

EARLY MAMMALIAN RADIATIONS

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INTRODUCTION

THE SEVENTY-FIFTH anniversary of the *Journal of Paleontology* presents a felicitous opportunity to review major changes in interpretation of mammalian phylogeny. Founding of the journal coincides with the nascence of the career of the most influential paleomammalogist of the past century, George Gaylord Simpson (1902–1984). It occurred at a time when now-archaic models for mammalian systematics and evolution, such as the aristogenesis of H. F. Osborn (1857–1935) and the typological concept of taxa, were prevalent (e.g., Simpson, 1945). These models were soon to give way to “new ways of going at things” (Laporte, 2000, p. 87); most significantly, the incorporation of quantitative methods and the evolutionary synthesis (Simpson, 1944). Subsequent decades witnessed the rise and/or sophistication of other applications and perspectives in fossil-based interpretation of mammalian systematics, including form-function analysis (e.g., Szalay, 1994) and, particularly, cladistic approaches (e.g., McKenna, 1975). Within these broad ideological frameworks, major paradigm shifts have resulted from new discoveries, conceptual changes, or (most commonly) a combination of both. Finally, mammalian systematics currently lie at the verge of a monumental paradigm shift, providing important direction for the future.

Given the brevity of this review, I focus mainly on the base and early branches of the mammalian tree: separate chapters would be required to undertake more than superficial coverage of Cenozoic radiations of placentals and marsupials. Likewise, despite the increasingly important role that molecular data have come to play in interpreting mammalian relationships (e.g., summary by Novacek, 1993), I deal here mainly with the primary subject matter of the journal itself: the fossil record. For organizational purposes, it is convenient to follow some broad systematic framework for mammals, notwithstanding the fact that placement of several major groups is unsettled and the subject of intense debate. Herein, I generally follow the phylogeny proposed by Luo et al. (2001). Taxonomic names for higher categories of mammals have proliferated in recent years, as a result of node-based naming. Herein, I restrict usage to such terms as are most appropriate in the present context. Where traditionally-recognized groups appear to be paraphyletic but the terms remain nonetheless useful in a descriptive sense, I have adopted the common practice (e.g., Nessov et al., 1998) of citing names in quotes. Quotes are not used, however, when the same terms are used in reference to morphology (e.g., a “triconodont” has molars with a triconodont cusp pattern).

EARLIEST AND EARLIEST-DIVERGING MAMMALS

What is a mammal? In the 1920s, as for a number of decades previously, certain mammal-like reptiles (tritylodontids) were included among Mammalia, partly because their strikingly advanced cheektooth pattern is similar to what is seen in multituberculates (Simpson, 1928). Tritylodontids later (e.g., Watson, 1942) became universally regarded as non-mammalian synapsids, though their relative proximity to mammals remains contentious (e.g., Rowe, 1993; Crompton and Luo, 1993; Hopson, 1994). The union card for membership in the Mammalia long was based exclusively on diagnostic characters or character systems, especially

those thought to have significant adaptive value. Pre-eminent among features observable in fossils are those related to the masticatory system, particularly the jaw joint(s). In primitive synapsids, the lower jaw is made of multiple elements, and articulation occurs between one of the so-called postdentary elements (the articular) and the quadrate of the skull; in advanced mammals, these elements are incorporated into the auditory system, and the jaw joint is instead formed by the tooth-bearing bone of the lower jaw (dentary) and an element on the side of the skull (squamosal). Complexity arose from new discoveries, together with reinterpretation of previously-known fossils. These showed that both jaw joints were actually present in some Triassic and Jurassic taxa generally considered to be mammals (e.g., K. A. Kermack and Mussett, 1958; K. A. Kermack et al., 1973). Concomitantly, an early suggestion that mammals may have had a polyphyletic origin (Simpson, 1928, 1929a) became widely adopted by the mid-twentieth century, as a result of detailed studies of non-mammalian synapsids, as well as newly-discovered mammals from the Triassic–Early Jurassic (e.g., Olson, 1944, 1959; Simpson, 1959, 1960; see review by Hopson and Crompton, 1969). More recent studies have universally upheld a monophyletic origin for Mammalia (e.g., Rowe, 1988); the presence of a well-developed or dominant dentary–squamosal joint has remained either the principal defining character (Hopson, 1994), or one of a system of features relating to masticatory function (Crompton and Jenkins, 1973, 1979; Crompton, 1995). This definition has been challenged in recent years, however, by those advocating phylogenetic taxonomy, wherein taxa are defined on the basis of contents or subordinate taxa, rather than on characters or character complexes. Rowe (1988, 1993), for example, has proposed a node-based, crown group definition of Mammalia: that is, the most recent common ancestor of the three living groups (monotremes, marsupials, and placentals), plus all of its descendants. In this case, fossil relatives presumed to fall outside of this major clade are relegated to a hierarchy of other, successively more inclusive taxa, some of which have been named. This scheme has received mixed support, being followed by some authors (e.g., Wible et al., 1995; Rougier et al., 1996a) and ignored by others (e.g., Hopson, 1994). One of the problems inherent to phylogenetic nomenclature (see Lucas, 1992; Benton, 2000), instability of contents, is particularly acute with early mammals—the position of several key groups with respect to living taxa is highly uncertain. For the purposes of this general review, it is practical to view the contents of Mammalia in a traditional, inclusive sense. This is consistent with node-based definitions that include fossil taxa lying outside of the crown group (e.g., Lillegraven and Krusat, 1991; Cifelli and Mui-zon, 1997). Thus conceived, mammals are represented by rather complete, informative fossils dating back to the Early Jurassic, with other possible records as old as Carnian, or early Late Triassic (Lucas and Luo, 1993; Datta and Das, 1996).

A cornerstone of Simpson’s (1928) view was that mammalian specializations had occurred independently in various lineages, and that mammals therefore arose in polyphyletic fashion. He recognized four or more such lineages (Fig. 1.1). This view was enormously influential, and predominated in various forms through the early 1960s (e.g., Simpson, 1959, 1960; Olson, 1959; Van Valen, 1960). An important paradigm shift occurred by the

late 1960s, however, with detailed studies suggesting a monophyletic origin for mammals (Fig. 1.2). This view has not been seriously challenged since. Studies of this era commonly recognized a fundamental, early bifurcation in mammalian evolution (e.g., Hopson and Crompton, 1969), reflecting the dichotomy seen in living groups: some fossil taxa were allied with the monotremes while others were grouped with the living therians (marsupials and placentals). Ancestor–descendant relationships were also recognized where data permitted. Although details remain disputed, an important and enduring contribution of this era was identification, among the Mesozoic mammal radiations, of the morphologic and taxonomic antecedents to living therians, only hinted or tentatively suggested in earlier literature. Since the 1980s (e.g., Kemp, 1983, Rowe, 1988), analyses using cladistic methods have predominated in interpretation of the relationships among early mammals (Fig. 1.3). The affinities of several key groups have continued to elude a consensus agreement. However, most studies do not find support for a fundamental division into non-therian and therian clades. In particular, the non-therian taxa appear not to form a single monophyletic cluster, as previously envisaged. A second result of many recent studies is the recognition of the earliest (Late Triassic–Early Jurassic) mammals as a succession of sister taxa to later forms, rather than early members of groups that appeared later in the fossil record.

