

In quest for a phylogeny of Mesozoic mammals

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We propose a phylogeny of all major groups of Mesozoic mammals based on phylogenetic analyses of 46 taxa and 275 osteological and dental characters, using parsimony methods (Swofford 2000). Mammalia *sensu lato* (Mammaliaformes of some authors) are monophyletic. Within mammals, *Sinoconodon* is the most primitive taxon. *Sinoconodon*, morganucodontids, docodonts, and *Hadrocodium* lie outside the mammalian crown group (crown therians + Monotremata) and are, successively, more closely related to the crown group. Within the mammalian crown group, we recognize a fundamental division into australosphenidan (Gondwana) and boreosphenidan (Laurasia) clades, possibly with vicariant geographic distributions during the Jurassic and Early Cretaceous. We provide additional derived characters supporting these two ancient clades, and we present two evolutionary hypotheses as to how the molars of early monotremes could have evolved. We consider two alternative placements of allotherians (haramiyids + multituberculates). The first, supported by strict consensus of most parsimonious trees, suggests that multituberculates (but not other allotherians) are closely related to a clade including spalacotheriids + crown therians (Trechnotheria as redefined herein). Alternatively, allotherians can be placed outside the mammalian crown group by a constrained search that reflects the traditional emphasis on the uniqueness of the multituberculate dentition. Given our dataset, these alternative topologies differ in tree-length by only ~0.6% of the total tree length; statistical tests show that these positions do not differ significantly from one another. Similarly, there exist two alternative positions of eutriconodonts among Mesozoic mammals, contingent on the placement of other major mammalian clades. Of these, we tentatively favor recognition of a monophyletic Eutriconodonta, nested within the mammalian crown group. We suggest that the “obtuse-angle symmetrodonts” are paraphyletic, and that they lack reliable and unambiguous synapomorphies.

Key words: Mammalia, Allotheria, Australosphenida, Boreosphenida, Monotremata, Eutriconodonta, phylogeny, parsimony analysis.

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Introduction

Recent progress in study of Mesozoic mammals

The goal of this study is to encompass all groups of Mesozoic mammals in a single, comprehensive set of parsimony analyses, so that the resultant hypotheses of relationships will have taken into account most Mesozoic mammal clades, at the familial or the sub-ordinal level. We strive to cover the entire range of morphological diversity, as reflected by diverse dental specializations of Mesozoic mammals, and to take into consideration the empirical views of those taxonomic specialists who have in-depth knowledge relating to particular groups of fossils. It is only by taking into account the vast number of taxa represented solely by teeth that we can reconstruct an adequate picture of mammalian evolution during the Mesozoic.

The last five decades have witnessed fundamental changes in the conceptual and methodological basis for phylogenetic reconstruction. Willi Hennig's "*Phylogenetischen Systematik*" methods (W. Hennig 1950, 1966) gained wide application in mammalian paleontology in the 1970s (e.g., McKenna 1975), and have been followed by studies using algorithm-based cladistic methods to reconstruct higher-rank relationships among mammalian groups (e.g., Novacek 1986a; Rowe 1988). The methods have their enthusiasts and critics, and it would be beyond the scope of this paper to cite the enormous literature on the merits or shortcomings of algorithm-based analyses, even to a limited degree. Reconstruction of the phylogeny of major groups of fossil and living mammals by parsimony methods can be reliable and useful in an ideal situation where the chosen anatomical characters are accurate and informative, the sampling of characters is comprehensive, the selection of the taxa is pertinent to the phylogenetic problems at hand, and the sampled taxa are fairly complete.

However, the fossil record of Mesozoic mammals is far from ideal. Most families are represented only by teeth. Due to incomplete anatomical representation for the overwhelming majority of early mammal groups, many previous parsimony studies on the relationships of Mesozoic mammals have concentrated on the more complete taxa. As a consequence of limited taxonomic sampling, the published phylogenies of Mesozoic mammals (including our own) tend to lack sufficient coverage of the vast diversity of fossil taxa. Though incompletely known, taxa represented only by dentitions can offer crucial data on temporal and geographical distributions. Yet the majority of these have not been included in the previous high-level, parsimony-based phylogenies. Without consideration of these dental taxa, our understanding of early mammalian phylogeny remains incomplete and therefore susceptible to bias.

Attempts at establishing relationships of Mesozoic mammals using cladistic analyses began with McKenna (1975), who proposed a phylogenetic hierarchy of mammals. Much

of this hypothesis has received corroborative support in the last 25 years (e.g., Prothero 1981; Hopson 1994). In the 1980s, a series of studies established a framework for interpreting interrelationships among the synapsid groups in which mammals are nested (Kemp 1982, 1983; Hopson and Barghusen 1986; see also Kemp 1988; Hopson 1991). Kemp (1983) proposed a cladistic phylogeny that departed significantly from the prevailing interpretation of the 1960s and 1970s, wherein a fundamental division between "therian" and "prototherian" lineages was generally accepted. Rowe (1988) was the first to undertake a large-scale parsimony analysis that included broad taxonomic diversity and incorporated both cranial and postcranial characters. Beginning with these studies, many aspects of relationships among early mammals have been debated in cladistic terms.

Application of cladistic methods and discoveries of new mammals in the last decade have led to a much greater appreciation of the enormous taxonomic diversity and morphological divergence of Mesozoic mammals. In the 1960s to 1970s, all Mesozoic mammal groups were divided into the "prototherians" survived by monotremes, and "therians" that are survived by marsupials and placentals. The more recent parsimony phylogenies tend to show that most of the taxa formerly assigned to the "prototherians" are not closely related to monotremes after all, but instead represent basal branches that split off near the root of the mammalian tree (Rowe 1999). Diverse and enigmatic mammals from the Gondwanan landmasses have revealed some previously unknown endemic radiations (e.g., Bonaparte 1990; Rich et al. 1997; Rich, Flannery et al. 2001; Rich, Vickers-Rich, et al. 2001; Krause et al. 1998; Flynn et al. 1999). Many of the recently discovered taxa cannot be easily accommodated into the elegant evolutionary schemes that were widely accepted in the 1970s, such as a monophyletic origin of all tribosphenic mammals in the Laurasian landmasses (Chow and Rich 1982; Wang et al. 1998; Sigogneau-Russell, 1999; Rich et al. 1997; Rich, Vickers-Rich, et al. 2001; Flynn et al. 1999). A great conceptual advance in the studies of Mesozoic mammals is the understanding that the greatest diversification tends to appear in the earliest periods of the major clades, as reflected by the bushy topology of the trees of all major clades of Mesozoic mammals (Figs. 1 and 2).

Since 1979, numerous books have been published on various aspects of Mesozoic mammalian evolution, their relationships to non-mammalian synapsids, embryology of extant mammals, reviews of living faunas of the Australian region, evolution of mammalian enamel microstructure, etc. These have contributed greatly to our understanding of early mammal evolution. Notable single- or two-authored books include those of Kemp (1982), D.M. Kermack and K.A. Kermack (1984), Sigogneau-Russell (1991c), and Szalay (1994). At the same time at least 20 multiple-authored books or symposium proceedings that have bearings on Mesozoic mammals, were

published, including those edited by: Lillegraven et al. (1979), Kielan-Jaworowska and Osmólska (1983), Mengel (1984), Reif and Westphal (1984), Flanagan and Lillegraven (1986), Hotton et al. (1986), Archer (1987), Currie and Koster (1987), Kuhn and Zeller (1987a), Patterson (1987), Benton (1988), Russell et al. (1988), Genoways (1990), Kielan-Jaworowska et al. (1991), Schultze and Trueb (1991), Augee (1992), Szalay et al. (1993a), Fraser and Sues (1994), Sun and Wang (1995), Koenigswald and Sander (1997), Carpenter et al. (1998, 1999), Gillette (1999), Leanza (1999, 2001), and Benton et al. (2000).

Fossil discoveries since 1980 have substantially increased knowledge of the diversity and anatomy of Mesozoic mammals. The literature is comprehensive, and we cite here only selected works: Prothero (1981), Archibald (1982), Chow and Rich (1982, 1984), Hahn (1983), Dashzeveg (1984), Fox (1984, 1989), Archer (1985), Crompton and Sun (1985), Kielan-Jaworowska et al. (1986), Bonaparte and Rougier (1987), Cifelli and Eaton (1987), Hahn et al. (1987), Krause and Carlson (1987), Jenkins and Schaff (1988), Miao (1993), Hahn et al. (1989), Kielan-Jaworowska and Dashzeveg (1989, 1998), Sigogneau-Russell (1989a, b, 1991a, b, 1994, 1995, 1998, 1999), Bonaparte (1990), Krebs (1991, 1993, 1998), Kielan-Jaworowska and Ensom (1992), Pascual et al. (1992a), Rougier et al. (1992), Rougier, Wible, and Hopson 1996), Sigogneau-Russell et al. (1992), Archer et al. (1993), Cifelli (1993a, b, 1999a, b), Crompton and Luo (1993), Eaton (1993, 1995), Hahn (1993), Lucas and Luo (1993), Rougier (1993), Szalay (1993a), Butler and MacIntyre (1994), Hurum (1994, 1998a, b), Kielan-Jaworowska and Gambaryan (1994), Prasad et al. (1994), Flannery et al. (1995), Sereno and McKenna (1995), Meng and Wyss (1995), Wible et al. (1995), Archibald (1996), Datta and Das (1996, 2001), Prasad and Manhas (1997, 1999), Nessov et al. (1994, 1998), Gambaryan and Kielan-Jaworowska (1995, 1997), Cifelli and Muizon (1997), Hu et al. (1997), Jenkins et al. (1997), Nessov (1997), Novacek et al. (1997), Rich et al. (1997), Ensom and Sigogneau-Russell (1998), Heinrich (1998, 1999), K.A. Kermack et al. (1998), Nessov et al. (1998), Rougier et al. (1998), Sigogneau-Russell (1998, 1999), Wang et al. (1998), Cifelli and Madsen (1999), Engelmann and Callison (1999), Hahn and Hahn (1999), Flynn et al. (1999); Ji et al. (1999), Martin (1999a), Pascual and Goin (1999, 2001), Pascual et al. (2000), and McKenna et al. (2000).

The comparative anatomical data bearing on cladistic analysis of Mesozoic mammals have been re-evaluated and greatly expanded in recent years (e.g., Rowe 1988, 1993; Wible 1991; Novacek 1992b; Cifelli 1993b; Crompton and Luo 1993; Simmons 1993; Hahn 1993; Wible and Hopson 1993, 1995; Hopson and Rougier 1993; Hopson 1994; Luo 1994; Meng and Wyss 1995; Rougier, Wible, and Hopson 1996; Kielan-Jaworowska 1997; Kielan-Jaworowska and Hurum 1997, 2001; Wang et al. 1998; Sigogneau-Russell 1998, 1999; Wood et al. 1999; Butler 2000; Butler and Clemens 2001; Luo, Cifelli, and Kielan-Jaworowska 2001; Luo, Crompton, and Sun 2001). Additionally, new embryological

and other neontologically-based data have provided important insights in interpretation of mammalian relationships (e.g., Presley 1980, 1981, 1993; MacPhee 1981; Kuhn and Zeller 1987a; Lillegraven et al. 1987; Maier 1987, 1989, 1993, 1999; Wible 1987; Luckett and Zeller 1989; Renfree 1993; Zeller 1993, 1999a, b). Finally, recent molecular studies have revealed new issues regarding placement of monotremes (Janke et al. 1996, 1997; Kullander et al. 1997; Messer et al. 1998; Lee et al. 1999; Gilbert and Labuda 2000; Killian et al. 2000, 2001), timing of clade divergence for major groups of mammals, and biogeographic implications (Hedges et al. 1996; Springer 1997; Kumar and Hedges 1998; Messer et al. 1998; Eizirik et al. 2001; Liu et al. 2001; Madsen et al. 2001; Murphy et al. 2001).

In this paper, we provide an expanded comparative dataset comprising the dental, cranial, and postcranial anatomy for a wide range of advanced cynodonts, stem-mammals (those presumed to lie outside of the crown group), and major extinct groups within crown Mammalia, together with living and fossil representatives of the three living clades: Monotremata, Marsupialia, and Eutheria. Our parsimony analyses of this new dataset provide corroboration for several previous cladistic hypotheses, such as the paraphyletic nature of mammals with a triconodont molar pattern, and diphyletic origin for mammals with a tribosphenic molar pattern. We consider two alternative positions of Allotheria (multituberculates and, with some doubt, archaic groups such as haramiyids) among Mesozoic mammals, one based on strict parsimony criteria, the other according to the majority opinion of specialists of haramiyidans and early multituberculates. Results are also equivocal for relationships of Eutriconodonta (Triconodonta as conceived by Simpson 1928, 1929a; see K.A. Kermack et al. 1973), and we offer alternative placements for eutriconodonts in the context of mammalian phylogeny. We also suggest that the triangulation of molar cusps, long considered a unique specialization of living therians and their putative fossil allies (e.g., Hopson 1969), evolved more than once (see also Rougier, Wible, and Hopson 1996; Pascual and Goin 1999, 2001). Specifically, we hypothesize that “acute-angle symmetrodonts” (Spalacotheriidae) lie well within crown Mammalia, perhaps representing one of several stem lineages closer to living therians; whereas “obtuse-angle symmetrodonts” (Tinodontidae, Kuehneotheriidae) appear to represent some unrelated groups among stem mammals.

Terminology and conventions

Anatomical terms and abbreviations.—We use upper case characters (e.g., P, premolars; M, molars) for upper teeth and lower case (e.g., p, premolars; m, molars) for lower teeth. For homologies of molar structures, we follow Crompton (1971), Hopson (1994), Butler (2000, allotherians), Butler and Clemens (2001, “therians”), and Luo, Cifelli, and Kielan-Jaworowska (2001, australosphenidans). We adopted the basicranial terminology of MacPhee (1981), Wible and Hopson (1995), Kielan-Jaworowska et al. (1986), and Rougier, Wible, and

Hopson (1996). For other terms, together with general discussion on anatomy, we follow (where possible) the standard terminology as set forth in *Nomina Anatomica Veterinaria* (see Schaller 1992). For those structures not defined in this work, we have adopted the terminology used in recent paleontological-anatomical papers cited herein.

Taxonomic nomenclature.—Higher taxonomic groups that are used formally are given taxon-based definitions, together with diagnosing characters. Unless otherwise qualified, we employ stem-based concepts for each of the major groups of living mammals, Monotremata, Metatheria, and Eutheria. Within Metatheria, fossil taxa believed to be more closely related to living marsupials than to deltatheroidans are included in Marsupialia. We restrict formal usage of taxonomical names to those higher-level groups for which monophyly is supported by current evidence (albeit weakly, in many cases), and to instances where, in our judgment, such names are useful and meaningful. The first criterion eliminates paraphyletic taxa, discussed further below. An example of a name not meeting the second criterion is Holotheria, used informally by Hopson (1994), and subsequently formalized by Wible et al. (1995; see also McKenna and Bell 1997). The term Holotheria represents a slightly modified replacement for “Theria” *sensu lato* (see below), conceived as one of two clades representing an early, fundamental dichotomy in mammalian history (e.g., Hopson 1969). Results of this study, like those of several others in recent years (see discussion by Rougier, Wible, and Hopson 1996), suggest that the intended grouping (*Kuehneotherium*, as well as other archaic taxa with a reversed triangle molar pattern, including all extant mammals) is non-exclusive, if using the proposed taxon-based definition of Wible et al. (1995). Furthermore, *Kuehneotherium* itself is very incomplete and its phylogenetic position is unstable; hence, any group defined on the basis of it suffers from similar instability.

Use of traditional names that are not currently recognized as valid, or use of informal but widely understood names, is unavoidable in the context of our general review. Some paraphyletic taxa must be mentioned for historical reasons; in other cases, we have relied on usage of informal names as a linguistic convenience in referring to multiple outgroups, or to mammals sharing certain structural attributes. We follow convention in identifying these names by enclosing them in quotation marks, when the intended usage is taxonomic (but not morphologic). Hence, “Triconodonta” (or “triconodonts”) refer to mammals with a triconodont molar pattern.

Undoubtedly the name most susceptible to confusion is Theria Parker and Haswell, 1897, originally conceived to distinguish two of the living groups, Metatheria and Eutheria, from the third, Monotremata. Simpson (1945) recognized certain Mesozoic mammals as more closely related to living therians than to monotremes, and formalized an expanded concept of Theria by adding an infraclass “Pantotheria” (including “eupantotheres” as conceived herein, see K.A. Kermack and Mussett 1958). This concept was further refined and expanded in following years, ultimately leading to

a widespread acceptance of the reversed-triangle molar as a character-based definition for “therians” (e.g., K.A. Kermack 1967b; Hopson and Crompton 1969; McKenna 1975). In recent years, some workers have advocated a more restricted, taxon-based definition for Theria, to include the common ancestor of Metatheria and Eutheria, plus all of its descendants (e.g., Rowe 1988, 1993; Rowe and Gauthier 1992). Other recent classifications variably include certain fossil taxa presumed to lie outside the crown group (e.g., Szalay 1994; McKenna and Bell 1997). The “therian” concept is used in two ways; one is more restricted and the other more expansive. The first, crown therians (or living groups of therians) is equivalent to Theria as formally defined by Rowe (1988, 1993). The second, the paraphyletic “therians”, is used in order to convey the historically important (and still widely used) concept of a group including *Kuehneotherium* and other “symmetrodonts”, “eupantotheres”, Metatheria, and Eutheria, but excluding groups that are now nested cladistically within such a clade: monotremes, eutriconodonts, and multituberculates.

