crompton, 1969; Prothero, 1981) and as such, it was properly taken as evidence of the Triassic origin of mammals because it seemed to indicate that monotremes and therians had, by the Late Triassic, already diverged from their last common ancestor. However, using ancestry-based taxon definitions, it now appears that *Kuehneotherium* is neither a therian nor a mammal. The oldest fossils preserving characters derived within Theria are teeth of the marsupial *Pariadens kirklandi*, from Late Cretaceous (Cenomanian) Dakota Formation of Utah (Cifelli and Eaton, 1987), which is between 97 ± 3 and 90 ± 3 years old.

Constraints on the Positions of Unresolved Taxa

A number of additional taxa were treated in the analyses by Rowe and Simmons (unpublished), including *Masetognathus*, *Asioryctes*, Docodonta, *Triconodon*, *Triaracodon*, *Kuehneotherium*, *Dinnetherium*, Haramiyidae, and an unnamed "eupantothere" described briefly by Krebs (1987). These taxa were less complete than those described above, and their positions could not be unambiguously resolved. However, it was found that each

of these taxa ranged in position over finite segments of the tree depicted in Figure 10.2. *Massetognathus* was closer to Mammaliomorpha than either *Diademodon* and *Cynognathus*, but it was not as close as *Exaeretodon*. In a similar way, Docodonts, *Dinnetherium*, and *Kuehneotherium* each consistently varied between Nodes 7 and 9, while *Triconodon*, *Trioracodon*, and Krebs's unnamed "eupantothere" fell between Nodes 9 and 11. Haramiyidae was the least complete and the most labile taxon studied, ranging in positions between Nodes 6 and 13.

Conclusions

Methods of sampling taxa and characters for particular systematic problems can be a determining factor in the outcome of phylogenetic analyses, and they may be a major source of current conflicts in interpreting early mammalian phylogeny. Some of the most persistent systematic problems in early mammalian history have been the result of restricted character sampling, in part a result of the preservational bias toward dental data. But because different systems transform at different rates, we should not expect any particular region to be informative for phylogenetic questions at all temporal scales. Resolution of a host of long-standing systematic problems in early mammalian history, such as the position of multituberculates, has been gained by reference to a diverse data set and by filtering out artifacts attributable to sampling. Further examination of sampling and rates may be the most direct avenue to resolving many remaining conflicts.

The eucynodont phylogeny that has emerged from recent phylogenetic analyses is dominated by several patterns. One involves a great acceleration in the rate and complexity of dental evolution. The initiation of this trend can be traced to the ancestral eucynodont, which lived no later than the earliest Triassic, and in which appeared several structures critical to occlusion, most notably the periodontal ligament. From that ancestor evolved descendants with an enormous diversity of complex tooth morphologies and occlusal relationships. Because of its rapid transformation rate, the dentition in fossil and extant eucynodonts is most likely to be informative with respect to phylogenetic problems encompassing short temporal spans, such as relationships at low taxonomic levels. By reference to the more slowly evolving skull and postcranium, the broader history of the dentition can be unambiguously interpreted.

Another pattern, this one long recognized, involves a major reorganization of the skull involving repackaging of a greatly inflated brain and special sensory organs. This trend was manifested throughout eucynodont history, and during the Mesozoic it resulted in the complete and intimate osseous enclosure of the brain along

with some of its associated vessels. The brain expanded to nearly one-half the length of the skull and greatly increased in width. This was associated with ontogenetic fusions among bones that primitively remained separate throughout life, a great increase in the extent of both membranous and endochondral bone, and profound remodeling of inherited structures. The nasal capsule and associated structures also expanded enormously, extending backward to a subcerebral position, displacing the choana backward as well. The orbit, lying between the inflated nasal capsule and brain, became enclosed medially and was extensively reorganized in other respects.