Haramiyida, Theroteinida, and Eleutherodontida.—The first-known of the earliest mammals are peculiar taxa discovered in the 19th century and now referred to the Haramiyidae (see Simpson, 1947). Then-known specimens, isolated teeth only, were reviewed by Simpson (1928), who considered haramiyids to be probable mammals and very tentatively suggested a possible relationship to Multituberculata. Haramiyids vaguely resemble multituberculates in having rows of cusps on their cheek teeth, but even orienting these baffling specimens was problematic until a large sample was described from a single, Triassic locality in France (Sigogneau-Russell, 1989; Butler and MacIntyre, 1994). Resemblances of haramiyids (placed in their own order by Hahn et al., 1989) to multituberculates appeared closer with the description of primitive multituberculates from the Jurassic of Portugal (Hahn, 1973) and the recognition that haramiyids, like multituberculates, apparently chewed with a distinctive, longitudinal movement of the jaw (Butler and MacIntyre, 1994). Matters are further complicated by consideration of two other early mammal groups with vaguely similar multicusped teeth: the Late Triassic Theroteinida (Sigogneau-Russell, 1983; Hahn et al., 1989) and the Middle Jurassic Eleutherodontida (K. A. Kermack et al., 1998). These, like haramiyids, are known principally or only by isolated teeth. The most important recent discovery relevant to one or all three of these groups comes from the Triassic of Greenland. *Haramiyavia*, known by jaws, cranial pieces, and a partial skeleton, was initially interpreted as a haramiyid (Jenkins et al., 1997) and later compared favorably with Theroteinidae (K. A. Kermack et al., 1998). It presents a few multituberculate-like characters, though not, apparently, longitudinal jaw movement. Some recent studies tentatively recognize all of these groups as a monophyletic group, Allotheria, that also includes multituberculates (see Butler, 2000, and references therein). The rationale for considering these enigmatic and poorly known mammals in the present context is that this hypothesis is difficult to reconcile with the stratigraphic record and most of the recent, comprehensive hypotheses of mammalian relationships. These studies commonly place multituberculates high on the mammalian tree, usually within the crown group formed by living taxa (e.g., Rowe, 1988; Rougier et al., 1996a; Luo et al., 2001). Earliest evidence of crown mammals is Middle Jurassic (Rowe, 1993). But haramiyids are known from beds as old as Norian: hence, if they are related to multituberculates, an astonishingly early divergence of crown

mammals—not to mention a series of putative sister taxa to crown mammals—is implied.

Morganucodonts, Sinoconodonts, and Docodonts.—Regardless of how Mammalia are defined, the discovery of *Morganucodon* and similar taxa in the mid-20th century clearly ranks among the most important additions to knowledge of early mammal evolution. Fragmentary fossils are known from the Triassic, but rather complete specimens from the Early Jurassic of Britain, China, the USA, and southern Africa have provided detailed knowledge of virtually the entire skull and skeleton, together with ontogenetic details (e.g., Patterson and Olson, 1961; K. A. Kermack et al., 1973, 1981; Crompton, 1974; Jenkins and Parrington, 1976; Jenkins et al., 1983; Crompton and Sun, 1985; Gow, 1986; Crompton and Luo, 1993). Molars of these present variations based on a serially tricusate pattern. This pattern is similar in essential details to that of advanced, non-mammalian cynodonts, and is believed to be primitive for mammals (e.g., Crompton and Jenkins, 1968). A serially tricusate molar pattern is also found in geologically younger (Middle Jurassic through Late Cretaceous) mammals, long grouped into the Order Triconodonta (e.g., Simpson, 1928, 1929a). Thus, as morganucodonts and sinoconodonts were described and discussed in the mid-twentieth century, the “Triconodonta” was simply broadened to include them (e.g., Jenkins and Crompton, 1979). This referral was to become a conceptual stumbling block, in part because it was based on plesiomorphy, but more importantly because another mammal of similar geological age, *Kuehneotherium*, was viewed as being ancestral to therians (D. M. Kermack et al., 1968). Thus it was commonly believed that another major divergence in mammalian evolution, one involving living mammals, had taken place by the Late Triassic (Crompton and Jenkins, 1973; see Fig. 1.2). Triconodonta, including morganucodonts and sinoconodonts, were viewed as broadly ancestral to the extinct Docodonta and to living monotremes, collectively grouped (often with Multituberculata) as Prototheria (e.g., Hopson, 1969; Hopson and Crompton, 1969). Confidence in this scheme began to erode when it was realized that certain later mammals with a triconodont dentition were remarkably advanced in some features of the skull and skeleton (Jenkins and Crompton, 1979), resembling therians and not morganucodonts. Recent discoveries (e.g., Ji et al., 1999) have sharpened these distinctions. Though significant uncertainties remain as to the relationship of later “triconodonts” with respect to various mammalian clades, recent analyses generally place them near living therians, whereas Late Triassic–Early Jurassic taxa fall at or near the base of the mammalian tree (e.g., Rowe, 1988, 1993; Wible et al., 1995; Rougier et al., 1996a; Luo et al., 2001; but see Hopson, 1994; Luo, 1994).