A number of traditionally used taxa now appear to be paraphyletic. For present purposes, we identify the contents of these groups, as previously used by many workers, in the following. “Prototherians”: “triconodonts”, multituberculates, docodonts, and monotremes. “Triconodonts”: Sinoconodontidae, Morganucodontidae, and Eutriconodonta (see Jenkins and Crompton 1979; K.A. Kermack et al. 1973); but not Docodonta, as advocated by K.A. Kermack et al. (1973). “Plagiaulacidans”: Paulchoffatiidae and other generally primitive Jurassic–Early Cretaceous multituberculate groups not treated herein (see Kielan-Jaworowska and Hurum 2001). “Symmetrodonts”: Kuehneotheriidae, Tinodontidae, Spalacotheriidae, and other groups not treated herein (see Cassiliano and Clemens 1979; Sigogneau-Russell 1983, 1989a; Bonaparte 1990; Sigogneau-Russell and Ensom 1998). “Amphilestidae”: *Amphilestes*, *Gobiconodon*, and other genera not treated herein (see McKenna and Bell 1997; Chow and Rich 1984; Engelmann and Callison 1998; Godefroit and Guo 1999). “Eupantotheres”: Dryolestoidea, Amphitheriidae, Vincelestidae, “peramurids” (= Cladotheria of McKenna 1975; minus Boreosphenida of Luo, Cifelli, and Kielan-Jaworowska 2001; other included taxa are not treated herein, see e.g., Dashzeveg 1994). “Peramurids”: *Peramus* and structurally similar taxa not treated herein (see Sigogneau-Russell 1999; Martin in press). “Pre-tribosphenic therians”: an informal term referring to proximal relatives of Boreosphenida, including Vincelestidae, Amphitheriidae, and “peramurids” (= Prototribosphenida of Rougier, Wible, and Hopson 1996; minus Boreosphenida of Luo, Cifelli, and Kielan-Jaworowska 2001).

Sister-group of Mammalia

Reconstructing anatomical transformations among the earliest mammals and interpreting their interrelationships depend on a larger phylogenetic framework that must include non-mammalian cynodonts, from which mammals arose. An obvious

and critical aspect of this framework involves postulation of the cynodont groups that are, sequentially, the most proximal relatives of mammals. Postulation of the sister-taxon (and the topological order of other close relatives) to mammals is fundamental to appraisal of character transformations and evolutionary patterns among the earliest mammals.

Historically, five cynodont families have been proposed as being closely related to the common ancestry of mammals: Thrinaxodontidae (Hopson 1969; Hopson and Crompton 1969; Barghusen and Hopson 1970; Fourie 1974), Probainognathidae (Romer 1970; Crompton and Jenkins 1979; Hopson 1994), Dromatheriidae (Hahn et al. 1994; Sues 2001), Tritheledontidae (Hopson and Barghusen 1986; McKenna 1987; Shubin et al. 1991; Crompton and Luo 1993; Luo 1994), and Tritylodontidae (Kemp 1983; Rowe 1988, 1993; Wible 1991; Wible and Hopson 1993).

Dromatheriids (*Dromatherium* and *Microconodon*), although considered to be mammals in the 19th century, have uncertain phylogenetic affinities according to studies dating to the 1920s (Simpson 1926a, b). Several problematic taxa known only by isolated teeth from the Late Triassic to Early Jurassic of Europe have been assigned to the Dromatheriidae (Sigogneau-Russell and Hahn 1994; Hahn et al. 1994). In the latest study of *Microconodon*, Sues (2001) points out that several “mammal-like” features of dromatheriids are shared by tritheledontids and other cynodonts, and he explicitly suggests that Dromatheriidae be excluded from mammals. They are best regarded as a derived “eucynodont” group, but their affinities to mammals remain uncertain due to their incomplete fossils (Sues 2001). *Therioherpeton*, from the mid-Triassic of South America (Bonaparte and Barberena 1975), could belong either to this group (Hahn et al. 1994), to Tritheledontidae (Kemp 1982; Sues 2001), or to a stem mammal group (Bonaparte and Barberena 1975). Until its fossils are better described, affinities of *Therioherpeton* to mammals, and to other nonmammalian cynodonts, will remain uncertain (Sues 2001).

Of the more derived cynodont families with complete fossils, tritheledontids and tritylodontids share far more derived characters with mammals than do Probainognathidae, Thrinaxodontidae, and other advanced cynodonts. Tritylodontids, tritheledontids, and mammals form a monophyletic group (Mammaliaforma, modified from Rowe 1988, 1993). This clade can be diagnosed by several apomorphies in the petrosal (Wible 1991; Wible and Hopson 1993; Luo 1994), inner ear (Crompton 1995; Luo 2001), quadrate (incus) (Kemp 1983; Sues 1985; Rowe 1988; Luo and Crompton 1994), dentition (Kemp 1983; Rowe 1988; Crompton and Luo 1993), and postcranium (Kühne 1956; Sues 1983; Sun and Li 1985; Rowe 1993; Gow in press).

It has been debated whether tritheledontids or tritylodontids are the sister-taxon to Mammalia (= Mammaliaformes of Rowe 1988). The hypothesis that tritheledontids are more closely related to mammals was proposed by Hopson and Barghusen (1986; see also Hopson 1991; McKenna 1987). This hypothesis has received support from studies by Shubin et al. (1991), Crompton and Luo (1993), Luo (1994), and Luo

and Crompton (1994). The tritylodontid–mammal hypothesis was first implied by Kemp (1983, 1988), and later more fully documented by the more extensive parsimony analyses of Rowe (1986, 1988, 1993) on the basis of larger and much improved datasets. Early versions of the tritylodontid–mammal hypothesis did not explicitly address the phylogenetic position of tritheledontids (Kemp 1983; Rowe 1988: figs. 3, 4). Later, Rowe (1993) explicitly proposed that tritylodontids and mammals are more closely related than either group is to tritheledontids, a postulation supported by a re-analysis of the cranial data by Wible (1991; see also Wible and Hopson 1993).

Each of these competing hypotheses is supported by a large number of apomorphies in the dentition, skull, and postcranial skeleton. The apomorphic characters of the orbital wall and sphenoid region predominantly support the tritylodontid–mammal hypothesis (Luo 1994). By contrast, the apomorphies of the craniomandibular joint, lower jaw, and palate predominantly support the tritheledontid–mammal hypothesis. But each hypothesis is also contradicted by a substantial amount of anatomical evidence (Luo 1994). If tritylodontids are more closely related to mammals than are tritheledontids, then the apomorphies shared by tritheledontids and mammals in the temporomandibular joint, jaw occlusion, and palate would represent homoplasies. Acceptance of the tritheledontid hypothesis, on the other hand, implies that the apomorphies in the orbital and sphenoid regions shared by tritylodontids and early mammals are homoplasies. The characters of the rest of the skull and the postcranium do not provide any unilateral, unambiguous support for either hypothesis (Luo 1994), instead supporting the inclusion of both Tritylodontidae and Tritheledontidae in a monophyletic clade (Mammaliaforma of Rowe 1988) with Mammalia.

Monophyly of Mammalia

We recognize Mammalia (Mammaliaformes in the usage of Rowe 1988; McKenna and Bell 1997) as a monophyletic group, defined as including the common ancestor of *Sinoconodon*, living monotremes, and living therians, plus all its descendants (Crompton and Sun 1985; Crompton and Luo 1993). This stem-group definition is stable because the taxonomic content or membership of this clade has been very stable. This clade has been supported by a large number of diagnostic apomorphies, identified in numerous studies (Crompton and Sun 1985; Lucas and Luo 1993; Rowe 1993; Luo and Crompton 1994; Hopson 1994; Wible and Hopson 1995; Rougier, Wible, and Hopson 1996; Luo, Crompton, and Sun 2001; this study).

However, most workers in the 1930s through 1960s considered Mammalia as a polyphyletic grade, with various groups having evolved independently from different cynodont groups (e.g., Patterson 1956: fig. 16). This pervasive view was based on the influential work of Broom (1910), Matthew (1928), Simpson (1928), and Olson (1944), among others. Multituberculate mammals were hypothesized to have

evolved from dentally similar cynodonts, the tritylodontids, which are characterized by longitudinal rows of multiple cusps on their molariform postcanines (Simpson 1928; Olson 1944). Mammals with a triconodont molar pattern, on the other hand, were proffered as possible descendants of tritheledontids (“ictidosaur” of earlier usage, see Olson 1959). Monotremes, with their peculiar specializations, were accorded a separate crossing into the mammalian grade, arising from some unknown therapsid group. For decades, multiple origins for various Mesozoic mammal lineages from separate “mammal-like reptile” families were taken for granted (Olson 1959; Simpson 1959). An issue then was the accommodation of recognized polyphyly into a natural classification, and the possible extension of Mammalia to a more inclusive level among Synapsida, thereby permitting recognition of mammals as monophyletic (Simpson 1959; Reed 1960; Van Valen 1960; see historical review by Rowe and Gauthier 1992).

Notably, Gregory (1910: figs. 31, 32; see also Weber 1904, 1927, 1928) had earlier suggested that mammals, including monotremes, are monophyletic, based on numerous derived anatomical and reproductive features. Gregory (1910) emphatically pointed out that monotremes are more closely related to “triconodonts”, multituberculates, and living mammals than to cynodonts and *Dromatherium* (currently considered to be an advanced non-mammalian cynodont, see Hahn et al. 1994; Sues 2001). Gregory’s view of mammalian origin was almost identical to the main stream view of monophyletic Mammalia adopted in the 1970s and later, although his evidence at the time was quite limited. His proposal of mammalian monophyly was echoed by Broom (1914) but was later overwhelmed by the force of contrary views in the influential work of Simpson (e.g., 1928, 1929a, 1945, 1959), Matthew (1928), Olson (1944, 1959), Patterson (1956), and Romer (1966).

The polyphyletic concept of Mammalia has long been abandoned, in part because the dental characters on which the scheme was based are no longer tenable. The linear arrangement of molar cusps, shared by “triconodonts” and several cynodonts (such as *Thrinaxodon* and *Pachygenelus*) has proven to be primitive (Kemp 1983), and thus uninformative of their relationship. Tritylodontids, when known only from the dentition and incomplete skull, were at first considered to be mammals (Owen 1884; Broom 1910; Simpson 1928; Tatarinov 1985; see historical review by Parrington 1981). A putative origin of multituberculates from tritylodontids was

proposed when both groups were known mainly by dentitions (e.g., E. Hennig 1922). In the 1930s and 1940s, when complete skulls of tritylodontids (Young 1940, 1947) and multituberculates (Simpson 1937) became known, it was evident that a tritylodontid–multituberculate relationship is contradicted by a vast number of differences, in the mandible and braincase, between the two groups. Tritylodontids retain the primitive configuration of postdentary bones in the mandible, as is typical of most cynodonts, and lack the dentary–squamosal jaw hinge, which is well-developed in mammals (Watson 1942; Young 1947; Kühne 1956; Hopson 1964). The braincase (Simpson 1937; Kielan-Jaworowska 1971) and mandible (Clemens 1963; Hahn 1969) of multituberculates are clearly mammalian and are far more derived than those of tritylodontids (Hopson 1964; Crompton 1964a; Gow 1986b).

The consensus of several influential studies of the late 1960s to early 1970s is that Mammalia are monophyletic (see Hopson 1969; Hopson and Crompton 1969). In addition to the character traditionally viewed as diagnostic of mammals (a craniomandibular joint comprised of dentary condyle and squamosal glenoid), new dental and basicranial features also were marshaled in support of a monophyletic Mammalia. Functional studies of dental occlusion in a wide diversity of Mesozoic mammals demonstrated the presence of derived characters that are absent in most, if not all, non-mammalian cynodonts (Patterson 1956; K.A. Kermack and Mussett 1958; K.A. Kermack 1963; K.A. Kermack et al. 1965; D.M. Kermack et al. 1968; Crompton and Jenkins 1968, 1973; Hopson and Crompton 1969; Crompton 1971, 1974; Mills 1971). In mammals, the braincase structure around the trigeminal ganglion recess (the cavum epiptericum) is also derived relative to the condition in cynodonts (K.A. Kermack 1963; Hopson 1964, 1969; Hopson and Crompton 1969; K.A. Kermack and Kielan-Jaworowska 1971).

Monophyly of Mammalia (Mammaliaformes of Rowe 1988) has been strongly supported by all phylogenetic studies of the last two decades. Although some of the diagnostic characters in the dentition, craniomandibular joint, and ear have been shown to have intermediate character states in non-mammalian cynodonts (Crompton 1972a; Allin and Hopson 1992; Luo and Crompton 1994; Luo 1994, 2001) and are less distinctive than previously believed (Gow 1985), a monophyletic grouping of (*Sinococonodon* + Monotremata + crown Theria) has remained one of the best supported monophyletic groups in synapsid phylogeny.

Phylogenetic analyses

Sampling of anatomical characters

The current dataset totals 275 characters, including 92 dental, 28 mandibular, 92 cranial, and 63 postcranial characters (Appendix 1). 271 of these characters are informative for the relationships of the selected taxa. These characters have been

gathered for the purpose of estimating phylogenetic relationships of taxa ranging from advanced cynodonts through the crown groups of mammals. Only those characters informative for the 46 selected taxa are used in the actual analysis. The four uninformative characters are retained here for the purposes of comparison to previously published studies. This

is the most inclusive dataset that we have managed to gather so far, but we point out that it represents only a part of the total available evidence for estimating relationships of non-mammalian synapsids through the extant mammalian orders. Because the relationships within non-mammalian synapsid groups and within the living mammal orders lie outside the purview of this analysis, we refer the readers to several other analyses on synapsid evolution (pre-therapsid pelycosaur, pre-cynodont therapsids to nonmammalian cynodonts through selected mammalian clades, Kemp 1982, 1988; Hopson and Barghusen 1986; Rowe 1986, 1988; Gauthier et al. 1988; Hopson 1991; Reisz et al. 1992; Laurin 1993; Laurin and Reisz 1996; Sidor and Hopson 1998; Sidor 2001), on phylogeny of living placental orders (Novacek 1986b, 1992b; Novacek and Wyss 1986a; Novacek et al. 1988; Prothero 1993; Gaudin et al. 1996; McKenna and Bell 1997; Shoshani and McKenna 1998; Waddell et al. 1999; Liu et al. 2001; Madsen et al. 2001; Murphy et al. 2001; contributions and references in Szalay et al. 1993b), and on phylogeny of living marsupial orders (Marshall 1979; Aplin and Archer 1987; Marshall et al. 1990; Szalay 1993a, 1994; Kirsch et al. 1997; Springer et al. 1998; Burk et al. 1999).

Dental and mandibular features.—Many dental and mandibular features listed here are revised from Luo, Cifelli, and Kielan-Jaworowska (2001), which includes a recent compilation of dental and mandibular characters used for phylogenetic studies of Mesozoic mammals. Many of these characters have been discussed by Hopson and Crompton (1969), Parrington (1971, 1978), K.A. Kermack et al. (1973), Kay and Hiiemae (1974), McKenna (1975), Fox (1975), Prothero (1981), Kemp (1983), Archer et al. (1985, 1993), Crompton and Sun (1985), Clemens and Lillegraven (1986), Kielan-Jaworowska et al. (1987a), Rowe (1988), Hahn et al. (1989), Jenkins (1990), Kielan-Jaworowska (1992), Sigogneau-Russell et al. (1992), Cifelli (1993b), Luo (1994), Hopson (1994), Hu et al. (1997), Sánchez-Villagra and Smith (1997), Rich et al. (1997, 1999), Sigogneau-Russell (1998), Wang et al. (1998), Kielan-Jaworowska et al. (1998), and Ji et al. (1999). Dental characters of the therian crown group and close relatives are from Cifelli (1993a, b), Rougier et al. (1998), Flynn et al. (1999), and Averianov and Skutschas (1999). Dental and mandibular characters for basal eutherians are from Kielan-Jaworowska and Dashzeveg (1989), Archibald (1996), Novacek et al. (1997), Nessov et al. (1998), Cifelli (1999b), and Averianov and Skutschas (2000, 2001). Characters based on wear facets are modified from K.A. Kermack et al. (1965), D.M. Kermack et al. (1968), Crompton and Jenkins (1967, 1968), Crompton (1971, 1974), Mills (1971, 1984), Fox (1975), Crompton and Kielan-Jaworowska (1978), Chow and Rich (1982), Sigogneau-Russell (1989b, 1998, 1999), Wang et al. (1998), and Butler (1988, 2000). Features on occlusal modes are from Crompton and Hylander (1986), Wall and Krause (1992), and Crompton and Luo (1993).

Cranial characters.—The most recent surveys of basicranial characteristics of Mesozoic mammals are those of Wible et al.