The postcranium was also reorganized during this time as the vertebral column became fully differentiated and the limbs correspondingly transformed. The neck became markedly differentiated, enhancing mobility of the head. Specialization of thoracic and lumbar regions was accompanied by reorientation of the principal plane of flexure of the vertebral column, indicating a shift toward parasagittal gait. An associated transformation involved segmentation of the sternum, whose role in the shoulder girdle diminished over time, becoming functionally linked instead to the vertebral column. The appendicular skeleton was correspondingly modified as the limbs became long and slender, developing intricately sculpted articulations, and the girdles were modified to permit great ranges of stable excursion. These changes probably reflect coupling of breathing tides and gait cycles, and an expanded metabolic scope.

The various character states that record these transformations are not distributed equally along the phylogeny, pointing to yet another pattern. The greatest number of changes occurred in the last common ancestor of tritheledontids and mammaliomorphs (Node 5), in association with miniaturization. The early parts of cynodont history were carried out by relatively large animals. But, beginning at Node 5, a long segment of the mammalian history involved animals that fall into the smallest order of vertebrate size magnitudes. With this reduction in size occurred a rapid remodeling of virtually all parts of the skeleton, involving a complex interplay of both paedomorphosis and peramorphosis (Rowe, 1989, 1990). Similar changes have been described in other miniaturized tetrapod lineages, suggesting that developmental constraints common to all tetrapods had profound influence on the shape of mammalian history.

This general picture bears strong resemblance to older views, and the broader features of several of these patterns have long been recognized. However, the picture has also been altered in fundamental respects as our measures of the evolutionary properties of taxa have changed under phylogenetic systematics. In addition, many new details of evolutionary pattern have come to light, and entirely new patterns involving both

tempo and mode of evolution have been discovered through efforts to understand the effects of rate and sampling on the outcome of phylogenetic analyses. The picture will undoubtedly continue to change as we collect new data from extant and extinct forms, and as we further scrutinize the effects of our analytic methods on the patterns we seek to explain.