Docodonts, like other Mesozoic mammals, were regarded as marsupials until the now-classic work of Simpson (1929a). Their remarkably complex molars continue to evade a consensus agreement on homologies (Jenkins, 1969; Butler, 1986, 1997; Sigogneau-Russell and Hahn, 1995; Sigogneau-Russell and Godefroit, 1997). Simpson regarded the pattern as a variant of that belonging to “eupantotheres” (Pantotheria of his usage; a paraphyletic grouping of proximal relatives to living therians, see Prothero, 1981). Recognition that docodont teeth are of fundamentally different design (Butler, 1939; Patterson, 1956) and that the jaw retains certain reptilian features (K. A. Kermack and Mussett, 1958), together with discovery of morganucodonts as appropriate structural antecedents (Kühne, 1950), led to the recognition of Docodonta as a distinct, early-diverging clade of mammals. By the 1970s, origin of docodonts from a specified or unspecified ancestor among morganucodonts became generally accepted (e.g., Crompton, 1974; Kron, 1979; see Fig. 1.2). Important new data for interpreting the relationships of these and other early mammals were presented by Lillegraven and Krusat (1991), based on

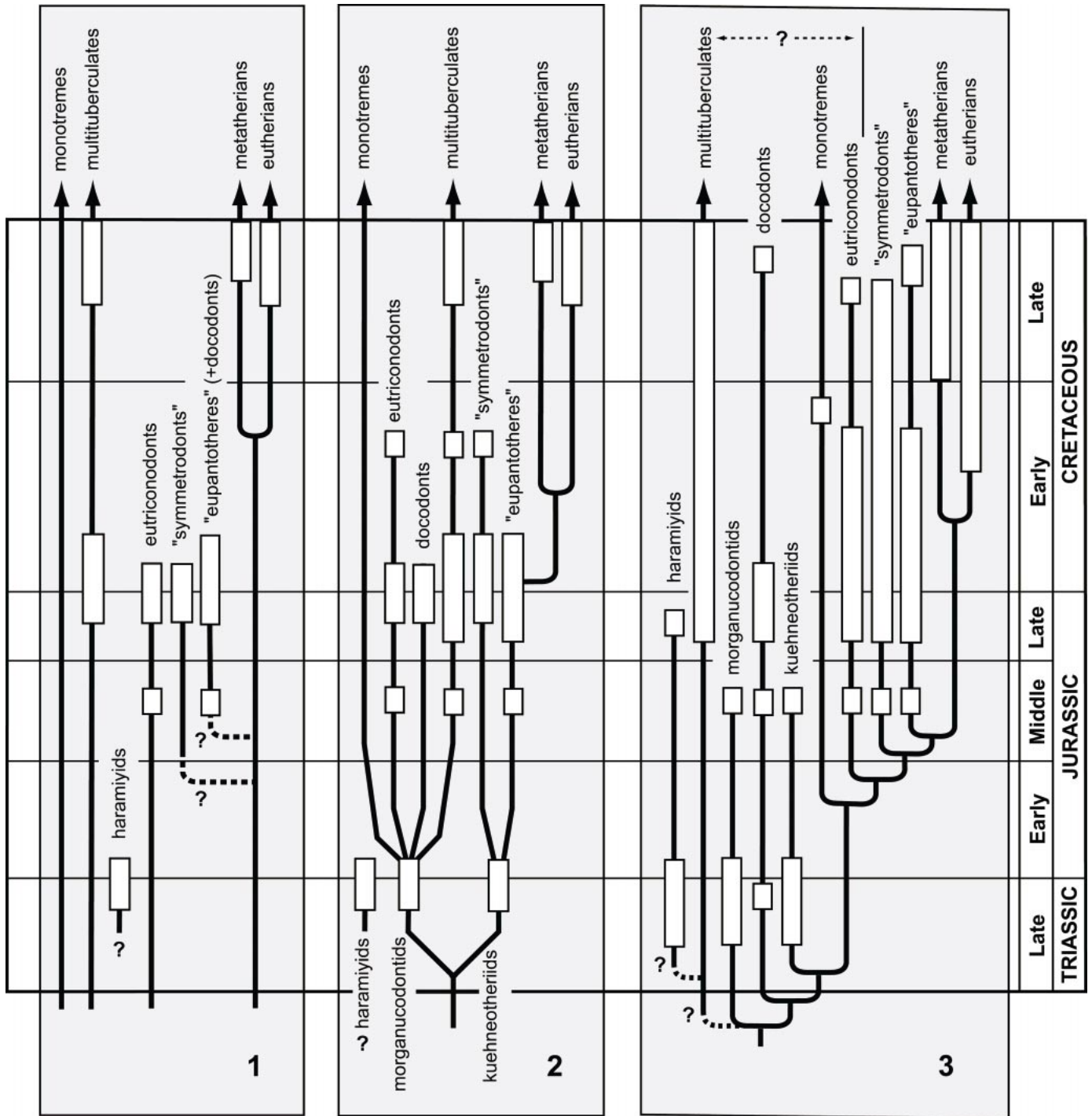


FIGURE 1—Changing interpretation of relationships among early mammals. These diagrams illustrate some of the conceptual shifts, together with improvements in the fossil record (range extensions, addition of new groups), in leading phylogenetic hypotheses. 1 is based mainly on Simpson (1928); variations of this view were widely accepted through the early 1960s (e.g., Simpson, 1959). The central thesis is that major groups of mammals arose independently from synapsid ancestors; four separate origins (monotremes, multituberculates, eutriconodonts (Simpson’s Triconodonta), living therians) are depicted here. “Eupantotheres” (Simpson’s Pantotheria, which included docodonts) and “symmetrodonts” (only Tinodontidae and Spalacotheriidae are included for the purposes of this figure) were very tentatively allied with the living therians; the position of the enigmatic haramiyids was (and remains) highly uncertain. An important shift came in the late 1960s (2, after Hopson and Crompton, 1969), with widespread acceptance of a monophyletic origin for mammals. Significant new information was available, based on recently-described fossils from the Late Triassic and Early Jurassic. Knowledge of these early mammals, together with comparative studies of the skull and dentition, led to the second notable feature of this hypothesis: the recognition of a fundamental, very early division between non-therian and therian lineages. Morganucodontids were hypothesized as ancestral to four major non-therian groups: monotremes, eutriconodonts, multituberculates, and docodonts (now removed from “eupantotheres”). Integrity of a broadly-construed Theria (to include several fossil taxa as well as the two living groups) was based mainly on presence of, or inferred elaboration from, the reversed-triangle pattern of molar cusps. Kuehneotheriids, in which this pattern is

relatively complete cranial remains of the Jurassic docodont *Haladanodon*. Their results suggest an even more remote position for docodonts, as sister taxon to all other mammals, including sinocondodonts and morganucodonts. Other recent analyses including docodonts generally place them as sister taxon to one or another of the morganucodonts (e.g., Hopson, 1994; Wible et al., 1995), or higher up the tree, proximal to crown Mammalia (e.g., Rougier et al., 1996a).