(1995, 2001) and Rougier, Wible, and Hopson (1996), which summarized many characters of the petrosal, squamosal, and exoccipital. Additional characters used herein are from MacIntyre (1972), MacPhee (1981), Novacek (1986b), Rowe (1988), Wible (1990, 1991), Wible and Hopson (1993), Lucas and Luo (1993), Luo (1994), Gambaryan and Kielan-Jaworowska (1995), and Hurum (1998a). Characters of ear structures are from Allin (1975, 1986), Novacek and Wyss (1986b), Graybeal et al. (1989), Allin and Hopson (1992), Luo and Crompton (1994), Luo et al. (1995), Meng and Fox (1995b, c), Meng and Wyss (1995), Hurum et al. (1996), Rougier, Wible, and Hopson (1996), Fox and Meng (1997), Hurum (1998b), McKenna et al. (2000), and Luo (2001). The brain endocast characters are based on Kielan-Jaworowska (1986, 1997) and Rowe (1996a, b). The temporo-orbital characters are from Sues (1985), Miao (1988), Rougier et al. (1992), Hopson and Rougier (1993), Luo (1994), and Wible and Hopson (1995). Characters of the rostral and facial parts of the skull are from Kemp (1983), Sues (1985), Rowe (1988), Wible et al. (1990), and Marshall and Muizon (1995). Characters of the cranio-mandibular joint are from Crompton (1972a), Crompton and Hylander (1986), Crompton and Luo (1993), and Luo, Crompton, and Sun (2001).

Postcranial characters.—The study by Kemp (1983) was the first attempt to make extensive use of postcranial characters in the analysis of cynodont–mammal phylogeny. Rowe (1986, 1988) provided a comprehensive survey of postcranial characters for taxa ranging from therapsids through living mammals. Many of these features were initially introduced by Jenkins (1971, 1973, 1974), and were subsequently reviewed and re-assessed by Szalay (1993b) and Kielan-Jaworowska and Gambaryan (1994). In the 1990s, additional postcranial characters were introduced in a series of studies, including those treating the “eupantothere” *Henkelotherium* (Krebs 1991), the prototribosphenidan *Vincelestes* (Rougier 1993), multituberculates (Krause and Jenkins 1983; Kielan-Jaworowska and Gambaryan 1994; Sereno and McKenna 1995, 1996; Gambaryan and Kielan-Jaworowska 1997; Kielan-Jaworowska 1998), “symmetrodonts” (Hu et al. 1997, 1998), eutriconodonts (Ji et al. 1999), eutherians (Novacek et al. 1997; Horovitz 2000), and marsupials (Szalay 1994; Marshall and Sigogneau-Russell 1995; Szalay and Trofimov 1996; Muizon 1998; Szalay and Sargis 2001).

Selection of taxa

Non-mammalian cynodonts.—Three non-mammalian cynodont groups, *Probainognathus*, tritylodontids, and trihedontids, are included: 1) to provide a more accurate assessment of the distributions of relevant anatomical characters outside mammals; 2) to insure a more comprehensive documentation for anatomical evolution through the cynodont–mammal transition; and 3) to use *Probainognathus* as outgroup for rooting the tree by the phylogenetic algorithms.

Probainognathus.—This taxon is represented by relatively complete fossils, and its cranial anatomy has been described in detail (Romer 1970; Crompton 1972a; Allin 1986; Rougier et al. 1992; Luo and Crompton 1994; Wible and Hopson 1995). Several recent cladistic studies have placed *Probainognathus* among the derived cynodonts, although not so close to mammals as tritylodontids and tritheledontids (Kemp 1982, 1983; Rowe 1988, 1993; Luo and Crompton 1994).

Tritheledontids.—This group has been hypothesized to represent the sister-taxon to mammals (Hopson and Barghusen 1986; Shubin et al. 1991; Crompton and Luo 1993; Luo 1994; Crompton 1995; Sidor and Hopson 1998). Its cranial and dental anatomy have been well described (Crompton 1958, 1995; Gow 1980; Shubin et al. 1991; Allin and Hopson 1992; Wible and Hopson 1993; Hopson and Rougier 1993; Luo and Crompton 1994). Postcranial materials have been found (Gow in press), although not formally described. However, some postcranial characters have been coded in published matrices (Rowe 1993; Sidor and Hopson 1998).

Tritylodontids.—This group has an extensive fossil record. Among the derived cynodonts, Tritylodontidae are the best described for all aspects of the dentition, skull, and skeleton. Well represented taxa include *Oligokyphus* (Kühne 1956; Crompton 1964b; 1972b), *Bienotherium* (Young 1947; Hopson 1964), *Kayentatherium* (Sues 1983, 1985, 1986), *Bienotheroides* (Sun 1984; Sun and Li 1985), *Yunnanodon* (Luo 2001), *Bocatherium* (Clark and Hopson 1985; also see Rowe 1988; Szalay 1993b; Wible and Hopson 1993; Luo 1994; Luo and Sun 1993). Several studies have placed Tritylodontidae near the Mammalia (Kemp 1983, 1988; Rowe 1988; Wible 1991; Luo 1994; but see contrasting opinions of Hopson and Barghusen 1986; Hopson 1991). Some (e.g., Wible 1991; Rowe 1993) have further argued that tritylodontids represent the sister-taxon to mammals, to the exclusion of tritheledontids—hence the relevance of tritylodontids to estimation relationships among Mesozoic mammals.

Mammalian taxa.—We selected 43 mammalian taxa, including representatives of stem lineages generally believed to lie outside the mammalian crown group, as well as extinct and living taxa presumed to lie within the crown, to include putative crown and stem members of Monotremata, Marsupialia, and Placentalia. Selection was based on four considerations.

1) Morphological informativeness. Among generally accepted, higher-level monophyletic groups, the most completely known taxa were selected as representatives for their respective clades (e.g., *Haldanodon* for Docodonts, *Zhangheotherium* for Spalacotheriidae, *Henkelotherium* for Paurodontidae, etc.).

2) Within-group morphological diversity. It is often a difficult task to choose a taxon as the representative (operational taxonomic unit) for an entire group with diverse taxa. Most studies on higher-level phylogeny of fossil groups have followed the convention of using the best preserved (and most complete) taxon. However, in cases where the most complete representative happens to be the most derived member of a

group (e.g., *Lambdopsalis* for the multituberculate superfamily Taeniolabidoidea), selection of only the relatively complete taxon out of a diverse group may risk bias (Weil 1999). A challenge is to balance the choice of a more primitive (although not necessarily the most complete) taxon with the benefit of better character sampling from a more complete taxon that could be potentially too specialized (Weil 1999). To overcome this problem, we made an effort to include multiple representatives of taxonomically diverse groups, in order to sample the range of morphological diversity for the respective clade. For example, multituberculates are represented by the Jurassic and Early Cretaceous Paulchoffatiidae (assigned to paraphyletic “plagiaulacids”), together with Late Cretaceous cimolodontans, e.g., Djadochtherioidea; and eutriconodonts are represented by two or more families, including the genera *Jeholodens*, *Amphilestes*, *Gobiconodon*, *Priacodon*, and *Trioracodon*.

3) Within-group geological age. Where feasible, early members of respective lineages were included (e.g., *Steropodon* and *Teinolophos* for Monotremata, *Obdurodon* for Ornithorhynchidae, *Aegialodon* and *Pappotherium* for Boreosphenida, *Kokopellia* for Metatheria, *Prokennalestes* for Eutheria, etc.).

4) Consideration of anatomical transformation. An effort was made to sample morphologically distinctive taxa, particularly those with a potential bearing on structural transformations. Several taxa falling into this category are very incompletely known, yet they were included because of their potential bearing on the evolution of specific anatomical systems, particularly the molar pattern. The “obtuse-angle symmetrodonts” *Kuehneotherium* and *Tinodon*, for example, have an incipient triangulation of molar cusps, and thus provide a plausible intermediate character state between the molars of “triconodonts” and those of crown therians. *Aegialodon*, *Kielantherium*, *Ausktribosphenos*, *Bishops*, and *Ambondro* were included because of their bearing on the evolution of the tribosphenic molar pattern; and *Adelobasileus*, for which the dentition has not yet been described, was included owing to its implications for evolution of ear structures.

Although we included certain living and fossil members of the three living crown groups, sampling the enormous diversity of orders within crown Theria is beyond the scope of this study. Mesozoic eutherians have been treated by Kielan-Jaworowska (1977, 1978, 1981, 1984), Kielan-Jaworowska, Bown, and Lillegraven (1979), Novacek (1986a, 1992b; Novacek et al. 1997), Kielan-Jaworowska and Dashzeveg (1989), Archibald (1996), Nessov et al. (1998), Cifelli (1999b), and McKenna et al. (2000). Selected sources on early marsupials include works by Clemens (1966, 1979a), Fox (1971, 1981, 1987), Marshall (1987), Marshall et al. (1990), Kielan-Jaworowska and Nessov (1990), Cifelli (1990a, b, 1993a, b), Marshall and Kielan-Jaworowska (1992), Eaton (1993), Trofimov and Szalay (1994; see also Szalay and Trofimov 1996), Szalay (1994), Muizon (1994, 1998), Muizon et al. (1997), Muizon and Argot (in press), Marshall and Sigogneau-Russell (1995), Marshall and Muizon (1995), Johanson (1996), Cifelli et al. (1996),

Cifelli and Muizon (1997), Rougier et al. (1998), and Argot (2001). Surveys of early monotremes have been given by Pascual et al. (1992a), Archer et al. (1992, 1993, 1999), Flannery et al. (1995), and Musser and Archer (1998). The most recent, comprehensive systematic survey of fossil and recent mammals is that of McKenna and Bell (1997). Relationships among living orders of placental mammals are, in part, controversial, though recent molecular studies have yielded well-resolved, mostly concordant results (e.g., Liu and Miyamoto 1999, 2001; Liu et al. 2001; Madsen et al. 2001; Murphy et al. 2001). Phylogeny of living marsupial orders is covered by several recent molecular (Kirsch et al. 1997; Burk et al. 1999; Palma and Spotorno 1999) and morphological studies (see Szalay and Sargis 2001 and references therein). The merits of the taxa selected for this study are discussed individually below.

Adelobasileus.—This taxon is represented by a partial cranium, described by Lucas and Hunt (1990) and Lucas and Luo (1993). *Adelobasileus* was included because previous studies have consistently placed it between advanced cynodonts and primitive mammals (Lucas and Luo 1993; Rougier, Wible, and Hopson 1996). With respect to several important characters, *Adelobasileus* shows an intermediate condition between cynodonts and mammals (Lucas and Luo 1993; Luo et al. 1995). Additional dental fossils have been discovered (personal communication from S.G. Lucas) but not yet described.

Sinoconodon.—This genus is widely recognized as representing one of the most primitive mammalian stem groups (Crompton and Sun 1985; Crompton and Luo 1993; Zhang et al. 1998). The dental and cranial anatomy of *Sinoconodon* has been described in detail (Patterson and Olson 1961; Zhang and Cui 1983; Crompton and Luo 1993; Luo 1994; Luo et al. 1995; Zhang et al. 1998). Parts of the postcranium have also been examined for this study (courtesy of G.-H. Cui).

Morganucodon.—Represented by abundant fossils, *Morganucodon* is one of the best-known early mammals. Virtually all aspects of its dental and cranial anatomy have been documented (Mills 1971; K.A. Kermack et al. 1973, 1981; Parrington 1973, 1978; Crompton 1974; Graybeal et al. 1989; Crompton and Luo 1993); parts of the postcranium have also been described (Jenkins and Parrington 1976; Lewis 1983; Rowe 1988).

Megazostrodon.—Dentition and mandible are well-known (Crompton 1974; Gow 1986a; Rowe 1986); some cranial (Crompton 1974; Gow 1986a; Rowe 1986) and postcranial materials (Jenkins and Parrington 1976; Gow 1986a) have been described.

Dinnetherium.—Dentition and mandible are well described (Jenkins et al. 1983; Jenkins 1984), and some petrosal and basicranial features are also known (Crompton and Luo 1993).

Haldanodon.—Chosen as a representative of Docodonta, *Haldanodon* is, by far, the best-known member of the group: the dentition, mandible (Krusat 1973, 1980), cranium (Lillegraven and Krusat 1991), and incomplete postcranium

(Henkel and Krusat 1980; Krusat 1980, 1991) have been described. Two alternative schemes of homology have been proposed for docodont molars. Most students follow a scheme whereby the lower labial principal cusps of *Haldanodon* are considered to be homologous with the lower labial cusps of morganucodontids (Patterson 1956; K.A. Kermack and Mussett 1958; Hopson and Crompton 1969; Jenkins 1969; Gingerich 1973; Krusat 1980; Butler 1988; Pascual and Goin 1999, 2001; Pascual et al. 2000). K.A. Kermack et al. (1987) and Butler (1988) noted a resemblance between molars of docodonts and those with reversed triangulation of cusps. Butler (1997) proposed an alternative scheme whereby some features of *Haldanodon* and kuehneotheriids are considered to be homologous (but see Sigogneau-Russell and Hahn 1995). However, Pascual and colleagues (1999, 2000, 2001) considered the “triangulated pattern” of docodont molar cusps to be homoplastic. We experimented with alternative coding according to each scheme of homology (Patterson 1956; Butler 1997) and found that the position of *Haldanodon* relative to other basal mammals is not significantly affected. Here we follow the interpretation of Patterson (1956), and the majority of workers since, in the homologies of docodont molar cusps.

Hadrocodium.—This recently described mammal from the Early Jurassic of China is known by a complete skull and dentition. Previous work suggests that *Hadrocodium* lies phylogenetically between stem lineages (such as morganucodontids) and crown Mammalia, and that it provides important evidence on evolution of cranial and mandibular characteristics (Luo, Crompton, and Sun 2001).

Gobiconodon.—This Early Cretaceous mammal is the best-represented of “amphilestid” eutriconodonts. The dentition and mandible have been thoroughly described (Jenkins and Schaff 1988; Kielan-Jaworowska and Dashzeveg 1998); parts of the skeleton (Jenkins and Schaff 1988) and an incomplete skull (Luo et al., unpublished data on new Chinese materials) are known. The recently described mammal *Repenomamus* (Li et al. 2000) is most likely a gobiconodontid, or a taxon closely related to the currently known gobiconodontids.

Amphilestes.—This genus is included as a representative of “Amphilestidae”, a generally plesiomorphic and possibly paraphyletic group of “triconodonts”. Data are limited to characters from the lower dentition and mandible (Simpson 1928; Mills 1971; Crompton 1974; Freeman 1979).

Jeholodens.—This taxon, which is presumed to lie close to or within Triconodontidae, is included as a representative of Eutriconodontia. *Jeholodens* is known by a complete skeleton (Ji et al. 1999).

Priacodon.—We include this genus as a representative of Late Jurassic, North American Triconodontidae. Virtually the entire dentition, most of the mandible, and parts of the skull are known (Simpson 1929a; Rasmussen and Callison 1981; Rougier, Wible, and Hopson 1996; Engelmann and Callison 1998).

Trioracodon.—The dentition, mandible (Simpson 1928a, 1929a), and incomplete cranium (see Simpson 1928; K.A.

Kermack 1963; Wible and Hopson 1993; Rougier, Wible, and Hopson 1996) are known for *Trioracodon*. We include it as a representative of earliest Cretaceous, European Triconodontidae.

Kuehneotherium.—This genus was selected as a representative of the several earliest-known mammals with a reversed-triangle pattern of molar cusps. Data are limited to parts of the dentition and mandible (D.M. Kermack et al. 1968; Crompton 1971; Mills 1971, 1984; Gill 1974; Godefroit and Sigogneau-Russell 1999).

Tinodon.—As a representative of “obtuse-angle symmetrodonts”. Data are limited to partial dentition and mandible (Simpson 1925c, 1929a; Crompton and Jenkins 1967, 1968; Prothero 1981). We follow consensus opinion in assuming that the upper molar assigned to “*Eurylambda*” represents *Tinodon* (see discussion by Simpson 1929a; Crompton and Jenkins 1967; Ensom and Sigogneau-Russell 2000).

Shuotherium.—Included as the sole representative of a clade with an unusual, “pseudo-tribosphenic” dentition. Data limited to incomplete dentition and mandible (Chow and Rich 1982; Sigogneau-Russell 1998; Wang et al. 1998).

Ambondro.—Selected because it is the earliest known mammal with a tribosphenic molar pattern. Represented by an incomplete mandible with three teeth (Flynn et al. 1999).

Ausktribosphenos.—Selected as an early and unusual tribosphenic mammal of debated affinities (e.g., Kielan-Jaworowska et al. 1998; Luo, Cifelli, and Kielan-Jaworowska 2001). Represented by incomplete lower dentition and mandibles (Rich et al. 1997, 1999). In x-rayed photographs of the first three dentaries of *Ausktribosphenos nyktos* (personal communication from Thomas H. Rich) there is no replacing bud under the ultimate premolar, which means that there are no deciduous premolars in these dentaries.

Bishops.—Included for the same reasons as *Ausktribosphenos*, from which it differs in several respects. Known by a virtually complete dentary and postcanine dentition (Rich, Flannery, et al. 2001).

Steropodon.—Selected as the earliest-known representative of ornithorhynchid-like monotremes. Known by a partial mandible with three molars (Archer et al. 1985, cast provided for this study, courtesy of Prof. M. Archer). In coding characters for *Steropodon*, we follow the interpretation of Kielan-Jaworowska et al. (1987) and Luo, Cifelli, and Kielan-Jaworowska (2001) regarding cusp homologies.