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References

- Alberch, P., and Alberch, J. 1981. Heterochronic mechanisms of morphological diversification and evolutionary change in the neotropical salamander *Bolitoglossa occidentalis* (Amphibia: Plethodontidae). *J. Morph.* 167:249–264.
- Allin, E.F. 1986. The auditory apparatus of advanced mammal-like reptiles and early mammals. In *Ecology and biology of mammal-like reptiles* (Hotton N.H. III, MacLean, P.D., Roth, J.J., and Roth, E.C., eds.). Washington, D.C.: Smithsonian Institution and National Institute of Mental Health, pp. 283–294.
- Anderson, H.M., and Cruickshank, A.R.I. 1978. The biostratigraphy of the Permian and Triassic. Part 5: A review of the classification and distribution of Permo-Triassic tetrapods. *Palaeontol. Afr.* 21:15–44.
- Aulie, R.P. 1974. The origin of the idea of mammal-like reptile. Parts I–III. *Am. Biol. Teacher* 36:476–485; 36:545–553; 37:21–32.
- Barbarena, M.C. 1974. *Contribuição ao conhecimento dos cinodontes gonfodontes (Cynodontia, Tritylodontidae) do Brasil*. Ph.D. thesis, University Federal do Rio Grande del Sul.
- Barghusen, H.R. 1986. On the evolutionary origin of the thetarian tensor veli palatini and tensor tympani muscles. In: *Ecology and biology of mammal-like reptiles* (Hotton N.H. III, MacLean, P.D., Roth, J.J., and Roth E.C., eds.). Washington, D.C.: Smithsonian Institution and National Institute of Mental Health, pp. 253–262.
- Barghusen, H.R., and Hopson, J.A. 1970. Dentary-squamosal joint and the origin of mammals. *Science* 168:573–575.
- Bonaparte, J.F. 1966. Sobre las cavidades cerebral, nasal y otras estructuras del cráneo de *Exaeretodon* sp. (Cynodontia-Traversodontidae), Tucuman. *Acta Geologica Lilloana* 8:5–31.
- Bonaparte, J.F., and Rougier, G. 1987. Mamíferos del Cretácico inferior de Patagonia. *IV Congreso Latinoamericano de Paleontología, Bolivia* 1:343–359.
- Bramble, D.M. 1989. Axial-appendicular dynamics and the integration of breathing and gait in mammals. *Syst. Zool.* 29:171–186.
- Bramble, D.M., and Jenkins, F.A. Jr. 1989. Structural and functional integration across the reptile-mammal boundary: The locomotor system. In: *Complex organismal functions: Integration and evolution in vertebrates* (Wake, D.B., and Roth, G., eds.). New York: John Wiley, pp. 133–146.
- Broom, R. 1932. *The mammal-like reptiles of South Africa and the origin of mammals*. London: H. F. & G. Witherby.
- Cifelli, R.L., and Eaton, J.G. 1987. Marsupial from the earliest late Cretaceous of western U.S. *Nature* 325:520–522.
- Clark, J.M., and Hopson, J.A. 1985. Distinctive mammal-like reptile from Mexico and its bearing on the phylogeny of the Tritylodontidae. *Nature* 315:389–400.
- Cloutier, R. 1991. Patterns, trends, and rates of evolution within the Actinistia. In: *Environmental biology of fishes*. Netherlands: Kluwer Academic Publishers, 32:23–58.
- Crompton, A.W. 1963. Tooth replacement in the cynodont *Thrinaxodon liorhinus*. *Ann. S. Afr. Mus.* 46:479–521.
- Crompton, A.W. 1972. Postcanine occlusion in cynodonts and tritylodontids. *Bull. Br. Mus. Nat. Hist. (Geol.)* 21:27–71.
- Crompton, A.W. 1989. The evolution of mammalian mastication. In: *Complex organismal functions: Integration and evolution in vertebrates* (Wake, D.B., and Roth, G., eds.). New York: John Wiley, pp. 23–40.
- Crompton, A.W., and Jenkins, F.A. Jr. 1973. Mammals from reptiles: A review of mammalian origins. *Annual Review of Earth and Planetary Sciences* 1:131–155.
- Crompton, A.W., and Jenkins, F.A. Jr. 1979. Origin of mammals. In: *Mesozoic mammals: The first two thirds of mammalian history* (Lillegrave, J.A. Kielan-Jaworowska, Z., and Clemens, W.A., eds.). Berkeley: University of California Press, pp. 59–73.
- Crompton, A.W., and Sun, A.-L. 1985. Cranial structure and relationships of the Liassic mammal *Sinoconodon*. *Zool J. Linnean Soc.* 85:99–119.
- de Beer, G.R. 1937. *The development of the vertebrate skull*. Oxford: Oxford University Press.
- de Queiroz, K. 1988. Systematics and the Darwinian revolution. *Philos. Sci.* 55:238–259.
- de Queiroz, K., and Gauthier, J.A. 1990. Phylogeny as a central principle in taxonomy: Phylogenetic definitions of taxon names. *Syst. Zoo.* 39:307–322.
- Donoghue, M.J., Doyle, J.A., Gauthier, J., Kluge, A.G., and Rowe, T. 1989. The importance of fossils in phylogeny reconstruction. *Ann. Rev. Ecol. Syst.* 20:431–460.
- Doyle, J.A., and Donoghue, M.J. 1987. The importance of fossils in elucidating seed plant phylogeny and macroevolution. *Rev. Paleobot. Palynol.* 50:63–95.
- Farris, J.S. 1986. Hennig 86, version 1.5. Computer software distributed on 5-inch diskette by J.S. Farris.
- Farris, J.S. 1989a. The retention index and the rescaled consistency index. *Cladistics* 5:417–419.
- Farris, J.S. 1989b. The retention index and homoplasy excess. *Syst. Zool.* 38:406–407.
- Fink, W.L. 1981. Ontogeny and phylogeny of tooth attachment modes in actinopterygian fishes. *J. Morph.* 167:167–184.
- Fourie, S. 1974. The cranial morphology of *Thrinaxodon liorhinus* Seeley. *Ann. S. Afr. Mus.* 65:337–400.
- Gauthier, J.A. 1986. Saurischian monophyly and the origin of birds. In: *The origin of birds and the evolution of flight* (Padian, K., ed.). *Mem. Calif. Acad. Sci.* 8:1–55.
- Gauthier, J.A., Cannatella, D., de Queiroz, K., Kluge, A.G.,