Early "Symmetrodonts".—Mesozoic mammals having rather simple molars with the three principal cusps arranged in a reversed (upper to lower) triangular pattern have long been relegated to the Order Symmetrodonta, based on the influential work of Simpson (1925, 1928, 1929a), dating from the beginning of the historical period under review. It has also long been recognized that this molar pattern represents a significant elaboration from the simpler arrangement seen in "triconodonts." In this respect the symmetrodont pattern is believed to represent an early step in the evolution of mammalian molar design, and that it is structurally antecedent to the complex pattern of living therians and their presumed fossil relatives (Butler, 1939; Patterson, 1956).

As noted above, the discovery that "symmetrodonts" were among the earliest known (Late Triassic–Early Jurassic) mammals, coupled with their triangulated molar pattern, immediately suggested that "symmetrodonts" (with or without therians) attained mammalian grade separately from various other groups (Patterson, 1956; Simpson, 1959); or (a later and more widely endorsed view) that they belong on the therian side of a fundamental, prototherian-therian dichotomy that took place early in the evolution of mammals (Crompton and Jenkins, 1968; Hopson, 1969, 1994; Parrington, 1971; Cassiliano and Clemens, 1979). It is important to note that the discovery of Late Triassic–Early Jurassic "symmetrodonts" coincided not only with the growing consensus that mammals had a polyphyletic origin (above), but also with the discovery (see K. A. Kermack and Mussett, 1958) that a number of early mammals retained a reptilian-style jaw (with postdentary elements still attached). Among these is the early "symmetrodont" *Kuehneotherium* (see D. M. Kermack et al., 1968). Conceptually, then, phyletically independent achievement of the mammalian configuration of the jaw and middle ear was accepted with little issue (Simpson, 1959; Crompton and Jenkins, 1973). Conversely and curiously, the apparently simple transformation of molar cusps from a serially-cusped triconodont pattern to the reversed triangles of "symmetrodonts" and other mammals grouped as Theria was regarded as an event of such fundamental significance that it could have occurred but once in mammalian history. This view was broadly adopted in following years. Some workers ignored the implied homoplasies for characters of the jaw and middle ear (D. M. Kermack et al., 1968; Crompton, 1971; McKenna, 1975; Prothero, 1981), though they have been explicitly discussed by others (Hopson, 1966; K. A. Kermack et al., 1981; Crompton and Hylander, 1986; Allin, 1986;

Allin and Hopson, 1992). McKenna and Bell (1997) imply reversal to explain the combination of primitive jaw structure with advanced teeth in *Kuehneotherium*, while developmental studies by Rowe (1996) suggest a single origin for the mammalian middle ear. Which condition arose independently: molars with a reversed-triangle pattern of cusps, or elaboration of jaw and suspensory bones into elements of the mammalian middle ear? The issue remains uncertain (see review by Rougier et al., 1996a), though some studies suggest that the molar pattern evolved iteratively (Rougier et al., 1996b), and it is possible that independent transformations occurred in both character complexes. A notable discovery in recent decades is that of Middle Jurassic *Shuotherium*. Like *Kuehneotherium*, it retains a primitive jaw structure in combination with a triangular arrangement of principal molar cusps (Chow and Rich, 1982). However, the lower molars bear an additional structure that is functionally analogous to the heel of marsupials and placental molars, but instead is placed in front of the tooth (see also Sigogneau-Russell, 1998).

Monotremes.—The monotremes, platypus and echidnas, have long and (almost) universally been regarded as comprising the outlier group among living mammals (Griffiths, 1978). They have fascinated evolutionary biologists for many reasons, not the least of which is the fact that they present a combination of reptilian and mammalian characteristics, together with their own striking specializations (Jenkins, 1990). While monotremes are generally regarded as an early-diverging clade relative to living therians, considerable uncertainty has long existed as to whether various extinct groups represent still more remote clades, whether they are monotreme relatives, or whether they are more closely related to therians than are monotremes. These uncertainties persist to the present, despite important additions to knowledge through the 20th century. Part of the problem, at least, stems from the nature of the fossil record: until recently, Mesozoic mammals were known almost exclusively by teeth and jaws, and hence comparison to characteristics of the monotreme (and living therian) skull and skeleton could not be made. Conversely, the dental evidence for living monotremes is limited to ephemeral and highly modified vestigial teeth in the platypus. These are so dissimilar to those of other mammal groups that, lacking intermediate links, they are of little utility in assessing monotreme relationships (Simpson, 1929b).

One argument developed in the mid-twentieth century is that monotremes are closely related to marsupials (Gregory, 1947; see also Kühne, 1973). Molecular studies bearing on this hypothesis have yielded conflicting results (Penny and Hasegawa, 1997; Lee et al., 1999; Killian et al., 2001), and evaluation of the morphological evidence suggests that most of the touted marsupial-monotreme similarities are plesiomorphic (Luo et al., in press). By the 1950s, the prevailing view was that monotremes represent a fundamentally different lineage from that leading to other living mammals (Simpson, 1945, 1959; see Fig. 1.1). As mammalian

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present, were viewed as ancestral to two major lineages, "symmetrodonts" and "eupantotheres," with the latter giving rise to metatherians and eutherians. Most recent studies (e.g., 3, based mainly on Luo et al., 2001, in press) are based on cladistic principles. Important developments here are: 1, the recognition that the non-therian groups do not represent a monophyletic clade; and 2, the disassociation of Late Triassic–Early Jurassic taxa from later groups. As a result, the hypothesis of relationships more closely matches sequential appearance of groups in the fossil record. Two major radiations of early mammals are recognized, the older being in the Late Triassic–Early Jurassic (morganucodontids, docodonts, kuehneotheriids). The second apparently took place by the Middle Jurassic and appears to include the ancestry of modern forms, with eutriconodonts, "symmetrodonts," and "eupantotheres" forming sequential sister taxa leading to the living therian groups. The position of multituberculates remains highly uncertain. Butler (2000) allies them with haramiyids (and several other groups), to the exclusion of all other mammals; whereas algorithm-based studies (e.g., Rowe, 1988) suggest placement much higher in the mammalian tree (see range of recent interpretations, top). Time scale is after Palmer and Geissman (1999). All distributions are based on current interpretation of age; vertical placement of group origin or cladogenesis is arbitrary and is not intended to indicate timing of such events.

monophyly became generally accepted (Hopson and Crompton, 1969), studies including newly discovered fossils revealed similarities (particularly of the braincase) between monotremes and several groups of early mammals, including morganucodonts, triconodontids, and multituberculates (K. A. Kermack, 1963, 1967; Hopson and Crompton, 1969; K. A. Kermack and Kielan-Jaworowska, 1971; Kielan-Jaworowska, 1971). As a result, a fundamental prototherian-therian dichotomy in mammalian evolution was widely accepted (e.g., McKenna, 1975; see Fig. 1.2). Later cladistic studies, beginning with that of Kemp (1983), called into question the integrity of a broadly conceived "Prototheria." A result common to these works (Fig. 1.3) is the broad separation of morganucodonts (placed near the base of the tree) from monotremes (placed closer to Theria), but there remain fundamental points of disagreement as to relationships of various extinct groups (e.g., Rowe, 1988; Wible and Hopson, 1993; Rougier et al., 1996a).