Teinolophos.—Selected as one of the earliest known monotremes. Represented by an incomplete dentary with one molar (Rich et al. 1999; Rich, Vickers-Rich, et al. 2001).

Obdurodon.—Selected because an included species, *O. dicksoni*, is represented by a skull, the oldest known for Ornithorhynchidae and Monotremata (Archer et al. 1993; Musser and Archer 1998). Additional data for the dentition and mandible are available for *O. insignis* (see Woodburne and Tedford 1975; Archer et al. 1993; Musser and Archer 1998). In coding molar characters, we follow the assumption

of cusp homologies given by Kielan-Jaworowska et al. (1987) and Luo, Cifelli, and Kielan-Jaworowska (2001).

Ornithorhynchus.—Included as a living representative of monotremes. In coding characters, we have relied on the descriptions and interpretations of Simpson (1929b) and Woodburne and Tedford (1975) for the deciduous teeth, Hopson and Crompton (1969) for characteristics of the mandible; and Gregory (1951), Klima (1973, 1987), Lewis (1983), Rowe (1988), Zeller (1988, 1989), Szalay (1993b), and Wible and Hopson (1995) for cranial and postcranial features.

Haramiyavia.—Selected as a representative of haramiyidans, an early alloverian group with a Laurasian distribution in the Late Triassic–Early Jurassic (and surviving into the Late Jurassic of Africa, see Heinrich 1999). The most extensive information on haramiyidans was provided by Sigogneau-Russell (1989) and Butler and MacIntyre (1994). *Haramiyavia* is the best-represented member of the group, and is known by the dentary and parts of the dentition (Jenkins et al. 1997). Additional analysis and discussion of dental characteristics are given by Butler (2000).

“*Plagiaulacida*”.—This group includes the oldest uncontested multituberculates. Paulchoffatiidae, which represent a basal but distinctive clade placed in the suborder “*Plagiaulacida*” (see Kielan-Jaworowska and Hurum 2001), include genera represented by complete dentitions and partial skulls (Hahn 1969, 1977b, 1981, 1985, 1988; Clemens and Kielan-Jaworowska 1979). Some dental characters used herein are based on Hahn et al. (1989) and Butler (2000).

Cimolodonta.—A clade of advanced multituberculates, including remarkable taxonomic and morphologic diversity from the Late Cretaceous and early Tertiary. The dentition, skull, and postcranium have been extensively studied. Characters were coded primarily from the Late Cretaceous Djadochtatherioidea (see Kielan-Jaworowska and Hurum 1997; Kielan-Jaworowska and Hurum 2001; Wible and Rougier 2000), supplemented by other taxa (Clemens 1963; Clemens and Kielan-Jaworowska 1979). Any anatomical differences for individual characters were coded as polymorphic. Sources for anatomical descriptions and characters are as follows. Skull: Kielan-Jaworowska (1971), Kielan-Jaworowska et al. (1986), Miao (1988), Lillegraven and Hahn (1993), Gambaryan and Kielan-Jaworowska (1995), Meng and Wyss (1995), Wible and Hopson (1995), Hurum (1994, 1998a, 1998b), Rougier et al. (1997), and Wible and Rougier (2000). Mandible: Wall and Krause (1992), Gambaryan and Kielan-Jaworowska (1995), Weil (1999). Postcranial features, Ptilodontidae: Krause and Jenkins (1983). *Lambdopsalis*: Kielan-Jaworowska and Qi (1990), Meng and Miao (1992). Djadochtatherioidea, Taeniolabidoidea, and Eucosmodontidae: Kielan-Jaworowska and Gambaryan (1994), Gambaryan and Kielan-Jaworowska (1997). *Bulganbaatar*: Sereno and McKenna (1995). General characters: Clemens and Kielan-Jaworowska (1979), Rowe (1988), Luo (1989), Simmons (1993), Wible and Rougier (2000), and Kielan-Jaworowska and Hurum (2001).

Zhangheotherium.—Included as the best-known representative of Spalacotheriidae (“acute-angle symmetrodonts”). Represented by the dentition, mandible, incomplete cranium, and almost complete postcranium (Hu et al. 1997, 1998). Additional data supplemented from other spalacotheriids (Cifelli 1999a; Cifelli and Madsen 1999).

Henkelotherium.—As the best representative of the highly distinctive paurodontid “eupantotheres”. Represented by most of the dentition and mandible, as well as incomplete cranium and incomplete skeleton (Krebs 1991).

Dryolestes.—Included as a representative of Dryolestidae, the most diverse group of “eupantotheres”. Primary information for the dentition and mandible from Martin (1997, 1999a), supplemented by additional data from Simpson (1928, 1929a), Krebs (1971, 1993, 1998), Prothero (1981), and Martin (2000).

Amphitherium.—As a representative of amphitheriid “eupantotheres”. Data limited to the lower dentition and dentary (Simpson 1928; Mills 1964; Clemens and Mills 1971; Crompton and Jenkins 1968; Prothero 1981; Butler and Clemens 2001).

Vincelestes.—As the best known representative of “pre-tribosphenic therians”. *Vincelestes* is known by the dentition, mandible (Bonaparte and Rougier 1987; Rougier 1993; Sigogneau-Russell 1999), cranium (Rougier et al. 1992; Hopson and Rougier 1993; Rougier 1993), and postcranium (Rougier 1993).

Peramus.—Included as a representative of advanced “eupantotheres”, with a molar pattern widely regarded as structurally antecedent to that of tribosphenic mammals (e.g., Clemens and Mills 1971). Data limited to characters of the dentition and mandible (Simpson 1928; Clemens and Mills 1971; Sigogneau-Russell 1999). We interpret postcanine formula in *Peramus* as P/p5 M/m3, but it cannot be excluded that the P/p5 in *Peramus* are deciduous or represent M/m1.

Kielantherium.—Included because its molar structure is widely regarded as plesiomorphic among mammals with the tribosphenic pattern (e.g., Kielan-Jaworowska and Cifelli 2001) and because of its putative phylogenetic position as a stem boreosphenidan. Known only by the lower molars and incomplete dentary (Dashzeveg 1975; Crompton and Kielan-Jaworowska 1978; Dashzeveg and Kielan-Jaworowska 1984, Kielan-Jaworowska, unpublished data).

Aegialodon.—Selected because it is among the earliest of putative boreosphenidans, and because it has figured prominently in discussions on the origin of the tribosphenic molar pattern (e.g., K.A. Kermack et al. 1965; Crompton 1971). The sole known specimen consists of an abraded lower molar.

Deltatheridium.—Included as a relatively well-known, putative stem taxon of Metatheria (Kielan-Jaworowska and Nessov 1990; Marshall and Kielan-Jaworowska 1992; Rougier et al. 1998) or, alternatively, a stem boreosphenidan (“therian of metatherian–eutherian grade”, Cifelli 1993b). Described fossils include the dentition, rostral part of the

skull, mandible, and incomplete tarsals (Kielan-Jaworowska 1975a; Rougier et al. 1998; Horovitz 2000).

Pappotherium.—This taxon was selected because it is believed to be a proximal relative to, or basal member of, crown Theria (Cifelli 1993b; Rougier et al. 1998; Averianov and Skutschas 1999), regarded by some as a stem member of Eutheria (Slaughter 1971, 1981; Fox 1975). *Pappotherium* is known only by upper molars, referred lower molars, and (possibly) a referred distal lower premolar (Butler 1978).

Kokopellia.—As the earliest-known, generally accepted representative of basal Marsupialia. Data are limited to characters of the dentition and mandible (Cifelli and Muizon 1997).

Asiatherium.—As the earliest known putative metatherian known by an associated skeleton (Trofimov and Szalay 1994). *Asiatherium* is of further interest because its dentition is strikingly unlike that of North American, Cretaceous marsupials (Cifelli and Muizon 1997) and because features of its auditory region have a bearing on the evolution of characteristics typically associated with Marsupialia (Szalay and Trofimov 1996). *Asiatherium* is represented by the dentition, poorly preserved skull, and nearly complete skeleton.

Pucadelphys.—As the best-known Paleocene marsupial, represented by virtually complete skulls and skeletons that have been described in detail (Marshall and Muizon 1995; Marshall and Sigogneau-Russell 1995; Muizon 1998; Argot 2001; Muizon and Argot in press).

Didelphis virginiana.—As a living representative of Marsupialia. Cranial features after Wible (1990) and Wible and Hopson (1995). Postcranial characters after Szalay (1993a, 1994; Szalay and Trofimov 1996) and personal observations (Z.-X.L.) on several specimens housed in the Carnegie Museum of Natural History, Pittsburgh.

Prokennalestes.—As the best-represented of Early Cretaceous Eutheria, and among the oldest from Asia. Data are limited to characters of the dentition, mandible (Kielan-Jaworowska and Dashzeveg 1989; Sigogneau-Russell et al. 1992), and petrosal (Wible et al. 2001).

Montanalestes.—As the earliest-known representative of Eutheria from North America. Known only by parts of the lower dentition and dentary (Cifelli 1999b).

Asioryctes.—As a representative of the Late Cretaceous radiation of Asian Eutheria, recently suggested to lie outside the crown group, Placentalia (Novacek et al. 1997). *Asioryctes* is relatively well-known and is represented by the dentition, complete cranium and mandible, and parts of the postcranium (Kielan-Jaworowska 1975b, 1977, 1981).

Erinaceus europaeus.—Included as a rather generalized, living representative of Placentalia, and because Early Cretaceous *Ausktribosphenos* is dentally similar in some respects, leading to the suggestion of a possible relationship (Rich et al. 1999). Coding based on personal observations (Z.-X. L., Z. K.-J.) of several specimens housed at the Carnegie Museum of Natural History, Pittsburgh; and the Institute of Paleobiology, Polish Academy of Sciences, Warsaw.

Analyses

Incomplete taxa.—Relatively few Mesozoic mammals are represented by cranial fossils, and taxa known also by postcranial materials are extremely rare. The vast majority of Mesozoic mammals is represented only by teeth and incomplete jaws. Because the overwhelming majority of the fossil record consists of teeth, and because evolution of the dentition is widely accepted as a fundamental aspect of mammalian history, any comprehensive and objective assessment of the phylogeny and biogeography of early mammals must include sampling of dental taxa.

In the quest to sample the entire diversity of Mesozoic mammals at the subordinal level, or family level where warranted and practical, we have included 20 taxa known only by the dentition and, for some, incomplete mandible. The missing cranial and postcranial characters for these dental taxa are coded as the requisite “?”. This practice is consistent with the approach employed in constructing a super matrix, in which different datasets are combined and missing data are incorporated for the incomplete taxa (Wiens and Reeder 1995). It has been shown that missing data, by themselves, are not misleading (Wiens 1998). This allows as broad a sampling as possible of known taxonomic diversity among Mesozoic mammals, while at the same time incorporating the relatively complete (but also relatively few) taxa, known by cranial and postcranial characters in addition to dentition and jaws, for corroboration of a robust phylogeny. It is axiomatic that future discovery of more complete and informative fossils will serve to test our phylogenetic placement of the taxa currently known only by teeth and jaws.

Not-preserved *versus* not-applicable characters.—PAUP (Swofford 2000) and other algorithms currently available for phylogenetic analysis treat both missing and inapplicable characters as “missing”. Hence, the algorithms treat characters that are “not preserved” in the same manner as those that are “not applicable”, despite the fact that these character states are clearly distinct on the basis of empirical observation. A recent study on this issue (Strong and Lipscomb 1999: 363) concludes: “Coding inapplicables as ‘?’, although flawed, is currently the best way to analyze data sets that contain inapplicable character states.” The ultimate solution depends on “development of new algorithms that properly distinguish between inapplicable characters and missing data” (Lee and Bryant 1999: 378). Lacking such a solution at present, we can do no more than simply acknowledge the limitation of PAUP in this regard.

Uncertainty in anatomical interpretation.—In some cases, there are alternative, and even conflicting, interpretations of a given character for a given taxon. For example, there exist differing opinions as to the homology of the lower lingual cusp “g” (Krusat 1980) of docodonts, the designation of upper cusp “C” (metacone) of some “eupantotheres” (Crompton 1971; Hopson 1997), and the postcanine dental formula of *Peramus* (see review by Clemens and Lillegraven 1986).

When we selected one alternative over the other, we present our rationale in the character description. If a character state is variable among different individuals of the same taxon, or among members of a terminal taxon for the analysis, then the feature is coded as polymorphic (see below).

Polymorphic characters.—Characters with known morphological variation (two or more character states present) within a terminal taxon were regarded as “polymorphic”. Polymorphic features of the terminal taxa were treated as polymorphisms in the search algorithms.

Definition of characters and division of character states.—Definition of characters and division of character states are always open to further discussion because anatomically oriented systematists commonly have differing views as to character utility and relevance (compare, for example, studies by Kemp 1983, 1988; Sues 1985; Rowe 1988; Hopson 1991; Wible 1991). Where there exist alternative ways of defining a character or splitting character states, we have added a brief note (within space limitations) discussing the alternatives and the basis for our treatment of the character (Appendix 1). While we have made every effort to establish logical, reasoned definitions for characters and their various states (Appendix 1), we emphasize that neither our treatment, nor any other based on similar data, should be taken as authoritative interpretations for given anatomical characters. See “Selection of characters” for further explanation.

Ordered *versus* unordered multistate characters.—Initial searches were run with all multi-state characters treated as unordered; in second runs, all multi-state characters were treated as ordered. The difference in tree topology between the unordered *versus* ordered searches is small. Trees are longer for the ordered search than for the unordered search, but our main phylogenetic conclusions are not affected. Our preferred trees are based on the unordered searches because they involve no *a priori* assumption as to the direction of character evolution.

PAUP search settings and results.—PAUP Version 4.0b (Swofford 2000). Tree topology is based on 1000 replicates of an heuristic search. The strict consensus (Figs. 1, 2) of the equally parsimonious and shortest trees are presented. The discussion on the diagnoses of the major clades of Mesozoic mammals is based the unambiguous synapomorphies on a fundamental tree.

Tests of alternative hypotheses.—The relationships of allotherians (haramiyidans and multituberculates) and eutriconodonts are controversial. There is also disagreement as to the affinities of the earliest-known tribosphenic mammals from southern landmasses. Alternative placements of these groups have been proposed by studies that emphasized some character complexes but not all characters available. For example, the placement of *Ausktribosphenos* by Rich et al. (1997, 1999) and the hypothesis on placement of Allotheria by Butler (2000) are based entirely on dental characteristics. The placement of *Jeholodens* outside the crown Mammalia was based primarily on postcranial characters (Ji et al. 1999).

Alternative hypotheses on the relationships of these groups can be compared by nonparametric tests (Templeton 1983; Swofford 2000), provided that the correct assumption for such testing could be met (Goldman et al. 2000). To consider the relative merits of these alternative views, we used constrained searches to obtain the sub-optimal trees that have alternative and controversial placements for these groups, as was used in some recent systematic studies (e.g., Murphy et al. 2001). We then compared our preferred and the most parsimonious topologies for these groups to the alternative and sub-optimal trees using nonparametric tests (Templeton 1983; Swofford 2000), in order to assess the statistical difference between the preferred placements of specific clades and

their alternative placements (Appendix 2). These alternative placements were selected *a priori* for testing, as proposed by previous and independent work (e.g., Rich et al. 1997; Ji et al. 1999; Butler 2000). Nonparametric comparisons were made between the consensus trees and the fundamental (the equally parsimonious) trees. We also evaluated the effect of ordered multi-state characters *versus* unordered multi-state characters on the test statistics for each pairwise comparison. Results from the permutation of these testing parameters are provided in Appendix 2, and their implications are evaluated in the discussions on relationships of allotherians (including multituberculates), eutriconodonts, and the southern tribosphenic mammals and monotremes.

Definitions, diagnoses, and placements of major clades

Based on the analyses of our dataset (46 taxa by 275 characters), we support the monophyly of a number of clades of Mesozoic mammals. These clades are defined and diagnosed below. Our study also provides corroborative support for the consensus view on the placement of several major clades, as well as the paraphyletic status of several previously recognized groups. These are also discussed below.

Paraphyly of “Prototheria”

A monophyletic grouping of all non-“therian” mammals was widely accepted in the 1970s. According to this hypothesis, morganucodontids, triconodontids, monotremes, multituberculates, and possibly also docodonts, were thought to represent a major, early-diverging clade (“prototherians” of Hopson and Crompton 1969; Hopson 1970; or “atherians” of K.A. Kermack et al. 1973; D.M. Kermack and K.A. Kermack 1984) of Mammalia. This grouping was based largely on the structure of the lateral wall of the braincase and the configuration of principal molar cusps. In “prototherians”, the lateral wall of the braincase is formed by an intramembranous ossification, the anterior lamina of the petrosal (Watson 1916); and the principal molar cusps are mesiodistally aligned. In “therians”, by contrast, the lateral wall of the braincase is formed by an endochondral element, the alisphenoid, and the principal molar cusps form reversed triangles. Mammals with a triangulated pattern of molar cusps (such as *Kuehneotherium*) appear together with “prototherians” (such as morganucodontids and haramiyids) in the geologically oldest mammal faunas, and for this reason the divergence of “prototherians” and “therians” was regarded as a fundamental dichotomy in mammal evolution. This basic division among Mesozoic mammals (K.A. Kermack and Mussett 1958; K.A. Kermack 1963) was endorsed by the majority of students on the subject (K.A. Kermack 1967a; Hopson 1969, 1970; Hopson and Crompton 1969; Kielan-Jaworowska 1971; K.A. Kermack and Kielan-Jaworowska 1971; K.A.