- and Rowe T. 1989. Tetrapod phylogeny. In: *The hierarchy of life: Molecules and morphology in phylogenetic analysis* (Fernholm, B., Bremer, K., and Jornvall, H., eds.). Amsterdam: Nobel Symposium 70, Excerpta Medica, pp. 337–354.
- Gauthier, J.A., Kluge, A.G., and Rowe, T. 1988. Amniote phylogeny and the importance of fossils. *Cladistics* 4:105–209.
- Ghiselin, M.T. 1984. "Definition," "character," and other equivocal terms. *Syst. Zool.* 33:104–110.
- Gidley, J.W. 1909. Notes on the fossil mammalian genus *Ptilodus*, with descriptions of new species. *Proc. U.S. Nat. Mus.* 36:611–626.
- Gow, C.E. 1980. The dentitions of the Trithelodontidae (Therapsida: Cynodontia). *Proc. Roy. Soc. London* B208:461–481.
- Greenwald, N.S. 1989. *Phylogeny and systematics of multituberculate mammals*. Ph.D. Dissertation, University of California, Berkeley.
- Haeckel, E. 1897. *The evolution of man*, vols. 1 and 2. New York: Appleton and Co.
- Hahn, G. 1973. Neue Zähne von Haramiyiden aus der deutschen Ober-Trias und ihre Beziehungen zu den Multituberclaten. *Palaeontographica Abt. A* 142:1–15.
- Hanken, J. 1983. Miniaturization and its effects on cranial morphology in plethodontid salamanders, genus *Thorius* (Amphibia, Plethodontidae): II. The fate of the brain and sense organs and their role in skull morphogenesis and evolution. *J. Morph.* 177:255–268.
- Hanken, J. 1984. Miniaturization and its effects on cranial morphology in plethodontid salamanders, genus *Thorius* (Amphibia: Plethodontidae). I. Osteological variation. *Biol. J. Linn. Soc.* 23:55–75.
- Harland, W.B., Armstrong, R.L., Cox, A.V., Craig, L.E., Smith, A.G., and Smith, D.G. 1990. *A geological time scale 1989*. Cambridge: Cambridge University Press.
- Hopson, J.A. 1969. The origin and adaptive radiation of mammal-like reptiles and non-therian mammals. *Ann. New York Acad. Sci.* 167:199–216.
- Hopson, J.A. 1984. Late Triassic traversodont cynodonts from Nova Scotia and southern Africa. *Palaeontol. Afr.* 25:181–201.
- Hopson, J.A., and Barghusen, H.R. 1986. An analysis of therapsid relationships. In: *Ecology and biology of mammal-like reptiles* (Hotton N.H. III, MacLean, P.D., Roth, J.J., and Roth, E.C., eds.). Washington, D.C.: Smithsonian Institution and National Institute of Mental Health, pp. 83–106.
- Hopson, J.A., and Crompton, A.W. 1969. Origin of mammals. *Evol. Biol.* 3:15–72.
- Hopson, J.A., and Kitching, J.W. 1972. A revised classification of cynodonts. *Palaeont. Afr.* 14:71–85.
- Hull, D.L. 1976. Are species really individuals? *Syst. Zool.* 25:174–191.
- Jenkins, F.A. Jr. 1969. The evolution and development of the dens of the mammalian axis. *Anat. Rec.* 164:173–184.
- Jenkins, F.A. Jr. 1971. The postcranial skeleton of African cynodonts. *Bull. Peabody Mus. Nat. Hist.* 36:1–216.
- Jenkins, F.A. Jr., and McClearn, D. 1984. Mechanisms of hind foot reversal in climbing mammals. *J. Morph.* 182:197–219.
- Johnson, A. 1983. The physiology of tooth eruption. *Birth Defects: Original Article Series* 19:67–82.