Dental evidence bearing on monotreme relationships finally emerged in 1985, with the discovery of *Steropodon* from the Early Cretaceous of Australia. An unquestioned monotreme, *Steropodon* has molars that are surprisingly similar to those of marsupials and placentals, suggesting a closer relationship to living therians than had generally been thought (Archer et al., 1985; Kielan-Jaworowska et al., 1987). Recent discoveries on southern landmasses have been equally or more iconoclastic: both *Ambondro* (Middle Jurassic, Madagascar) and *Ausktribosphenos* (Early Cretaceous, Australia) have fully advanced ("tribosphenic") molars like those of living therians (Rich et al., 1997; Flynn et al., 1999). Analyses reported by Luo et al. (2001, in press) suggest, however, that this pattern was independently achieved, and that the extinct taxa are related to monotremes, forming a clade that originated from a primitive "symmetrodont" and that is only remotely related to therians.

LATER JURASSIC RADIATIONS

Although one or more faunas and some individual mammal specimens are known from the Middle Jurassic (e.g., Evans and Milner, 1994; Clark et al., 1994; Flynn et al., 1999), a hiatus in the fossil record separates well-known taxa and assemblages from the Early and Late epochs of that period (Rowe, 1993). As noted above, the Late Triassic–Early Jurassic mammals have long been grouped with structurally similar, later-appearing taxa: haramiyids with multituberculates (Allotheria), morganucodonts with other "triconodonts," and *Kuehneotherium* with other "symmetrodonts." These allocations result in long stratigraphic ranges for groups of early mammals, and imply great antiquity for divergence of lineages (Fig. 1.2). Despite varied interpretations as to the relative placement of later "triconodonts," "symmetrodonts," and multituberculates, recent analyses suggest that they are more closely related to the crown group Mammalia than are the Late Triassic–Early Jurassic forms noted above (Fig. 1.3). Hence, at present there appears to be a cladistic basis for organizing treatment of these early mammals on a stratigraphic basis, as done here.

Multituberculates.—Discoveries through the twentieth century include a great wealth of multituberculate fossils, and as a result this group is incomparably the best known of all Mesozoic mammals. Late Cretaceous taxa from Mongolia are especially well represented, with the skull and skeleton being known in exquisite detail (Kielan-Jaworowska, 1971, 1986; Kielan-Jaworowska and Gambaryan, 1994; Hurum, 1994, 1998a, 1998b; Gambaryan and Kielan-Jaworowska, 1995, 1997; Hurum et al., 1996; Rougier et al., 1996b, 1997; Wible and Rougier, 2000). Well-represented dentitions and skulls are also known for some of the earliest and most primitive multituberculates, from the Late Jurassic of Portugal (Hahn, 1969, 1977a, 1977b, 1978, 1981, 1985, 1987, 1988;

Hahn and Hahn, 1994). In view of the extraordinary breadth and detail of data now available, it is a great irony that multituberculate relationships, both of and within the order, remain elusive.

Multituberculates are highly distinctive and autapomorphic, even at first appearance in the Late Jurassic: any potential scenario for their origin requires substantial morphological transformation that is not convincingly bridged by available fossils. When mammalian polyphyly was a dominant hypothesis, multituberculates were accorded a synapsid ancestry separate from that of therians and (variably) other groups of mammals (Simpson, 1937a, 1959; see Fig. 1.1). As noted, recognition of skull resemblances to monotremes and triconodonts led to later referral to "Prototheria," within a monophyletic Mammalia (e.g., McKenna, 1975). Challenges to this view began in the 1980s, with the application of cladistic methodology (Kemp, 1983). These studies universally result in some separation of the main components of "Prototheria," otherwise there is little consensus. Many of the comprehensive, algorithm-based analyses place multituberculates within the crown group of living mammals, in some cases tentatively united with monotremes (Wible and Hopson, 1993; Wible et al., 1995; Rougier et al., 1996a, 1996b; Hu et al., 1997; Ji et al., 1999). An extreme in this regard is Rowe (1988, 1993), who places multituberculates well within crown mammals, close to living therians. Other studies place multituberculates well outside of crown mammals (Miao, 1988, 1993; Allin and Hopson, 1992; Hopson, 1994), some even suggesting that multituberculates comprise a sister taxon to all other mammals, including morganucodonts and docodonts (McKenna, 1987; Butler, 2000). A related issue is the aforementioned possibility of a relationship between multituberculates and one or another earlier-occurring groups, such as haramiyids, implying early divergence of an allotherian clade (Fig. 1.3). Despite the accumulation of significant new fossil evidence in the past few decades, the concept of an expanded Allotheria remains uncertain (e.g., Hahn, 1973; Sigogneau-Russell, 1989; Butler and MacIntyre, 1994; Jenkins et al., 1997; Butler, 2000).

Equally confounding are relationships within the Multituberculata. Known taxa were simply grouped into three families by Simpson (1945). Later, the early and primitive forms were grouped into the suborder Plagiaulacoidea, with more advanced taxa being placed in the suborders Taeniolabidoidea and Ptilodontoidea (see summary by Hahn and Hahn, 1983). The "Plagiaulacida" (emended name) are now recognized as a paraphyletic assemblage, with advanced multituberculates recognized as a monophyletic Cimolodonta (Simmons, 1993; see review by Kielan-Jaworowska and Hurum, 2001). A major advance in recent years has been the recognition that most Late Cretaceous multituberculates of Asia, previously grouped in Taeniolabidoidea, represent their own, endemic radiation that is only distantly related to other cimolodontans (Kielan-Jaworowska and Hurum, 1997; Rougier et al., 1997). However, relationships within Cimolodonta remain highly uncertain. As an apparent result of high levels of missing data with widespread homoplasy, cladistic analyses have resulted in enormous numbers of equally parsimonious trees, yielding very poor resolution (Simmons, 1993; Rougier et al., 1997; see review by Kielan-Jaworowska and Hurum, 2001).