Kermack et al. 1973; Crompton and Jenkins 1973, 1979; McKenna 1975; Zhang and Cui 1983), despite some minority opposition (e.g., MacIntyre 1967).

As first articulated by Kemp (1983), however, the linear arrangement of molar cusps seen in “prototherians” is a primitive character shared by cynodonts, and cannot be used for characterizing a monophyletic group within Mammalia. Evidence presented by braincase structure, also cited in support of a monophyletic “Prototheria”, was called into question by the embryological observations of Presley and Steel (1976; see also Presley 1980, 1981). Presley (1980) noted that the lamina obturans, the embryonic precursor to the ascending process of the alisphenoid of “therians” and the anterior lamina of the petrosal in monotremes, is formed within the spheno-obturator membrane in both monotremes and marsupials. The lamina obturans has several ossification centers that may either fuse first with the otic capsule, as in the case of the anterior lamina of the petrosal of monotremes; or with the ala temporalis, as in the case of the ascending process of the alisphenoid, seen in “therians”. The early embryonic development appears to be the same for both living therians and monotremes, so that the difference in structure of the adult braincase appears to be far less significant than initially thought (Watson 1916).

Further embryological studies (Kuhn and Zeller 1987b; Maier 1987, 1989; Zeller 1989) show a clear difference between crown therians and monotremes in the timing and sequence of fusion of these embryonic structures to surrounding structures. It has been argued (Hopson and Rougier 1993) that the reduced alisphenoid and the enlarged anterior lamina are derived features shared by monotremes and multituberculates (but see Miao 1988). Several additional derived conditions of the ear region may also be shared by groups formerly assigned to “Prototheria”, such as enclosure or partial enclosure of the geniculate ganglion into the cavum epipericum (Crompton and Sun 1985; Luo 1989; Zeller 1989), and the ventral projection of the posterior paroccipital process (Luo 1989).

However, these braincase features shared by “Prototheria” are vastly out-numbered by the derived cranial characters shared by monotremes, multituberculates, and crown therians, or some sub-group thereof, to the exclusion of *Morganucodon* and *Sinoconodon* (Crompton and Luo 1993; Wible and Hopson 1993). Recent phylogenetic analyses of the cranial characters, including the anterior lamina of the petrosal, consistently resolve monotremes, triconodontids, and multituberculates into a suite of nested (and even pectinate) clades toward the living therians (Wible and Hopson 1993; Wible et al. 1995; Rougier, Wible, and Hopson 1996). Analyses of the combined dental, cranial, and postcranial data (Rowe 1988; Hu et al. 1997; Ji et al. 1999; Luo, Cifelli, and Kielan-Jaworowska 2001) also show that “Prototheria” cannot be supported as a monophyletic group, unless crown therians are nested within it. The present study, based on a larger dataset with more comprehensive sampling of different character systems (Appendix 1), has reaffirmed the paraphyletic status of “prototherians” (Figs. 1 and 2).

Paraphyly of “triconodont-like” mammals (“Triconodonta” *sensu lato*)

Previous studies have shown that morganucodontids are far more primitive than eutriconodonts in features of the basicranium (Rowe 1988; Wible and Hopson 1993; Rougier, Wible, and Hopson 1996) and skeleton (Ji et al. 1999), despite their similarities in some (although not all) dental characters. Based on the dental features, K.A. Kermack et al. (1973) included *Morganucodonta* (*Morganucodon* and dentally similar taxa from the Rhaeto–Liassic), *Docodonts*, and *Eutriconodonts* (= “amphilestids” + triconodontids) as suborders within the order *Triconodonta*. The placement of morganucodontids in “*Triconodonta*” was widely accepted (reviewed by Jenkins and Crompton 1979; see also Miao and Lillegraven 1986; Hopson 1994: fig. 8). Subsequently it was shown that *Sinoconodon* (see Patterson and Olson 1961), although generally placed in *Morganucodonta* (Mills 1971; K.A. Kermack et al. 1973), has a far more primitive dentition than any other mammal (Crompton and Sun 1985; Crompton and Luo 1993; Zhang et al. 1998). Because *Sinoconodon* is phylogenetically more distant from the mammalian crown group than are morganucodontids, it was removed from the “*Triconodonta*”. More recent phylogenetic studies have placed morganucodontids in a far more remote position than eutriconodonts (Rowe 1988; Wible and Hopson 1993; Rougier, Wible, and Hopson 1996). This is reflected in the latest classification of McKenna and Bell (1997), wherein both morganucodontids and *Sinoconodon* are removed from the “*Triconodonta*”, in recognition of the consensus view that they are not closely related to triconodontids and “amphilestids” (Rowe 1988; Wible 1991; Wible and Hopson 1993; Crompton and Luo 1993; Luo 1994; Rougier, Wible, and Hopson 1996). The current study of a larger dataset, with

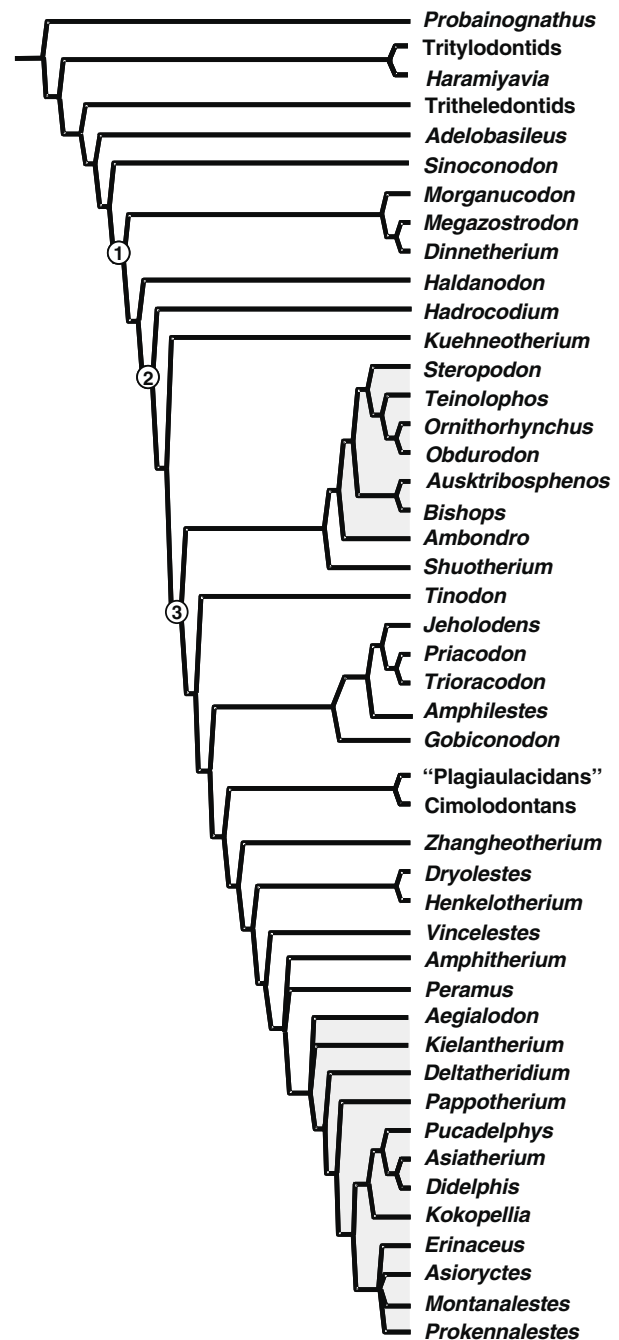


Fig. 1. Phylogenetic relationships of all major Mesozoic mammal lineages (strict parsimony from unconstrained searches). Each of the 42 equally parsimonious trees has: TreeLength = 935; CI = 0.499; RI = 0.762. Multi-state characters unordered; PAUP4.0b5 heuristic search (stepwise addition) 1000 runs. Numbers in circles (1 and 2) denote the nodes of two unnamed clades, described on p. 20 and 21 respectively, (3) crown-group Mammalia. Shaded areas denote: Australosphenida (upper shading) and Boreosphenida (lower shading).

more comprehensive sampling of characters (Appendix 1), reaffirms (Figs. 1 and 2) the paraphyletic status of “*Triconodonta*” (*sensu lato*, e.g., K.A. Kermack et al. 1973). Problems relating to monophyly and placement of eutriconodonts are discussed below.

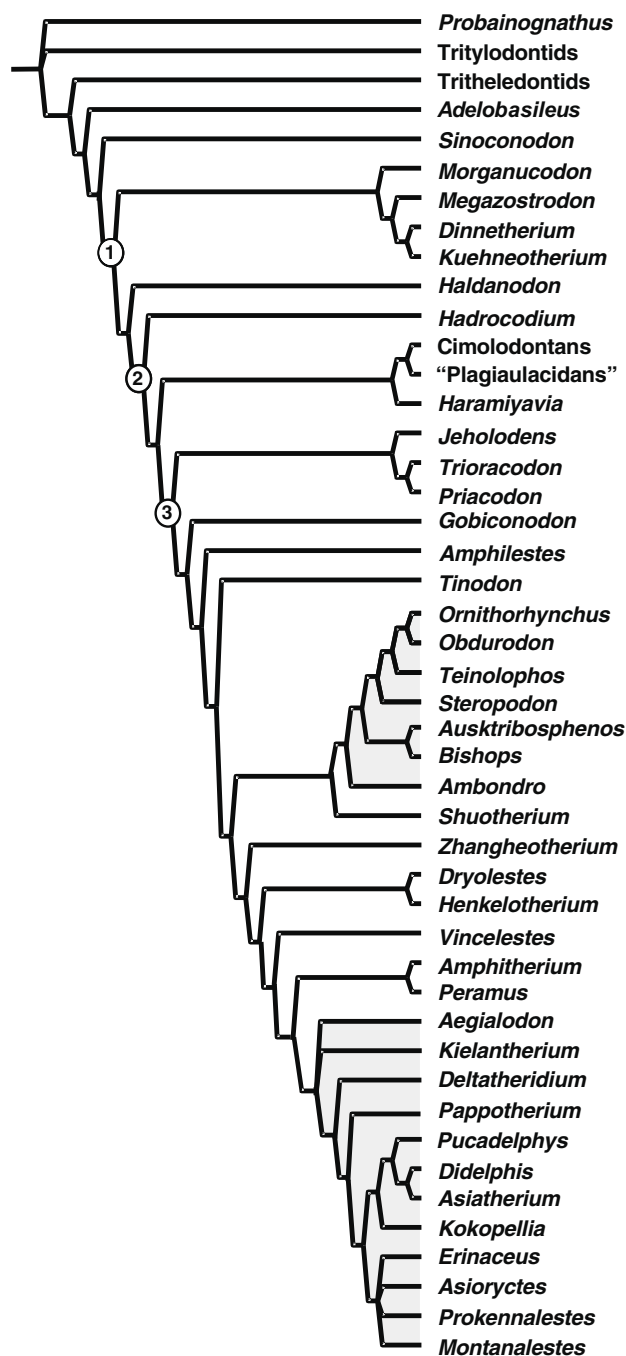


Fig. 2. Phylogenetic relationships of all major Mesozoic mammal lineages. Alternative topology from constrained searches for allotherians. Search constrained to retain the trees compatible with an allotherian clade (*Haramiyavia* + multituberculates) outside mammalian crown group. By nonparametric tests, the alternative placement of allotherian clade here is not significantly different from that in Fig. 1. Our nonparametric tests did not show a significant difference between the alternative placement of allotherians clade outside (here in Fig. 2) or multituberculates within (compare to Fig. 1) the mammalian crown group. Test results are summarized in Appendix 2. Each of the 21 equally parsimonious trees has: Tree Length = 942; CI = 0.496; RI = 0.759. All multi-state characters run as unordered; PAUP4.0b5 heuristic search (stepwise addition) 1000 runs. Numbers in circles (1 and 2) denote the nodes of two unnamed clades, described on p. 20 and 21 respectively, (3) crown-group Mammalia. Shaded areas denote: Australosphenida (upper shading) and Boreosphenida (lower shading).

Relationships of Docodonta

Simpson (1928, 1929a) and a number of workers before him (e.g., Marsh 1887; Osborn 1888) placed docodonts among “pantotheres”, which in turn were considered to be the basal stock to living therians. Simpson (1929a: figs. 27, 36) pointed out some general similarities in the upper molars between the dryolestid “pantotheres” and docodonts. He implied that the transverse alignment of labial and lingual cusps on upper molars of dryolestids might be comparable to the cusp pattern of a docodont.

Patterson’s (1956) interpretation of cusp homologies for dryolestid upper molars identifies the main labial cusp as the stylocone. This homology has been accepted by all subsequent workers who have revisited the issue (see reviews by Prothero 1981; Butler 1988). Patterson (1956) also proposed that the longitudinal cusps in the labial row of docodont upper molars are homologous to the mesiodistally aligned principal cusps seen in upper molars of morganucodontids and eutriconodonts. Following this scheme, the large lingual cusp of docodont upper molars is not homologous to the protocone, as Simpson (1928) implied and Butler (1939) explicitly designated. Rather, it is a hypertrophied homologue to a lingual (cingular) cusp of morganucodontids (Patterson 1956). Based on Patterson’s (1956) observation, docodonts are no longer considered to be related to “pantotheres”.

Patterson’s interpretation of cusp homologies for docodonts and morganucodontids has been accepted by subsequent workers (K.A. Kermack and Mussett 1958; K.A. Kermack 1967a; Hopson and Crompton 1969; Jenkins 1969; Hopson 1970; Kühne and Krusat 1972; Krusat 1980; Pascual et al. 2000). This scheme is consistent with extensive observations on cusp wear facets and with inferences on occlusion (Jenkins 1969; Gingerich 1973; Krusat 1980; Butler 1988; Pascual et al. 2000). Based on the plausible derivation of docodont molar structure from the triconodont pattern, together with the primitive jaw structure shared by docodonts and morganucodontids (K.A. Kermack and Mussett 1958), Docodonta were placed among “Prototheria” (K.A. Kermack and Mussett 1958; Hopson 1969, 1970; Hopson and Crompton 1969; Krusat 1980) and were commonly considered to be morganucodontid descendants (see review by K.A. Kermack et al. 1973).

Docodonts are unusual among Mesozoic mammals in the development of a wear surface on the mesio-lingual part of the lower molar (Jenkins 1969; Gingerich 1973; Krusat 1980; Butler 1988, 1989; Sigogneau-Russell and Hahn 1995). In at least in one genus, *Simpsonodon*, this developed into a basined surface and assumed a grinding function (K.A. Kermack et al. 1987). *Shuotherium*, from the Jurassic of China (Chow and Rich 1982; Wang et al. 1998) and Britain (Sigogneau-Russell 1998), is the only other Mesozoic mammal that has a comparable structure (pseudo-talonid anterior to the trigonid) and occlusal pattern (with the lingual aspect of the upper molar, represented by the pseudo-protocone of *Shuotherium*, Wang et al. 1998; Sigogneau-Russell 1998).

K.A. Kermack et al. (1987) suggested a possible relationship between *Shuotherium* and docodonts. More recently, Butler (1997) pointed out several similar features of docodonts and the Late Triassic mammal *Woutersia*. Butler (1997) suggested that the molar pattern of *Woutersia* (described as an early and somewhat unusual “symmetrodont”, see Sigogneau-Russell 1983; Sigogneau-Russell and Hahn 1995) could be an evolutionary precursor to the more specialized molars of docodonts. This view, not endorsed by Sigogneau-Russell and Hahn (1995), implies that docodonts have an ancestry characterized by reversed triangulation of molar cusps and their oblique wear facets (see also Sigogneau-Russell and Godefroit 1997).

Pascual and Goin (1999, 2001; Pascual et al. 2000) proposed a different hypothesis from that of Butler (1997) for the evolution of oblique wear facets in docodonts. They suggest that the pattern seen in docodont lower molars evolved through hypertrophy of a lingual cusp (cingular cusp of morganucodontids) and the secondary development of oblique ridges between it and the labial cusps in the “triconodont-like” and linear alignment. In this evolutionary scenario, the obliquely oriented, elaborate wear surfaces of docodont molars evolved in different ways from those of mammals with a molar cusp triangulation (e.g., kuehneotheriids). These authors implied that the reversed triangulation of wear surfaces in docodonts is derived from a morganucodont-like precursor and is functionally analogous to the molar of “therians” (for further discussion see “obtuse-angle symmetrodots”).

Detailed study by Lillegraven and Krusat (1991) showed that the skull of *Haldanodon* is more primitive than morganucodontids in a number of features. These authors placed *Haldanodon* (and, by implication, Docodonta) outside all mammals, including *Sinoconodon*. In subsequent parsimony analyses (Luo 1994; Wible et al. 1995; Rougier, Wible, and Hopson 1996), *Haldanodon* assumed a slightly higher position on the mammalian tree, being placed closer to the mammalian crown group than both morganucodontids and *Sinoconodon*.