- Kemp, T. 1979. The primitive cynodont *Procynosuchus*: Functional anatomy of the skull and relationships. *Phil. Trans. Roy. Soc. London* B285:73–122.
- Kemp, T. 1980. The primitive cynodont *Procynosuchus*: Structure, function and evolution of the postcranial skeleton. *Phil. Trans. Roy. Soc. London* B288:217–258.
- Kemp, T. 1982. *Mammal-like reptiles and the Origin of mammals*. London: Academic Press.
- Kemp, T., 1983. The relationships of mammals. *Zool. J. Linn. Soc. London* 77:353–384.
- Kemp, T. 1988a. A note on the Mesozoic mammals, and the origin of therians. In: *The phylogeny and classification of the tetrapods, vol. 2: Mammals* (Benton, M. J., ed.). Syst. Assoc. Spec. Vol. No. 35B. Oxford: Clarendon Press, pp. 23–29.
- Kemp, T. 1988b. Interrelationships of the Synapsida. In: *The phylogeny and classification of the tetrapods, vol. 2: Mammals* (Benton, M.J., ed.). Syst. Assoc. Spec. Vol., No. 35B. Oxford: Clarendon Press, pp. 1–22.
- Kielan-Jaworowska, Z., Presely, R., and Poplin, C. 1986. The cranial vascular system in taeniolabidoid multituberculate mammals. *Phil. Trans. Roy. Soc. London* B313:525–602.
- Kitching, J.W. 1977. The distribution of the Karroo vertebrate fauna. Mem. No. 1, Bernard Price Institute for Palaeontological Research, University of Witwatersrand, pp. 1–131.
- Kluge, A.G. 1989. A concern for evidence and a phylogenetic hypothesis of relationships among *Epicrates* (Boidae, Serpentes). *Syst. Zool.* 38:7–25.
- Krebs, B. 1987. The skeleton of a Jurassic eupantothere and the arboreal origin of modern mammals. In: *Fourth symposium on Mesozoic terrestrial ecosystems, short papers* (Currie, P.M., and Koster, E.H., eds.). Occ. Pap. No. 3., Tyrell Museum of Paleontology, Drumheller, pp. 132–137.
- Kühne, W.G. 1956. *The Liassic therapsid Oligokyphus*. London: Brit. Mus. (Nat. Hist.).
- Lillegraven, J.A., Thompson, S.D., McNab, B.K., and Patton, J.L. 1987. The origin of eutherian mammals. *Biol. J. Linn. Soc.* 32:281–336.
- Marshall, L.G. 1979. Evolution of metatherian and eutherian (mammalian) characters: A review based on cladistic methodology. *Zool. J. Linn. Soc. London* 66:369–410.
- Marshall, L.G., and Corruccini, R.S. 1978. Variability, evolutionary rates, and allometry in dwarfing lineages. *Paleobiology* 4:101–119.
- McMahon, T.A., and Bonner, J.T. 1983. *On size and life*. New York: Scientific American Books, Inc.
- Miao, D., and Lillegraven, J.A. 1986. Discovery of three ear ossicles in a multituberculate mammal. *Nat. Geograph. Res.* 2:500–507.
- Mickevich, M.F., and Platnick, N.I. 1989. On the information content of classifications. *Cladistics* 5:33–47.
- Noble, H.W. 1969. Evolution of the mammalian periodontum. In: *Biology of the Periodontium* (Melcher, A.H., and Bowen, W.H., eds.). London, New York: Academic Press, pp. 1–26.
- Novacek, M.J. 1986. The skull of leptictid insectivorans and the higher-level classification of eutherian mammals. *Bull. Am. Mus. Nat. Hist.* 183:1–112.
- Novacek, M.J. 1989. Higher mammalian phylogeny: The