Later "Triconodonts" and "Symmetrodonts"; "Eupantotheres".—Molar pattern has always figured prominently in interpretation of mammalian relationships. The elaboration of molar pattern through triconodont, symmetrodont, and eupantotheres stages, ultimately leading to the complex, multifunctional (tribosphenic) molars of marsupials and placentals, has traditionally been central to understanding early mammal phylogeny (Patterson, 1956; Crompton, 1971). This morphological transition remains unchallenged, and molar pattern justifiably continues to figure prominently in debates about the relationships of early mammals.

However, the fossil record has been significantly augmented in recent decades by discovery of relatively complete specimens, permitting the extension of comprehensive comparisons to the skull and skeleton. In addition, the application of cladistic methodology has provided tests of traditional hypotheses of relationships and generation of new hypotheses. Several important points emerge: 1) some formal groups, such as “Pantotheria” or “Eupantotheria” represent paraphyletic grades rather than monophyletic groups; 2) other groups, such as “Symmetrodonta” and “Triconodonta,” are likely polyphyletic if Late Triassic–Early Jurassic taxa are included in them; and 3) simple, triconodont and symmetrodont molar patterns probably appeared independently, either through homoplasy or reversal.

The core of “Triconodonta,” Amphilestidae and Triconodontidae (Eutriconodonta of K. A. Kermack et al., 1973), collectively range from Middle Jurassic through Late Cretaceous. Important, recent discoveries bearing on eutriconodont relationships include specimens of *Priacodon* (Late Jurassic), an unnamed triconodontid, *Gobiconodon*, and *Jeholodens*, the last three all of Early Cretaceous age (Jenkins and Crompton, 1979; Jenkins and Schaff, 1988; Rasmussen and Callison, 1981; Rougier et al., 1996a; Kielan-Jaworowska and Dashzeveg, 1998; Ji et al., 1999). Despite some primitive retentions in the axial skeleton and hind limb, these taxa share a number of advanced characters of the skull and fore limb with therians, to the exclusion of morganucodonts—thus belying the simple, serially tricusate molar pattern common to “triconodonts” (Jenkins and Crompton, 1979; Jenkins and Schaff, 1988; Wible et al., 1995; Rougier et al., 1996a; Ji et al., 1999), and contradicting earlier hypotheses of a monophyletic “Triconodonta,” noted above. Notwithstanding this apparent advance in understanding, the monophyly of eutriconodonts remains uncertain, as does their placement (collectively or individually) with respect to crown mammals and later “symmetrodonts” discussed in this section (see Luo et al., in press). As intimated earlier, the consensus view that these “triconodonts” occupy a more proximal place to therians than do the archaic “symmetrodonts” implies either reversal of the reversed triangle molar pattern (Luo et al., 2001), or independent origin of the symmetrodont cusp configuration (Rougier et al., 1996b).

Knowledge of Late Jurassic and younger “symmetrodonts,” which are among the most poorly represented of Mesozoic mammals, has advanced significantly in recent years (Hu et al., 1997; Sigogneau-Russell and Ensom, 1998; Cifelli and Madsen, 1999). Despite dental similarity (presumably primitive) of some taxa to archaic “symmetrodonts” (Fox, 1985), the two best-known groups (tinodontids and spalacotheriids) have advanced features of the lower jaw and presumably had a characteristically mammalian three-boned middle ear (Cifelli and Madsen, 1999). This, together with postcranial evidence, suggests placement of the geologically younger “symmetrodonts” well within the crown group of living mammals, proximal to “eupantotherians” and living therians (Luo et al., in press), as envisaged in the middle 20th century (Patterson, 1956). “Eupantotheres,” encompassing a variety of taxa such as dryolestids, amphitheriids, paurodontids, and paramurids, have long been interpreted to be structurally antecedent to tribosphenic therians (Simpson, 1928, 1929a; Butler, 1939; Patterson, 1956). This view has been upheld by detailed studies of the dentition (Mills, 1964; Clemens and Mills, 1971; Butler and Clemens, 2001). Cladistic analyses suggest that “eupantotheres” form a paraphyletic grade rather than a monophyletic assemblage (e.g., Prothero, 1981; Martin, in press), and relationships among them remain somewhat unstable. Nonetheless, new knowledge of cranial and postcranial anatomy in taxa such as *Vincelestes* and *Henkelotherium* (see Krebs, 1991; Rougier, 1993) has provided substantial support for a proximal relationship of “eupantotheres” to tribosphenic therians (Luo et al., in press and

references therein). The diversity of the dentition among “eupantotheres” has also become better known as a result of discoveries in recent years (e.g., Bonaparte, 1990; Dashzeveg, 1994; Martin, 1997, 1999, in press; Ensom and Sigogneau-Russell, 1998; Sigogneau-Russell, 1999).

BOREOSPHENIDA

The living groups of therian mammals, Marsupialia and Placentalia, are readily distinguished on the basis of numerous anatomical features, both “soft” and “hard” (Lillegraven et al., 1987). Dental criteria have long proven useful in recognizing the affinities of many fossils of Late Cretaceous and younger age (Simpson, 1929a; Lillegraven et al., 1979). The water became muddied with the recovery of geologically older (Early Cretaceous) tribosphenic mammals, however: many of these, as well as problematic younger fossils, cannot be reliably placed on one side or the other of the marsupial-placental divide. A taxonomic netherworld, “Theria of metatherian-eutherian grade” (Patterson, 1956) or “Tribotheria” (Butler, 1978), was created to accommodate such mammals (Kielan-Jaworowska et al., 1979; Cifelli, 1993a). Taxa of this grade have proliferated as the Cretaceous record has improved (e.g., Clemens and Lillegraven, 1986; Fox, 1980, 1982). Most celebrated of early tribosphenic mammals is Valanginian *Aegialodon* (see K. A. Kermack et al., 1965), though older (Berriasian) fossils are now known (Sigogneau-Russell, 1994; Sigogneau-Russell and Ensom, 1994). Luo et al. (2001) recognize these and other taxa as proximal relatives (Boreosphe-nida) of Marsupialia + Placentalia, regarding them as distinct from early tribosphenic mammals of southern landmasses (see above).