In summary, all studies since Patterson (1956) indicate that docodonts represent one of the stem branches of the mammalian tree, despite their precociously specialized dentition. Recent parsimony analyses (Hopson 1994; Luo 1994; Rougier, Wible, and Hopson 1996; Luo, Crompton, and Sun 2001) explicitly place Docodonta closer to crown Mammalia than morganucodontids and *Sinoconodon*, but more basal than triconodontids, multituberculates, and *Hadrocodium* (Luo, Crompton, and Sun 2001). Our analysis of the currently available dataset (Appendix 1) supports this placement of docodonts (Figs. 1 and 2).

Paraphyly of the “obtuse-angle symmetrodots”

Kuehneotheriidae and Tinodontidae include generally similar taxa (see Fox 1975), with principal molar cusps arranged

in an obtuse triangle (in occlusal view), and upper triangles reversed with respect to lowers. This pattern has long been viewed as representing a major functional advance in the evolution of mammalian molar occlusion (e.g. Butler 1939; D.M. Kermack et al. 1968; Crompton and Jenkins 1967, 1968; Parrington 1973; Crompton 1995). As noted in the review of “prototherians”, this pattern has also been widely regarded as a key feature linking “obtuse-angle symmetrodots” to “eupantotheres” and, ultimately, to marsupials and placentals (e.g., Butler 1939; Patterson 1956; Crompton 1971; McKenna 1975). The Late Triassic to Early Jurassic *Kuehneotherium*, however, retains a number of plesiomorphies in the mandible. Most notable of these is the presence of a postdentary trough and a medial ridge on the dentary, indicating that the postdentary elements were associated with the mandible, as in cynodonts, rather than being incorporated into the middle ear, as in living mammals (see D.M. Kermack et al. 1968; Allin and Hopson 1992; Rowe 1993; Hopson 1994; Rougier, Wible, and Hopson 1996; Kielan-Jaworowska et al. 1998). This paradoxical combination of important characters – molars of advanced design, together with mandible characterized by primitive “reptilian” features – poses an obvious conflict for any placement of *Kuehneotherium* in mammalian phylogeny: either a triangulated molar cusp pattern evolved more than once, or the separation of middle ear from the mandible occurred more than once (see discussions by Miao and Lillegraven 1986; Allin and Hopson 1992; Rowe 1993; Hopson 1994; Rougier, Wible, and Hopson 1996). It is also possible that both the molar cusp triangulation and the derived mandibular characters are homoplastic.

Traditionally, the reversed triangulation of molar cusps has been favored and the conflicting mandibular features have been considered to be homoplasies. The discoveries of early “symmetrodots” having cusp triangulation (Kühne 1950), as well as mammals with the postdentary elements attached to the mandible (K.A. Kermack and Mussett 1958), occurred in the conceptual framework of independent acquisition of key mammalian characteristics through polyphyletic origin, which was then widely accepted (e.g., Simpson 1959). The assumption of phyletically independent transformations in the postdentary bones into the middle ear was not perceived as conceptually daunting, and remained largely unchallenged (Hopson 1966; Allin 1986; Allin and Hopson 1992; see summary by Cifelli 2001). One recent work (McKenna and Bell 1997), for example, still emphasizes the molar triangulation of *Kuehneotherium*, and explains its mandibular plesiomorphies as atavistic reversals.

Recent large-scale phylogenetic analyses, however, have supported the alternative interpretation that the reversed-triangle pattern of molar cusps evolved more than once (see reviews by Rowe 1993; Rougier, Wible, and Hopson 1996; also Pascual and Goin 1999, 2001; Pascual et al. 2000). The postulation of homoplasies of molar cusp triangulation would be consistent with the following observations.

The molar cusp triangulation is quite variable among “obtuse-angle symmetrodots”. The degree of cusp triangulation

varies through the molar series in *Kuehneotherium* (see Parrington 1978). In *Tinodon*, it is clear that the posterior lower molars show more prominent triangulation than the first lower molar, which is hardly triangulated at all (Crompton and Jenkins 1967). A similar variability in triangulation of cusps is now also documented in *Gobiotheriodon* (Averianov in press).

Similar variability of molar cusp triangulation is present in several non-“symmetrodont” mammals. In *Gobiconodon*, the anterior upper molars have a typical triconodont cusp pattern, while a gradient of increasing triangulation characterizes more posterior molars (Jenkins and Schaff 1988; Kielan-Jaworowska and Dashzeveg 1998). The same is true, to a lesser degree, in *Megazostrodon* (Crompton 1974; Parrington 1978). In both cases, this variable triangulation is present in the upper but not lower molar series.

A recent hypothesis by Pascual and Goin (1999, 2001; Pascual et al. 2000) invokes homoplasy to explain the presence of cusp triangulation among disparate mammalian groups, and suggests how it might have been independently achieved. For docodonts, they hypothesize that triangulation in lower molars occurred through a secondary development of oblique ridges connecting the primary labial cusps (aligned in “triconodont” fashion) to an enlarged lingual (originally cingular) cusp. According to this model, the obliquely oriented wear surfaces of docodont lower molars constitute a “pseudo-trigonid” that is not homologous to the trigonid of “therians”. These authors further suggest that this same, alternative model may be used to explain the origin of the V-shaped “trigonid” and “talonid” among toothed monotremes. The hypothesis of Pascual and Goin (1999, 2001; Pascual et al. 2000) calls for separate origins of molar cusp triangulation in docodonts, toothed monotremes, and “therians”. It highlights the uncertainties surrounding the evolution of molar cusp triangulation, calls into question the long-held reverence for (and reliance upon) this single character complex, and underscores the need for evaluating the molar triangulation in the parsimony context of other, non-molar characters.

Our analysis has included all known dental and mandibular features of *Kuehneotherium* and *Tinodon*, two important taxa overlooked in most previous parsimony analyses. Results of this study (Figs. 1, 2) show that there are simply no synapomorphies to support a broadly conceived “Symmetrodonta” that include these genera, and that the “obtuse-angle symmetrodonts” themselves are not closely related. The structurally more advanced (in terms of mandibular characters; Appendix 1) of the two, *Tinodon*, lies within (Fig. 1) or basal to (Fig. 2) the mammalian crown group, but it is not proximal to the trechnotherian clade (spalacotheriids + crown Theria) characterized by “acute-angle” molars (see also Ji et al. 1999). In summary, we consider that these archaic, “obtuse-angle symmetrodonts” represent a heterogeneous evolutionary grade, and that they lack reliable diagnostic features. All that can be said is that they are probably unrelated to each other or to “acute-angle symmetrodonts”. They occupy some basal positions in mammalian phylogeny that

are not very well resolved by the limited anatomical data known from their currently incomplete fossils.

Holotheria (see Hopson 1994) are defined as the shared common ancestor of *Kuehneotherium* and living therians, plus all its descendants (McKenna and Bell 1997). Anatomical data for *Kuehneotherium* are very incomplete, and include a mosaic of primitive (such as the presence of a postdentary trough on the mandible) and advanced (triangulated molar cusps) characteristics. Unsurprisingly, these conflicting characters result in great instability for placement of *Kuehneotherium* in mammalian phylogeny. By definition, the taxonomic contents of Holotheria are also highly unstable, if the clade is to be defined by *Kuehneotherium*. The most important apomorphy of *Kuehneotherium* is the triangulation of molar cusps, but our parsimony analyses show that this feature is not sufficient to link *Kuehneotherium* to other mammals with triangulated molar cusps. For these reasons, we do not treat Holotheria as stable clade herein, as we did previously (Luo, Cifelli, and Kielan-Jaworowska 2001).

Relationships of Monotremata

Living monotremes are very distinctive from other mammals and are also highly specialized in their own right (Kuhn 1971; Griffiths 1978; Zeller 1989, 1999a, b). They are so different from other mammals that Matthew (1928), Simpson (1928, 1937), and Olson (1944: 124) accorded monotremes an ancestry from some unknown pre-cynodont therapsid, independent of other living and fossil mammals, as a part of the now-abandoned concept of mammalian polyphyly.

Gregory (1910) pointed out that monotremes and crown therians share many derived anatomical and reproductive features. He argued that monotremes and crown therians comprise a natural group (Gregory 1910: figs. 31, 32), and that monotremes are more closely related to living therians than to any non-mammalian cynodonts. More recent studies have documented an enormous body of evidence on the derived reproductive and ontogenetic features that are shared by all living mammals (Luckett 1977; Griffiths 1978; Zeller 1999a, b) to the exclusion of the living non-mammalian amniotes. Within the framework of a monophyletic Mammalia, there are several hypotheses as to the relationships of monotremes to other mammalian groups.

Monotremes and marsupials.—Gregory (1910) emphasized the anatomical resemblance of monotremes and marsupials, and later (Gregory 1947) went on to argue for placement of Monotremata within Marsupialia, as possible relatives of phalangerids. His classification places marsupials and monotremes in their own subclass, “Marsupionta”. Since then, a close relationship of monotremes and marsupials has been rejected by most students of mammalian phylogeny (see review by Parrington 1974), a notable exception being Kühne (1973a, b, 1977).

Subsequent discoveries of more complete fossils of advanced cynodonts and Mesozoic mammals showed that all

osteological characters cited by Gregory (1947) in support of monotreme–marsupial affinities are primitive. These features have a broad distribution outside monotremes and marsupials. For example, the similarities between monotremes and marsupials in the tympanic and malleus, emphasized by Gregory (1947), are also applicable to *Morganucodon* (K.A. Kermack et al. 1981; K.A. Kermack and Mussett 1983) and to a wide range of non-mammalian cynodonts (Allin and Hopson 1992). The columnar stapes of the platypus and *Didelphis* is also a primitive feature (Doran 1878; Novacek and Wyss 1986b; Meng 1992; Hurum et al. 1996; Rougier, Wible, and Novacek 1996a). The number of thoraco-lumbar vertebrae (19–20) is also known for some placentals and the eutriconodont *Jeholodens* (Ji et al. 1999). The pectoral girdle features shared by monotremes and transiently in marsupial embryos (Klima 1973, 1987) have been shown to be present in numerous advanced cynodonts (Jenkins 1971, 1974; Sues 1983; Sun and Li 1985). Gregory (1947; also Kühne 1973a, b) emphasized the epipubic bone and its anatomical relationships to the “marsupial” pouch, then only known for monotremes and marsupials. Now the epipubic bone has been documented in eutriconodonts (Jenkins and Schaff 1988; Ji et al. 1999), multituberculates (Kielan-Jaworowska 1969; Krause and Jenkins 1983; Kielan-Jaworowska and Gambaryan 1994), a wide variety of stem group “therians” (Krebs 1991; Rougier 1993; Hu et al. 1997) and Cretaceous eutherians (Novacek et al. 1997), possibly also in morganucodontids (Jenkins and Parrington 1976; but see reinterpretation of Evans 1981). In summary, none of the osteological features emphasized by Gregory (1947) is a shared derived character for monotremes and marsupials.

Of the soft-tissue anatomical features noted by Gregory (1947), only the marsupial pouch can be considered as shared exclusively by monotremes and (almost all) marsupials. However, it remains possible that the pouch existed also in a number of fossil taxa, e.g., in multituberculates, as suggested by Kielan-Jaworowska (1979). The comparison of the enlarged rhinarium seen in certain marsupials (wombat, phalangers) to the beak of *Ornithorhynchus* (Gregory 1947; Penny and Hasegawa 1997) is misleading because the enlarged rhinarium of vombatids and phalangerids is not a basal condition for marsupials, or even for Diprotodonta, within which vombatids and phalangerids are nested. Most recently, Zeller (1999a, b) has pointed out that characteristics of embryogenesis and lactation shared by monotremes and marsupials are primitive for all mammals (including eutherians), and that these primitive features offer no support for a close relationship of monotremes and marsupials, to the exclusion of placentals.

Kühne (1973a, b, 1977) was the only morphologist to support the “Marsupionta” hypothesis. Reinterpreting Green’s (1937) work on the milk dentition of *Ornithorhynchus*, Kühne (1977) postulated that only the first premolariform tooth in *Ornithorhynchus* is a true premolar with replacement, and that the second premolariform, regarded by Green (1937) as belonging to the milk dentition, is the first molar. Because marsupials replace only the last premolar (see review by Luckett

1993), Kühne (1977) argued that *Ornithorhynchus* and marsupials share the same replacement pattern of the cheek teeth. Kühne’s controversial reinterpretation has been accepted by few (see the criticism by Griffiths 1978; Starck 1982). Luckett and Zeller (1989) re-evaluated the relevant embryological evidence, and concluded: 1) that there is no secondary dental lamina at the first premolar locus of *Ornithorhynchus*; and 2), in agreement with Green (1937), the tooth in question therefore belongs to the deciduous series. Luckett and Zeller (1989) also argued that the second tooth of the series in *Ornithorhynchus* is a premolar, not a molar as Kühne (1977) contended. The Miocene ornithorhynchids *Obdurodon insignis* (see Woodburne and Tedford 1975) and *O. dicksoni* (see Archer et al. 1992, 1993) show that ornithorhynchids primitively had two premolars and that the ultimate premolar was smaller than the first molar (Musser and Archer 1998). This corroborates Green’s (1937) proposed homologies for the cheek teeth of *Ornithorhynchus anatinus*, but contradicts the alternative interpretation of Kühne (1977). In summary, no unambiguous characters of dental developmental pattern are available to serve as synapomorphies of marsupials and monotremes to the exclusion of placentals.

Phylogenetic evidence from molecular sequence on the relationship of monotremes differs according to the types of molecules and genes examined, but most of the recent studies (1997–2001) are consistent with a monophyletic crown Theria, to the exclusion of monotremes. An earlier study on the globin protein sequence (Czelusniak et al. 1990) yielded an unresolved trichotomy for the three groups of living mammals. The most recent study on α -lactalbumin protein sequences excluded monotremes from a monophyletic crown Theria (Messer et al. 1998). The first studies on protamine DNA and protein sequences (Retief et al. 1993) also placed Monotremata outside of a monophyletic crown Theria. This topology was again corroborated by phylogenetic studies of neurotrophin genes (Kullander et al. 1997) and β -globin gene sequences (Lee et al. 1999) among monotremes, marsupials, and placentals. Recent studies on large datasets of imprint genes (Killian et al. 2000, 2001) and on CORE-SINES retroposons (Gilbert and Labuda 2000) again support the marsupial-placental clade to the exclusion of monotremes. To date, only the DNA–DNA hybridization (Kirsch et al. 1997) and mitochondrial sequence data (Janke et al. 1996, 1997; Penny and Hasegawa 1997) suggest an alternative topology, in which monotremes are sister-group to the living marsupials, to the exclusion of placentals. In sum, some types of molecular data have provided limited support for the “Marsupionta” hypothesis (Janke et al. 1996, 1997; Penny and Hasegawa 1997). The preponderance of evidence, including that provided by nuclear genes and retroposons (Retief et al. 1993; Kullander et al. 1997; Lee et al. 1999; Gilbert and Labuda 2000; Killian et al. 2000, 2001) and protein sequences (Messer et al. 1998), favors the traditional hypothesis of a monophyletic crown Theria (see also Szalay and Sargis 2001).

Monotremes and “pre-tribosphenic therians”.—The discovery of Australian, Early Cretaceous *Steropodon* in 1985 showed that early monotremes have surprisingly complex molars that are structurally closer to the tribosphenic pattern than had been previously envisaged. Archer et al. (1985) interpreted the dentition of *Steropodon* to represent a highly modified tribosphenic pattern, implying an origin of monotremes from a relatively advanced, tribosphenic stage of “therian” evolution. Kielan-Jaworowska et al. (1987; see also Jenkins 1990) observed that the molars of *Steropodon* are not fully tribosphenic (in lacking wear function within the talonid basin), and proposed an alternative origin for monotremes, among “pre-tribosphenic therians” (e.g., *Peramus*). Bonaparte (1990) emphasized the dental similarities between *Steropodon* and dryolestid “eupantotheres”, an observation endorsed by Pascual et al. (1992a) and Archer et al. (1993). Archer et al. (1992) argued that the dentition of early monotremes is characterized largely by plesiomorphic features lacking (and presumably lost) in “therian” mammals. Zeller (1993) proposed a more remote position for monotremes on the mammalian tree, suggesting origin of their clade prior to the appearance of basal “eupantotheres”.

Monotremes and other australosphenidans.—*Ausktribosphenos nyktos*, from the Early Cretaceous of Australia, has molars that are clearly of tribosphenic design, together with highly specialized premolars. Rich et al. (1997, 1999) and Rich, Flannery, et al. (2001) proposed that *A. nyktos* is a placental, possibly a member of the living Erinaceidae. To date, this view has not been accepted (e.g., Rougier and Novacek 1998). Musser and Archer (1998) suggested a relationship of *Ausktribosphenos* to “pre-tribosphenic peramurids” or, possibly, to monotremes. Kielan-Jaworowska et al. (1998) observed that *Ausktribosphenos* retains significant plesiomorphies in the mandible (such as the presence of a post-dentary trough), and suggested a far more remote origin for *Ausktribosphenos*, perhaps among early “symmetrodonts” (see counterarguments by Rich et al. 1998, 1999).