- morphological-molecular synthesis. In: *The hierarchy of life: Molecules and morphology in phylogenetic analysis* (Fernholm, B., Bremer, K., and Jornvall, H., eds.). Amsterdam: Nobel Symposium 70, Excerpta Medica, pp. 421–435.
- Novacek, M.J. 1990. Morphology, paleontology, and the higher clades of mammals. In: *Current mammalogy*, vol. 2 (Genarys, H.H., ed.). New York: Plenum, pp. 507–543.
- Novacek, M.J., and Wyss, A.R. 1986. Higher-level relationships of the Recent eutherian orders: Morphological evidence. *Cladistics* 2:257–287.
- Olsen, P.E., and Galton, P.M. 1984. A review of the reptile and amphibian assemblages from the Stormberg of southern Africa, with special emphasis on the footprints and the age of the Stormberg. *Palaeontol. Afr.* 25:87–110.
- Olson, E.C. 1959. The evolution of mammalian characters. *Evolution* 13:344–353.
- Olson, E.C. 1962. Late Permian terrestrial vertebrates, U.S.A. and U.S.S.R. *Trans. Am. Phil. Soc.* 52:1–224.
- Patterson, B., and Olson, E.C. 1961. A triconodontid mammal from the Triassic of Yunnan. In: *International colloquium on the evolution of lower and specialized mammals* Part 1 (Vandebroek, G., ed.). Kon. Vlaamse Acad. Wetensch. Lett. Schone Kunstten Belgie, Brussels, pp. 129–191.
- Presley, R. 1981. Alisphenoid equivalents in placentals, marsupials, monotremes and fossils. *Nature* 294:668–670.
- Prothero, D.R. 1981. New Jurassic mammals from Como Bluff, Wyoming, and the interrelationships of non-tribosphenic Theria. *Bull. Am. Mus. Nat. Hist.* 167:280–325.
- Reed, C.A. 1960. Polyphyletic or monophyletic ancestry of mammals, or: What is a class? *Evolution* 14:314–322.
- Rieppel, O. 1984. Miniaturization of the lizard skull: Its functional and evolutionary implications. *Symp. Zool. Soc. London* 52:503–520.
- Roberts, T.R. 1981. Sundasalangidae, a new family of minute freshwater salmoniform fishes from southeast Asia. *Proc. Calif. Acad. Sci.* 42:295–302.
- Romer, A.S. 1969. Cynodont reptile with incipient mammalian jaw articulation. *Science* 166:881–882.
- Romer, A.S. 1970. The Chanares (Argentina) Triassic reptile fauna VI. A chiniquodontid cynodont with an incipient squamosal-dentary jaw articulation. *Breviora* 344:1–18.
- Roth, J.J., Roth, E.C., and Hotton, N. III. 1986. The parietal foramen and eye: Their function and fate in therapsids. In: *Ecology and biology of mammal-like reptiles* (Hotton, N.H. III, MacLean, P.D., Roth, J.J., and Roth, E.C., eds.). Washington, D.C.: Smithsonian Institution and National Institute of Mental Health, pp. 173–184.
- Rowe, T. 1986. *Osteological diagnosis of Mammalia, L. 1758, and its relationship to extinct Synapsida*. Ph.D. Dissertation, University of California, Berkeley.
- Rowe, T. 1987. Definition and diagnosis in the phylogenetic system. *Syst. Zool.* 36:208–211.
- Rowe, T. 1988. Definition, diagnosis and origin of Mammalia. *J. Vert. Paleo.* 8(3):241–246.
- Rowe, T. 1989. Skeletal ontogeny and the origin of mammals. Amer. Soc. Mammal., Abstracts to 69th Ann. Meet., pp. 34.