How ancient is the marsupial-placental dichotomy (Lillegraven, 1969, 1974, 1975; Lillegraven et al., 1987)? Using stem-based definitions (and the respective terms Metatheria and Eutheria), generally-accepted eutherians are now known from the late Early Cretaceous of both Asia (Kielan-Jaworowska and Dashzeveg, 1989; Sigogneau-Russell et al., 1992; Averianov and Skutschas, 2000) and North America (Cifelli, 1999). The earliest uncontested metatherian is from the Albian-Cenomanian of North America (Cifelli, 1993b; Cifelli and Muizon, 1997). Recent studies suggest that Deltatheroidea, a predominantly Asiatic group, may be related to marsupials (Marshall and Kielan-Jaworowska, 1992; Rougier et al., 1998). Yet the teeth of deltatheroideans are of remarkably primitive construction (Cifelli, 1993a); if they are related to marsupials, an extremely early divergence of Metatheria and Eutheria is implied (Kielan-Jaworowska, 1982, 1992). Molecular studies (Kumar and Hedges, 1998; Penny et al., 1999) place the metatherian-eutherian dichotomy as far back as the Middle Jurassic, long before the first appearance of either group in the fossil record.

Metatheria.—Only a handful of metatherian fossils was known from the Mesozoic when the Journal of Paleontology was founded (Simpson, 1929a). That record underwent explosive expansion in the second half of the twentieth century, thanks in large part to widespread use of underwater screen-washing and associated techniques (e.g., Clemens, 1966; Lillegraven, 1969; Fox, 1971, 1979a, 1979b, 1989; Archibald, 1982; Storer, 1991; Eaton, 1993; Cifelli, 1990a, 1990b). In North America, a modest diversity of taxa (represented mainly by jaws and teeth) is now known for much of the Late Cretaceous. Metatheria did not fare well on this continent after the close of the Mesozoic, however (Archibald, 1996a), and their subsequent radiations were mainly a Gondwanan phenomenon. Metatherians have also recently been described from the Late Cretaceous of Asia (Szalay and Trofimov, 1996; Averianov and Kielan-Jaworowska, 1999), suggesting a much broader early distribution pattern than previously envisaged (Lillegraven, 1974).

The record of Mesozoic metatherians remains negligible or

non-existent for southern landmasses, though the Tertiary record has greatly improved. Particularly noteworthy are discoveries of Paleocene fossils from Brazil (Marshall, 1987; Szalay, 1994) and Bolivia, including remarkably complete skulls and skeletons (Muizon, 1995, 1998; Muizon et al., 1997). The Tertiary marsupial record from Australia has expanded dramatically, though problematic gaps persist (Archer, 1984; Archer et al., 1999), and fossil marsupials are now also known from Antarctica (Woodburne and Case, 1996; Goin et al., 1999). This vast increase in knowledge and appreciation of marsupial diversity, coupled with increased focus on relationships among major groups, has resulted in profound changes in systematics and taxonomy. Simpson's (1945) synthetic classification included only six superfamilies, all grouped within a single order. All workers since Ride (1964) have recognized the enormity of marsupial diversity by placing them in multiple orders, though relationships remain debated in many cases. An influential contribution is that of Szalay (1982; see also Szalay, 1994), who linked Australian taxa to one group (Microbiotheriidae) among the South American radiation, based on structure of the tarsus. Most later phylogenies and resultant classifications follow Szalay in recognizing a fundamental split of marsupials into australodelphian (including the microbiotheres) and ameridelphian clades. However, the results of these studies (e.g., Archer, 1984; Aplin and Archer, 1987; Marshall, 1987; Reig et al., 1987; Marshall et al., 1990) are at variance on many points, and the interordinal relationships among marsupials remain unstable, particularly when molecular data are considered (e.g., Burk et al., 1999).

Eutheria.—Early mammals bearing a tribosphenic dentition were almost universally referred to Marsupialia (e.g., Osborn, 1893) until the 1920s, when rather complete specimens from Mongolia unambiguously established the presence of eutherians in the Late Cretaceous (Gregory and Simpson, 1926). Shortly thereafter, development of dental criteria enabled referral to Eutheria of more fragmentary fossils from elsewhere (Simpson, 1929a, 1951). The small size and relatively primitive dentitions of these early taxa prompted referral to the closest living group, Insectivora (e.g., Simpson, 1945), which thus became utilized as a taxonomic wastebasket. As a partial remedy, Romer (1966) created within the Insectivora a suborder "Proteutheria," in which he placed most of the problematic taxa, essentially restricting the extent of the wastebasket. The nomen Insectivora is now commonly restricted to certain living taxa (Lipotyphla) and some fossil relatives (Novacek, 1986). *Paranyctoides*, known as far back as the early Campanian in North America (Fox, 1984; Cifelli, 1990c) and (possibly) the Coniacian in Asia (Nessov, 1993), is the oldest generally-accepted member of a living eutherian order.

An important conceptual advance came with the identification, from among Cretaceous "insectivores," of putative relatives of carnivores and (perhaps) creodonts (Van Valen, 1966; Lillegraven, 1969). This was a partial result of another conceptual change, one relating to ungulates. A number of features (now regarded as mainly primitive) of archaic ungulates ("condylarths") long suggested a possible relationship to carnivores (e.g., Matthew, 1937): the resulting group, Ferungulata (see Simpson, 1945), seems to have served as a partial encumbrance to interpreting the early history of both groups. Recent studies have yielded conflicting results as to the proximity of carnivores (and suspected relatives, collectively grouped as Ferae) to ungulates (e.g., Novacek et al., 1988; McKenna and Bell, 1997; Liu et al., 2001).

Since the 1970s, most morphologically-based phylogenies and resulting classifications have recognized a fundamental split among crown Eutheria, with one clade comprised of South American edentates (Xenarthra) and the other (Epitheria) including all remaining taxa (e.g., McKenna, 1975; Novacek, 1986; Novacek and Wyss, 1986; but see Gaudin et al., 1996). As noted below,

an alternative interpretation of xenarthran affinities is suggested by some molecular data. In practice, placement of many Mesozoic taxa with respect to this proposed dichotomy is problematic. However, another significant departure from the conventional allocation of early eutherians to Insectivora or "Proteutheria" is that of Novacek et al. (1997). These authors place some of the well-known fossils from the Cretaceous of Asia into their own group (Asioryctitheria), which they suggest represents an endemic radiation unrelated to later epitheres; this hypothesis has received some support from studies of the ankle (Horovitz, 2000).