Flynn et al. (1999) reported a new tribosphenic mammal, *Ambondro mahabo*, in the Middle Jurassic (Bathonian) of Madagascar. *Ambondro* is represented by a dentary fragment with the last premolar and two molars. The fossil extends the geologic age of mammals with tribosphenic molars back by some 25 million years. This allowed Rich and Vickers-Rich (1999) to develop new arguments supporting the placental nature of both *Ausktribosphenos* and *Ambondro*. More recently, Rich, Vickers-Rich, et al. (2001) reported *Bishops whitmorei*, a new taxon closely related to *Ausktribosphenos*. The discoveries of *Ambondro*, *Ausktribosphenos*, and *Bishops* challenge the long-held view that higher mammals and their descendants (including all living placentals and marsupials), which are similarly characterized by tribosphenic molars, arose on northern continents.

Phylogenetic analyses by Luo, Cifelli, and Kielan-Jaworowska (2001) suggest that the newly discovered southern tribosphenic mammals, *Ausktribosphenos* and *Ambondro*, are

representatives of an endemic, Gondwanan radiation of mammals that are related to monotremes rather than marsupials, placentals, and presumed fossil relatives from northern continents. These results imply that the hallmark specialization of higher mammals—the multifunctional tribosphenic molar pattern—arose not once but at least twice, and had vicariant geographic distribution in the Jurassic through Early Cretaceous. Based on their conclusions, Luo, Cifelli, and Kielan-Jaworowska (2001) erected two new mammalian infraclasses, both including taxa with tribosphenic molars: Boreosphenida, including “tribotheres”, marsupials and placentals (known only from northern continents prior to the latest Cretaceous); and Australosphenida, including *Ausktribosphenos*, *Ambondro*, and monotremes (restricted to Gondwanan landmasses). In the present study, we have also included the newly described southern tribosphenic mammal *Bishops* (Rich, Vickers-Rich, et al. 2001), as well as new characters on the premolar structure of *Obdurodon dicksoni*. Results of the new, expanded analyses (Figs. 1, 2) reaffirm a monophyletic clade including the southern tribosphenic mammals with toothed monotremes (see discussion under Australosphenida, below).

Definition of Mammalia

Mammalia as construed herein are a clade defined as the common ancestor to *Sinoconodon*, monotremes, and crown therians, plus all the extinct fossil mammals nested within these three taxa. This is equivalent to the Mammaliaformes of Rowe (Rowe 1988: fig. 4, but not Rowe, 1993: fig. 10.2). We opt for this inclusive definition of mammals (e.g., Hopson 1994) because it is consistent with widespread, traditional usage, and (as noted above) because it has the virtue of being relatively stable with respect to both living and fossil taxa. A crown-based definition of Mammalia (Rowe 1986; McKenna and Bell 1997) clearly offers certain advantages (Queiroz and Gauthier 1990, 1992; Rowe and Gauthier 1992), though there are merits to other definitions as well (Kemp 1982; Hopson and Barghusen 1986; Miao 1991; Lucas 1992; Rowe and Gauthier 1992; Bryant 1994; Hopson 1994; McKenna and Bell 1997). The current lack of consensus on definition of Mammalia is an example of the perennial debate surrounding vertebrate groups that have familiar, vernacular names, as well as reasonably good fossil records documenting early phylogenetic differentiation and anatomical transformations toward the crown groups (e.g., Sereno 1998; Lee 2001).

Based on the foregoing definition, a primary character diagnosing Mammalia is the presence of a craniomandibular joint comprised of dentary condyle and squamosal glenoid. The establishment of the dentary condyle to squamosal glenoid joint is correlated with an important functional pattern of mammalian jaw movement (Crompton 1964a; Crompton and Parker 1978; Crompton and Hylander 1986). It is also a crucial morphological feature shared by *Sinoconodon* and living mammals, plus all taxa nested among them. Of the three earliest (Late Triassic) mammalian lineages to appear

in the fossil record, morganucodontids and kuehneotheriids are nested within this clade (K.A. Kermack and Mussett 1958; Hopson and Crompton 1969; Crompton and Jenkins 1979; Gow 1985; Rowe 1988; Luo 1994). The haramiyidan *Haramiyavia* may also have this feature, as inferred from the preserved posterior part of the mandible (Jenkins et al. 1997).

The dentary–squamosal jaw contact is absent in all known non-mammalian cynodonts (Crompton 1972a) with exception of tritheledontids, generally considered to represent the sister-taxon to Mammalia (Hopson and Barghusen 1986; McKenna 1987; Shubin et al. 1991; Crompton and Luo 1993; Miao 1993; Luo 1994; this study). The lateral ridge of the dentary posterior peduncle contacts the base of the squamosal zygoma in tritheledontids (Crompton 1958; 1972a; Crompton and Luo 1993); but there is no dentary condyle, nor a clearly defined glenoid area on the squamosal (Crompton 1972a; Luo and Crompton 1994). Thus tritheledontids have an intermediate character state to the typical mammalian craniomandibular joint, and still differ from Mammalia in this feature.

Mammalia as defined herein are also diagnosed by presence of a petrosal promontorium, representing the external eminence of the pars cochlearis. The promontorium is the most distinctive feature of the mammalian basicranium (MacIntyre 1972; Crompton and Sun 1985; Gow 1985, 1986b; Hopson and Barghusen 1986; Rowe 1988; Wible 1991; Luo 1994; Luo et al. 1995). The promontorium is developed at the expense of the ventrolateral wing of the basi-sphenoid; it also partially displaces the basioccipital. Observations on living mammals show that presence of the promontorium is correlated with a neomorphic pattern of ossification of the embryonic otic capsule that is distinct from the pattern of living, non-mammalian amniotes (Kuhn 1971; Maier 1987, 1989; Zeller 1989). The pars cochlearis is the bony housing of the hearing organ, the cochlea; enlargement and emergence of the pars cochlearis on the ventral surface of the skull provide more internal space for the cochlea within the petrosal. The cochlea of basal mammals may have already had the capacity for high frequency hearing (Rosowski and Graybeal 1991; Rosowski 1992) as a result of this transformation in the bony structures.

Mammalia can also be diagnosed by a host of other basicranial apomorphies: the extensive development of a petrosal floor for the cavum epiptericum that houses the trigeminal ganglion (Crompton and Sun 1985), the presence of a separate tympanic aperture for the prootic canal that contains the prootic vein (Wible and Hopson 1995), the loss of the thickened rim of the fenestra vestibuli (Lucas and Luo 1993), and the separation of the hypoglossal foramen (cranial nerve XII) from the jugular foramen (cranial nerves IX, X, XI) (Lucas and Luo 1993). According to Hopson (1991, 1994), the presence of four lower incisors (instead of three) is also diagnostic for Mammalia (although reversed in multituberculates and *Gobiconodon*). Other, equivocal features in the palate and in the orbital wall can also diagnose Mammalia, depending on whether tritylodontids or tritheledontids

are considered to be the sister-taxon and the immediate out-group to mammals (Luo 1994).

Adelobasileus, from the Late Triassic (Carnian), also possesses an incipient petrosal promontorium, together with several other synapomorphies listed above. Initial analyses including *Adelobasileus* nested this genus within mammals (Lucas and Hunt 1990; Lucas and Luo 1993; Hopson 1994). Our results, like those of other recent analyses (Rougier, Wible, and Hopson 1996; Luo, Crompton, and Sun 2001), place *Adelobasileus* outside the clade of *Sinoconodon* and living mammals. The fossil of *Adelobasileus* is incomplete. We provisionally follow Lucas and Luo (1993) in considering it to be a basal mammal, noting that a well-supported appraisal of its status ultimately depends on discovery of additional fossils.

Within Mammalia, *Sinoconodon* is the sister-taxon to a clade that includes *Morganucodon* and the living mammals (Crompton and Sun 1985; Crompton and Luo 1993; Rowe 1993; Wible and Hopson 1993; Luo 1994; Rougier, Wible, and Hopson 1996). Below we define and diagnose major clades of Mesozoic mammals.

Unnamed clade 1 (node 1 in Figs. 1 and 2).—This clade is defined as the common ancestor of *Morganucodon*, living mammals, and all fossil taxa nested within this clade (= node 8 of Rowe 1993, minus *Sinoconodon*). *Morganucodon* is known by relatively complete, abundant fossils representing the dentition (Crompton 1971, 1974; Mills 1971; K.A. Kermack et al. 1973; Clemens 1980; Jenkins et al. 1983), skull (K.A. Kermack et al. 1973, 1981; K.A. Kermack and Mussett 1983; Young 1982; Crompton and Luo 1993; Luo and Crompton 1994), and skeleton (Jenkins and Parrington 1976). Because it is the most completely known of Late Triassic–Early Jurassic mammals and because its characteristics have received thorough coverage in previous phylogenetic analyses, the phylogenetic position of *Morganucodon* among basal mammals has remained very stable (Kemp 1983; Rowe 1988; Wible 1991; Hopson 1994; Rougier, Wible, and Hopson 1996; Luo, Crompton, and Sun 2001), compared to other less complete fossil taxa.

The clade including *Morganucodon* and living mammals is diagnosed by several derived dental characters that are unique among amniotes. Several of these apomorphies are associated with the presence of precise occlusion between upper and lower molars. These include one-to-one opposition of upper to lower molars, and the development of matching upper and lower facets associated with individual molar cusps as the results of occlusal wear (K.A. Kermack et al. 1965; D.M. Kermack et al. 1968; Crompton and Jenkins 1968; Crompton 1971, 1974; Mills 1971). The majority of taxa in this clade share an apomorphic condition of tooth replacement, wherein the anterior post-canines are diphyodont, but molars are not replaced (Parrington 1978; Krusat 1980; Luckett and Zeller 1989; Luckett 1993; Martin 1997; Cifelli 1999a; Cifelli et al. 1998; Martin and Nowotny 2000; Luo et al. 2001c). Known exceptions are *Gobiconodon* (see Jenkins and

Schaff 1988) and *Megazostrodon* (see Gow 1986a), where replacement occurs at one or more “molar” positions.

There is substantial evidence, based on large samples of fossil jaws and crania, that *Morganucodon* had achieved a determinate growth pattern in the upper and lower jaws with respect to the entire skull (Gow 1985; Luo 1994; Luo, Crompton, and Sun 2001). By comparison, *Sinoconodon* retains the primitive pattern of indeterminate skull growth, with successive replacement of molariforms at posterior loci while the skull continued to grow in size, as seen in cynodonts and most other non-mammalian amniotes (Crompton and Luo 1993; Luo 1994; Zhang et al. 1998). In *Sinoconodon*, as in non-herbivorous cynodonts, the molariform postcanines lack one-to-one opposition between respective upper and lower teeth.

The clade of *Morganucodon* and living mammals is also characterized by a large suite of basicranial features (see review by Rougier, Wible, and Hopson 1996). The anterior paroccipital process of the petrosal has a crista parotica for the articulation of the incus (Luo and Crompton 1994). The incus, reduced in size and suspended by the petrosal, has a greater degree of mobility that presumably facilitated sound transmission in the middle ear. By contrast, *Sinoconodon* and tritheledontids retain the primitive condition, wherein the incus (quadrate) is entirely suspended by the squamosal, as in all non-mammalian cynodonts except for tritylodontids (Crompton 1964a; Hopson 1964; Sues 1985, 1986; Luo and Crompton 1994). Other derived petrosal characters of this clade include an enlarged posterior projection of the posterior paroccipital process (Luo 1989; Crompton and Luo 1993; Wible and Hopson 1993; Rougier, Wible, and Hopson 1996), and a fully developed promontorium without any overlap of the basioccipital (Luo, Crompton, and Sun 2001). In correlation with the increased size of the promontorium, the cochlea is relatively longer in *Morganucodon* (Graybeal et al. 1989; Luo and Ketten 1991) and in the more derived taxa of this clade (Lillegraven and Krusat 1991; Lillegraven and Hahn 1993; Meng and Wyss 1995; Hurum 1998b) than in *Sinoconodon* and all non-mammalian cynodonts (Fourie 1974; Quiroga 1979; Allin 1986; Crompton 1995; Luo 2001).

The basal members of this clade are the morganucodontids, of which *Megazostrodon*, *Erytherotherium*, *Dinnetherium*, and *Morganucodon* are best represented by fossils. Several additional taxa are known only by teeth (and hence some are placed here with doubt), including *Eozostrodon* (not surely distinct from *Morganucodon*, see Clemens 1979b), *Brachyozostrodon* (see Hahn et al. 1991), *Helvetiodon* and *Hallaitherium* (see Clemens 1980), *Wareolestes* (see Freeman 1979), *Indotherium* (see Prasad and Manhas 1997), *Gondwanodon* (Datta and Das 1996) and *Indozostrodon* (Datta and Das 2001). They range from Late Triassic (Carnian) to Early Jurassic, with one questionable genus (*Wareolestes*) known from the Middle Jurassic. Morganucodontidae are notable in their early geological occurrence, global distribution, and relatively good representation in the fossil record. Our analyses (Figs. 1, 2) show that morganu-

codontids represent a monophyletic clade, and are not related to the geologically younger eutriconodonts.

Among Docodonta, *Haldanodon* is best-known (Krusat 1980, 1991; Lillegraven and Krusat 1991; see also Martin 1999b). Like other docodonts, the molars are highly derived (Hopson and Crompton 1969; Krusat 1980; Butler 1988, 1997). The pattern of tooth replacement is consistent with that seen in *Morganucodon* and derived mammals (Martin and Nowotny 2000), with single replacement of premolariforms and no replacement of molariforms, and unlike *Sinoconodon*, in which there is replacement of the posterior molariforms (Crompton and Luo 1993; Zhang et al. 1998). *Haldanodon* shares with morganucodontids and other derived mammals such features as the platform-like squamosal glenoid, with constriction of the base of squamosal zygoma (Lillegraven and Krusat 1991); the anterior placement of the pterygo-paroccipital foramen for the superior ramus of the stapedial artery (Rougier, Wible, and Hopson 1996); and a more extensive ventral floor of the cavum epiptericum. Our analysis nests *Haldanodon* within the clade of *Morganucodon* and living mammals, and indicates that it is more closely related to living mammals than to *Morganucodon*. By extrapolation, Docodonta as a group are hypothesized to be closer to the mammalian crown group than are morganucodontids. The additional dental and several postcranial characters in our dataset corroborate a placement of *Haldanodon* that is similar based exclusively on basicranial features (Rougier, Wible, and Hopson 1996).

Unnamed clade 2 (node 2 in Figs. 1 and 2).—Defined as the common ancestor of *Hadrocodium* (see Luo, Crompton, and Sun 2001) and living mammals, plus all of its descendants. The first suite of diagnostic apomorphies is on the medial side of the dentary: the absence of the postdentary trough and its medial ridge, together with loss of the concavity for the reflected lamina of the angular. By contrast, other Late Triassic–Early Jurassic mammals resemble cynodonts in having a prominent postdentary trough with an overhanging medial ridge for accommodation of the surangular, articular, and prearticular bones (Allin 1975; K.A. Kermack et al. 1973, 1981; Allin and Hopson 1992; Crompton and Luo 1993; Luo 1994). *Morganucodon* and *Sinoconodon* also have a conspicuous medial concavity on the mandibular angle for the reflected lamina of the angular (K.A. Kermack et al. 1973; Crompton and Luo 1993), although this concavity is less prominent in *Dinnetherium* and *Megazostrodon* (in which the mandibular angle is smaller), and in non-mammalian cynodonts. The absence of these features suggests the detachment of the postdentary bones from the dentary and the possible incorporation of these elements into the “cranial” middle ear in *Hadrocodium* and some eutriconodonts, as is demonstrably the case for multituberculates and living mammals. However, if *Haramiyavia* is proven to be related to multituberculates and if *Kuehneotherium* is a basal “therian”, then atavistic reversal would be required to account for the inferred attachment of the postdentary elements in these two genera (see Jenkins et al.

1997; McKenna and Bell 1997; and previous discussion on “holotherians”). We also notice that *Shuotherium* and some australosphenidans have retained the postdentary trough, although the trough in these taxa is reduced and lacks its overhanging medial ridge seen in most Late Triassic–Early Jurassic mammals. If *Shuotherium* and australosphenidans are nested with the crown mammalian group, as proposed herein, then there could be yet another case of homoplastic evolution of the postdentary (middle ear) elements in early mammals.

The second suite of diagnostic apomorphies for *Hadrocodium* and living mammals is related to the enlargement of the brain. The brain vault is wider in the parietal region of *Hadrocodium*, Triconodontidae (Simpson 1928), multituberculates (Kielan-Jaworowska 1986, 1997), and the mammalian crown group (Kielan-Jaworowska 1986, 1997; Rowe 1996a, b), than in cynodonts (Quiroga 1979), *Sinoconodon* (Patterson and Olson 1961; Crompton and Sun 1985; Crompton and Luo 1993; Luo 1994), *Morganucodon* (K.A. Kermack et al. 1981; Rowe 1996a, b), and *Haldanodon* (Lillegraven and Krusat 1991). Related to this expansion of the brain vault, the cerebellar portion of the brain cavity is expanded more posteriorly than the temporomandibular joint (TMJ). As a result, the occiput (the posterior wall of the brain cavity) is convex and extends back far beyond the TMJ. A distinctive postglenoid region is developed posterior to the TMJ in *Hadrocodium*. This is a derived feature shared by the monotremes *Tachyglossus* and *Obdurodon* (Musser and Archer 1998), although not *Ornithorhynchus*, by many (but not all) multituberculates (Kielan-Jaworowska and Hurum 1997; Wible and Rougier 2000), and by most trechnotherians (Krebs 1991; Rougier 1993; Hu et al. 1997). In contrast, all outgroups to this clade lack these derived features in the TMJ and the occipital region. Also related to the expanded brain vault is a more ventrolateral orientation of the fenestra vestibuli (Rowe 1988).