- Rowe, T. 1990. Tempo and mode in early mammalian morphogenesis. *J. Vert. Paleo.* 10 (Suppl. to No. 3):18A.
- Rowe, T., and Simmons, N. Unpublished. Early mammalian phylogeny and the effects of incompleteness on phylogenetic resolution.
- Sereno, P.C., and McKenna, M.C. 1990. The multituberculate clavicle and interclavicle, and the early evolution of the mammalian pectoral girdle. *J. Vert. Paleon.* 10 (Suppl. to No. 3):42A.
- Sigogneau-Russell, D. 1989. Haramiyidae (Mammalia, Allotheria) en Provenance du Trias Supérieur de Lorraine (France). *Palaeontographica, Abt. A.* 206:137–198.
- Simpson, G.G. 1959. Mesozoic mammals and the polyphyletic origin of mammals. *Evolution* 13:405–414.
- Simpson, G.G. 1960. Diagnosis of the classes Reptilia and Mammalia. *Evolution* 14:388–392.
- Simpson, G.G. 1961. Evolution of Mesozoic mammals. In: *International colloquium on the evolution of lower and specialized mammals*. Part 1 (Vandebroek, G., ed.). Kon. Vlaamse Acad. Wetensch. Lett. Schone Kunstten Belgie, Brussels, pp. 57–95.
- Simpson, G.G. 1971. Concluding remarks. In: Early mammals (Kermack, D.M., and Kermack, K.L., eds.). *Zool. J. Linn. Soc. London* 50 (Suppl. 1): 181–198.
- Simpson, G.G., and Elftman, H.O. 1928. Hind limb musculature and habits of a Paleocene multituberculate. *Novitates* 333:1–19.
- Sues, H.-D. 1985. The relationships of the Tritylodontidae (Synapsida). *Zool. J. Linn. Soc. London* 85:205–217.
- Sues, H.-D. 1986a. The skull and dentition of two tritylodontid synapsids from the Lower Jurassic of western North America. *Bull. Mus. Comp. Zool.* 151:217–268.
- Sues, H.-D. 1986b. Relationships and biostratigraphic significance of the Tritylodontidae (Synapsida) from the Kayenta Formation of northeastern Arizona. In: *The beginning of the age of dinosaurs* (Padian, K., ed.). New York: Cambridge University Press, pp. 279–284.
- Swofford, D.L. 1989. Phylogenetic analysis using parsimony [PAUP], Release 3. Macintosh computer software distributed on 31/2-inch diskette by the Illinois Natural History Survey.
- Ten Cate, A.R. 1969. The mechanism of tooth eruption. In: *Biology of the Periodontium* (Melcher, A.H., and Bowen, W.H., eds.). London, New York: Academic Press, pp. 91–103.
- Van Valen, L. 1960. Therapsids as mammals. *Evolution* 14:304–313.
- Wake, D.B. 1966. Comparative osteology and evolution of the lungless salamanders, family Plethodontidae. *Mem. S. Calif. Acad. Sci.* 4:1–111.
- Wible, J.R. 1987. The eutherian stapedial artery: Character analysis and implications for superordinal relationships. *Zool. J. Linn. Soc.* 91:107–135.
- Wible, J.R. 1990. Petrosals of late Cretaceous marsupials from North America, and a cladistic analysis of the petrosal in therian mammals. *J. Vert. Paleo.* 10:183–205.
- Wible, J.R. 1991. Origin of Mammalia: The craniodental evidence reexamined. *J. Vert. Paleont.* 11:1–28.
- Wible, J.R., Miao, D., and Hopson, J.A. 1990. The septomaxilla of fossil and recent synapsids and the problem of the septomaxilla of monotremes and armadillos. *Zool. J. Linn. Soc.* 98:203–228.