Simpson (1945) grouped various "insectivore" taxa into Ungulata, together with a number of other groups. Notable among these are primates, tree shrews, dermopterans, and bats. A special relationship among these latter groups (collectively termed Archonta), earlier proposed by Gregory (1910), has enjoyed resurgence among morphologists in recent years (e.g., McKenna, 1975; Szalay, 1977; Novacek, 1986; Sargis, 2000). Molecular data, on the other hand, suggest that bats, at least, are unrelated to the remaining archontan groups (Liu et al., 2001; Madsen et al., 2001; Murphy et al., 2001). The early history of Archonta (or a restricted Archonta), if it is a natural group, remains highly conjectural. The oldest proposed archontan, *Deccanolestes*, is from the Late Cretaceous of India (Godinot and Prasad, 1994; Prasad and Godinot, 1994) suggesting that this living clade also had its roots in the Mesozoic.

The most speciose group of mammals is Rodentia. Gregory (1910) suggested a relationship to lagomorphs, and Simpson united the two into a major division of Eutheria, the Glires. Morphological support for this grouping has grown through the years, with the suggestion that Glires in turn lie within a more inclusive group, Anagalida, that includes elephant shrews (Macroscelidea) and certain fossil taxa (Szalay, 1977; Novacek, 1985; Novacek et al., 1988; McKenna and Bell, 1997). A monophyletic Glires is supported by molecular data, but a relationship of Glires to Macroscelidea is not (e.g., Madsen et al., 2001).

The majority of fossil and living eutherian orders is comprised of ungulates. Morphological studies have led to their grouping in a supraordinal taxon, Ungulata (e.g., Prothero et al., 1988; Prothero, 1993). However, profoundly different results are suggested by molecular data. Central to the issue are the Paenungulata, a superordinal group erected by Simpson (1945) to include hyraxes, sirenians, proboscideans, and several groups of fossil "near ungulates." Later studies recognized a close relationship of paenungulates to the two most familiar ungulate groups, Artiodactyla and Perissodactyla, with the latter sometimes viewed as proximal to paenungulates, particularly hyraxes (e.g., McKenna, 1975; Prothero et al., 1988; Fischer and Tassy, 1993; Liu et al., 2001). Molecular data, on the other hand, support a monophyletic Paenungulata and their placement in a higher clade distant from that containing perissodactyls and artiodactyls (Springer et al., 1999; Madsen et al., 2001; Murphy et al., 2001; see below). The currently uncertain status of Ungulata as a whole must be borne in mind when considering putative early members or relatives in the fossil record.

Archaic ungulates ("condylarths") were long known to be among many eutherians to make their first appearance and proliferate in the Paleocene (Matthew, 1937; Simpson, 1937b). A possible range extension of Ungulata into the latest Cretaceous of North America (see Sloan and Van Valen, 1965; Lofgren, 1995), though interesting in many ways, has proven to be of little help in evaluating the origin and early biogeography of this major eutherian clade (Clemens, in press). The most significant new discoveries bearing on these issues resulted from the collecting activities of L. A. Nessov in beds of early Late Cretaceous age, middle Asia. Detailed study suggests that some dentally advanced taxa, "Zhelestidae," are ultimately related to ungulates. These,

plus a few North American and European forms, are now regarded as basal members of Ungulatomorpha, a superordinal group that also includes living ungulates and problematic taxa (“condylarths”) from the early Tertiary (Archibald, 1996b; Nessov et al., 1998). “Condylarthra” have long been recognized as a heterogeneous, paraphyletic assemblage that includes ancestry of modern ungulate orders (Simpson, 1945). Various attempts at phylogenetic analysis have yielded differing results (e.g., Rigby, 1980; Prothero et al., 1988; Archibald, 1998), in part because of widespread symplesiomorphy and limited data.

The affinities of cetaceans, with their extreme modifications for aquatic life, have long perplexed evolutionary biologists. Simpson (1945) considered any possible suggestion as implausible, and placed them in their own cohort. A major advance in subsequent decades has been the recognition that Cetacea are derived from ungulates, and that certain taxa previously considered “condylarths” (Mesonychidae) are close relatives of whales (Van Valen, 1966; Szalay, 1969). Some later authors have favored placement of Cetacea (and fossil relatives) closer to Perissodactyla among living orders (Novacek and Wyss, 1986; Prothero et al., 1988; Thewissen, 1994). Others suggest that cetaceans are more closely related to artiodactyls, with molecular data even suggesting that whales arose from within a paraphyletic Artiodactyla (see reviews by Lockett and Hong, 1998; O’Leary, 1999; O’Leary and Geisler, 1999; Liu and Miyamoto, 1999).

A radical and broad-based departure from earlier phylogenies of Eutheria has recently been proposed on the basis of molecular data. Most of the traditional supraordinal taxa noted above are rejected in favor of two new, major groupings. Afrotheria are conceived as a long-distinct clade endemic to Africa, and including elephant shrews, golden moles, aardvarks, elephants, sirenians, and hyraxes (Stanhope et al., 1998a, 1998b; Liu and Miyamoto, 1999; Springer et al., 1999). More iconoclastic yet, Waddell et al. (1999; see also Liu et al., 2001) propose that Xenarthra (otherwise generally regarded as an outlier group among eutherians, as noted above) are related to Afrotheria, having become distinct following the opening of the South Atlantic Ocean, well back into the Cretaceous. Unfortunately, the record of fossil mammals from sub-Saharan Africa prior to the Neogene is very poor (Maglio and Cooke, 1978). Laurasiatheria are hypothesized to include artiodactyls, whales, perissodactyls, bats, Ferae, and some (but not all) of the lipotyphlan insectivores (Madsen et al., 2001).

Mammalian systematics currently lie at one of the most important interpretive crossroads since the classification of Linnaeus (1766). Supraordinal groupings indicated by molecular data represent, with few exceptions, a monumental departure from more traditional hypotheses supported by morphological data, including fossils (e.g., Liu et al., 2001). The implications for mammalian history, particularly the timing and geography of radiations leading to the living groups, are profound, and not easily reconciled (nor addressed) with existing fossils. Estimated divergence times—for example, more than 170 Myr for the marsupial-placental dichotomy (Kumar and Hedges, 1998; Penny et al., 1999); perhaps as great as 111–118 Myr for the eutherian clades Laurasiatheria and Afrotheria (Madsen et al., 2001)—are staggering in light of current knowledge and inference based on the known record of early mammals. Recent fossil discoveries, too, challenge traditional interpretations of mammalian history (Archibald, 1996b; Rich et al., 1997, 1998; Rougier et al., 1998; Flynn et al., 1999; Luo et al., 2001). New paradigms are in the process of emerging in this flurry of activity. These new hypotheses assure a vibrant, exciting future for mammalian systematics, and point to the critical role of paleontology in providing new data from the fossil record.

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