The third suite of derived features shared by *Hadrocodium* and living mammals is in the petrosal. The paroccipital region of the petrosal lacks bifurcation of the paroccipital process into anterior and posterior parts. A shallow fossa incudis is well-developed lateral to the crista parotica. The pterygoparoccipital foramen for the superior ramus of the stapedial artery is completely enclosed by the petrosal. By contrast, most outgroups (*Morganucodon*, *Sinoconodon*, and tritylodontids) to this clade lack these apomorphies (Wible and Hopson 1993; Wible and Hopson 1995; Rougier, Wible, and Hopson 1996), although *Adelobasileus* may be an exception (Lucas and Luo 1993).

Crown-group Mammalia (node 3 in Figs. 1 and 2) (Mammalia of Rowe 1988; Rowe and Gauthier 1992; McKenna and Bell 1997).—This clade is defined as the common ancestor of all living mammals and all its descendants. A dental synapomorphy shared by all fossil and living members of this clade is the presence of occlusal surfaces that match precisely between upper and lower molars upon eruption. By comparison, precise molar occlusion in the stem taxa outside this clade is dependent on the development of extensive wear facets, wherein

a significant amount of the tooth crowns must be worn away in order to achieve matching occlusal surfaces between upper and lower molars (Crompton 1971, 1974; Mills 1971, 1984; Godefroit and Sigogneau-Russell 1999). A notable exception is presented by Docodonts, which have a complex pattern of occlusion (Jenkins 1969; Gingerich 1973; Krusat 1980; Butler 1988; Pascual et al. 2000). A mandibular synapomorphy of this clade is the presence of a distinctive masseteric fossa with a well-defined ventral margin. This fossa occupies the entire mandibular angle region and is far more expanded than in such stem taxa as *Sinoconodon*, morganucodontids, *Kuehneotherium* and *Hadrocodium*. This character is also absent in *Haramiyavia*, which is placed outside the crown group on the most parsimonious trees (Fig. 1, but also see the alternative placements of *Haramiyavia* and multituberculates in Fig. 2).

The cochlear canal is more elongate (although not always coiled) in all members of the mammalian crown group in which this feature is known (Luo and Ketten 1991; Meng and Wyss 1995; Fox and Meng 1997; Hurum 1998b), at least in comparison to *Sinoconodon* (Luo et al. 1995), *Morganucodon* (Graybeal et al. 1989), *Haldanodon* (Lillegraven and Krusat 1991) and cynodonts (Allin and Hopson 1992; Luo 2001). All clades of the mammalian crown-group lack an ossified pila antotica separating the cavum epiptericum from the braincase, with the notable exception of multituberculates (Hurum 1998a). The astragalus and calcaneus are in partial superposition in the majority of the taxa for which the tarsals are known (except *Ornithorhynchus*; also *Jeholodens* if the latter proves to lie among crown mammals). Most living orders of this group have greatly enlarged gyrencephalic cerebral hemispheres (with external gyri and sulci on the surface of endocast).

Australosphenida (*sensu* Luo, Cifelli, and Kielan-Jaworowska 2001).—This clade is defined as the common ancestor of *Ambondro*, *Ausktribosphenos*, living monotremes, and all its descendants. It includes all extinct taxa more closely related to living monotremes than to *Shuotherium*¹, or than to living therians. Fossil members of Australosphenida for which the dentition is known (*Ambondro*, *Ausktribosphenos*, *Bishops*, and the toothed monotremes) are diagnosed by a distinctive and shelf-like mesial cingulid (rather than individualized cingulid cusps) that wraps around the antero-lingual corner of the lower molar. This feature is well developed in *Ambondro* and *Ausktribosphenos*, but developed to a lesser extent in *Bishops*. It is better developed on m3 than on m1 in *Steropodon*. The toothed monotremes share with *Ausktribosphenos* and *Bishops* a unique condition in which the distal metacristid forms a sharp, V-shaped notch, with the crest extending anteriorly from cusp “d” (provisionally re-

¹ The “m1” of the holotype of *Shuotherium dongi* lacks the pseudo-talonid, characteristic of the succeeding molars. It cannot be ruled out that the tooth is, instead, an ultimate premolar (Chow and Rich 1982); if this proves to be true, then the two australosphenidan apomorphies (mesial cingulid and ultimate lower premolar with the trigonid, lacking the talonid) may be shifted to be the apomorphies of (*Shuotherium* + Australosphenida).

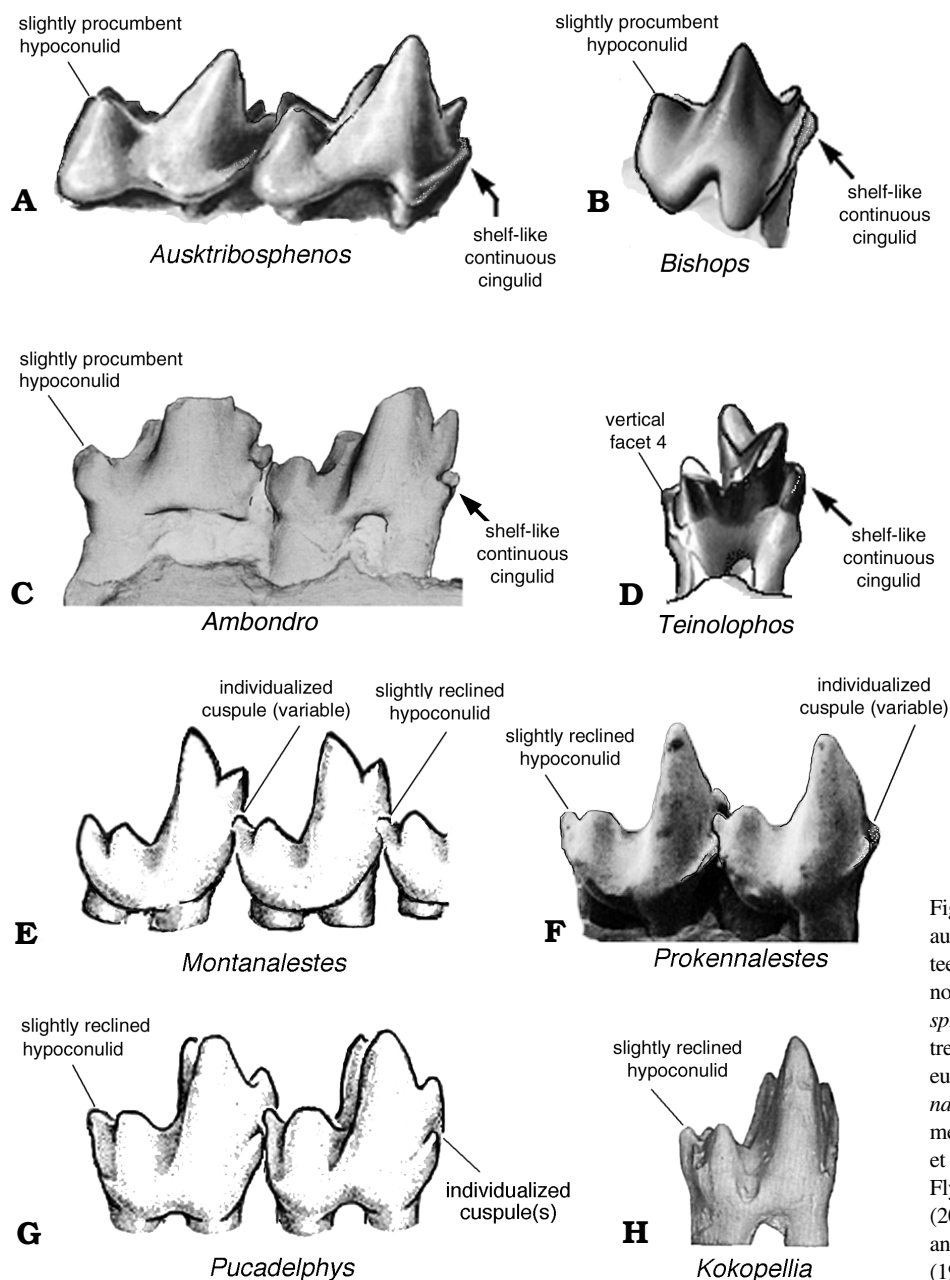


Fig. 3. Comparison of dental characters among australosphenidan and boreosphenidan mammals; all teeth are in labial view; anterior is to the right; teeth not to scale. **A–D.** Australosphenidans: *Ausktribosphenos* (**A**), *Bishops* (**B**), *Ambondro* (**C**), the monotreme *Teinolophos* (**D**). **E–H.** Boreosphenidans: the eutherian *Montanalestes* (**E**), the eutherian *Prokennalestes* (**F**), the marsupial *Pucadelphys* (**G**), the metatherian *Kokopellia* (**H**). Modified after: **A**, Rich et al. (1999); **B**, Rich, Flannery, et al. (2001); **C**, Flynn et al. (1999); **D**, Rich, Vickers-Rich, et al. (2001); **E**, Cifelli (1999b); **F**, Kielan-Jaworowska and Dashzeveg (1989); **G**, Marshall and Muizon (1995); **H**, Cifelli and Muizon (1997).

garded herein as the hypoconulid). Australosphenidans are more derived than contemporary pre-tribosphenic mammals, as well as all tribosphenic mammals from the Cretaceous of northern continents, in having a transversely wide talonid. The hypoconulid is procumbent and the posterior and labial walls of the talonid are developed into a prominent bulge (exoedaenodont condition; Fig. 3). None of these derived conditions is seen in any of the Laurasian pre-tribosphenic “eupantotheres”, or tribosphenic mammals (including metatherians and eutherians) before the early Tertiary (Puercan age). By contrast, in most northern Cretaceous tribosphenic mammals, the hypoconulid is slightly reclined posteriorly, slanting toward the root without much bulging. The hypoconulid of a preceding molar interdigitates with the individualized mesial cusps of the succeeding molar. Due to the

highly transformed features of the mesial cingulid of a succeeding molar and the distal cingulid of the preceding molar, the lower molars of australosphenidans lack the primitive interlocking mechanisms (Fig. 3) common to most Mesozoic mammals (except *Sinoconodon*, some “symmetrodonts”, and dryolestids).

The posterior lower premolars of *Ambondro*, *Ausktribosphenos*, and *Bishops* are also very derived. The main diagnostic features are: the great breadth of the posterior part of the premolar, with transverse distal cingulid present, and the presence of fully triangulated trigonid cusps on the penultimate and ultimate lower premolars. These derived premolar features are not seen in any other mammals of the Jurassic–Early Cretaceous. Premolars are not known for the earliest monotreme, *Steropodon*; but some derived conditions are

present in the premolar of *Obdurodon dicksoni* (see below), and we presume that the condition of living monotremes represents a secondary loss.

The ultimate lower right premolar of *Obdurodon dicksoni* (see Archer et al. 1993) has a weakly developed triangulate pattern. The labial face of the protoconid (cusp a) is convex, while the lingual face is slightly concave (Fig. 4). The two crests form an angle with the protoconid. The premolar is transversely wide in its posterior part, as in *Ambondro* and *Ausktribosphenos*. It also has both the transverse mesial and distal cingulids. By comparison, the distal part of the penultimate and ultimate premolars of most Cretaceous eutherians and metatherians are narrow and laterally compressed.

Most spalacotheriids and the pre-tribosphenic “eupantotheres” also have posterior lower premolars with laterally compressed crowns. None of these taxa has symmetrically triangulated premolars, or continuous mesial and distal cingulids. It should be noted that, although some Late Cretaceous and many early Tertiary eutherians have semi-molariform premolars, the molarization of the premolars is invariably expressed first through the presence of a talonid, not in the development of well-differentiated, symmetrically triangulated trigonid cusps, as in *Ambondro*, *Ausktribosphenos*, *Bishops*, and *Obdurodon dicksoni*. The molariform premolars of eutherians differ from those of australosphenidan mammals in numerous features.

The angular process of the mandibles of *Ausktribosphenos*, *Bishops*, and the monotreme *Teinolophos* are similar in that they are elevated dorsally, so as to be on the same level as (or higher than) an imaginary line drawn through the gum level of the postcanine alveoli (Fig. 5). In most of pre-tribosphenic “eupantotheres” and marsupials, the mandibular angle is more or less at the level of the ventral border of the mandible. In the majority of eutherians, the angle projects below the level of the horizontal ramus, pointing postero-ventrally (Fig. 5). A related apomorphic feature of *Bishops* and monotremes (e.g., *Teinolophos* and ornithorhynchids) is the more vertically directed dentary peduncle and condyle. In “eupantotheres” and boreosphenidans, these are more posteriorly directed (Fig. 5).

In other aspects, the mandibles of *Ausktribosphenos* and the monotreme *Steropodon* (Fig. 6) are more primitive than those of multituberculates, eutriconodonts, spalacotheriids, dryolestids, metatherians and eutherians. As pointed out by Kielan-Jaworowska et al. (1998) and Luo, Cifelli, and Kielan-Jaworowska (2001), both *Ausktribosphenos* and *Steropodon* retain a prominent Meckel’s sulcus (Fig. 6), which is also present in *Bishops* (Rich et al. 1999). The postdentary trough is well developed in *Ausktribosphenos*, and partially preserved in the incomplete mandible of *Steropodon* (Fig. 6). The posterior opening of the mandibular foramen is located within the postdentary trough (Fig. 6). The latter two characters are primitive features shared by *Morganucodon*, *Sinoconodon* and nonmammalian cynodonts (K.A. Kermack et al. 1973; Luo 1994). These primitive features of *Ausktribosphenos* do not support its placement

within trechnotherians (spalacotheriids + crown Theria) or within eutherians (more discussion below).

Living monotremes have unique features of the inner ear in which they differ from all living mammals and all extinct lineages of fossil mammals. In living monotremes, the membranous ductus cochlearis does not have a corresponding coiled bony tube. Instead the ductus cochlearis is coiled within a larger bony cochlear canal without internal bony supportive structures such as the primary bony lamina for the basilar membrane (Zeller 1989; Luo and Ketten 1991; Fox and Meng 1997). In living therians, by contrast, the coiled membranous ductus cochlearis is indivisibly associated with the coiled bony cochlear canal (Lewis et al. 1985; Meng and Fox 1995c); the coiled duct is supported by the primary bony lamina that is also coiled. It has been hypothesized that the coiled cochlea without internal bony lamina in monotremes is derived separately from that of the living therians (Zeller 1989; Hu et al. 1997). Living monotremes also differ from other mammals in that their tympanohyal contacts the promontorium (Kuhn 1971; Zeller 1989; Wible and Hopson 1995; Rougier, Wible, and Hopson 1996). The auditory region is unknown among stem australosphenidans. Future fossil discoveries may show that these characters (presence of a coiled cochlear duct without internal bony lamina, and the contact of tympanohyal to promontorium) may represent synapomorphies of a more inclusive group (e.g., Australosphenida) or, alternatively, a sub-clade of australosphenidans in which living monotremes are nested.

We evaluated the alternative (and controversial) placements of the southern tribosphenic mammals (Rich et al. 1997; Flynn et al. 1999; Luo, Cifelli, and Kielan-Jaworowska 2001) by nonparametric tests (Templeton 1983; Swofford 2000). We developed sub-optimal trees from PAUP’s search, constraining the position of *Ambondro* between *Peramus* and *Kielantherium* (as explicitly suggested by Flynn et al. 1999). Similar constraints were imposed for *Ausktribosphenos* and *Bishops*, which were placed within the placental crown group (as explicitly proposed by Rich et al. 1997, 1999). Our preferred tree topology (*Ambondro*, *Ausktribosphenos* and *Bishops* clustered with the toothed monotremes, and segregated from the earliest northern tribosphenic mammals) was then compared to the sub-optimal trees that are consistent with topologies implicit in the studies of Rich et al. (1997, 1999) and Flynn et al. (1999). Based on our dataset (46 taxa, 275 characters; see Appendix 1), these pairwise comparisons uphold the hypothesis of a dual origin for the tribosphenic molar pattern (Luo, Cifelli, and Kielan-Jaworowska 2001) as significantly different from (and better than) the suboptimal trees ($p < 0.05$) for all permutations of the tests (Appendix 2). Rich et al. (1999) also implied that the affinities of *Ambondro* may lie with erinaceomorph placentals (contra the interpretation of Flynn et al. 1999). We also evaluated this alternative placement. The topology including a cluster comprised of *Erinaceus*, *Ambondro*, *Ausktribosphenos*, and *Bishops* is significantly different from our preferred tree if the tests are based on the strict consensus trees (Appendix 2).

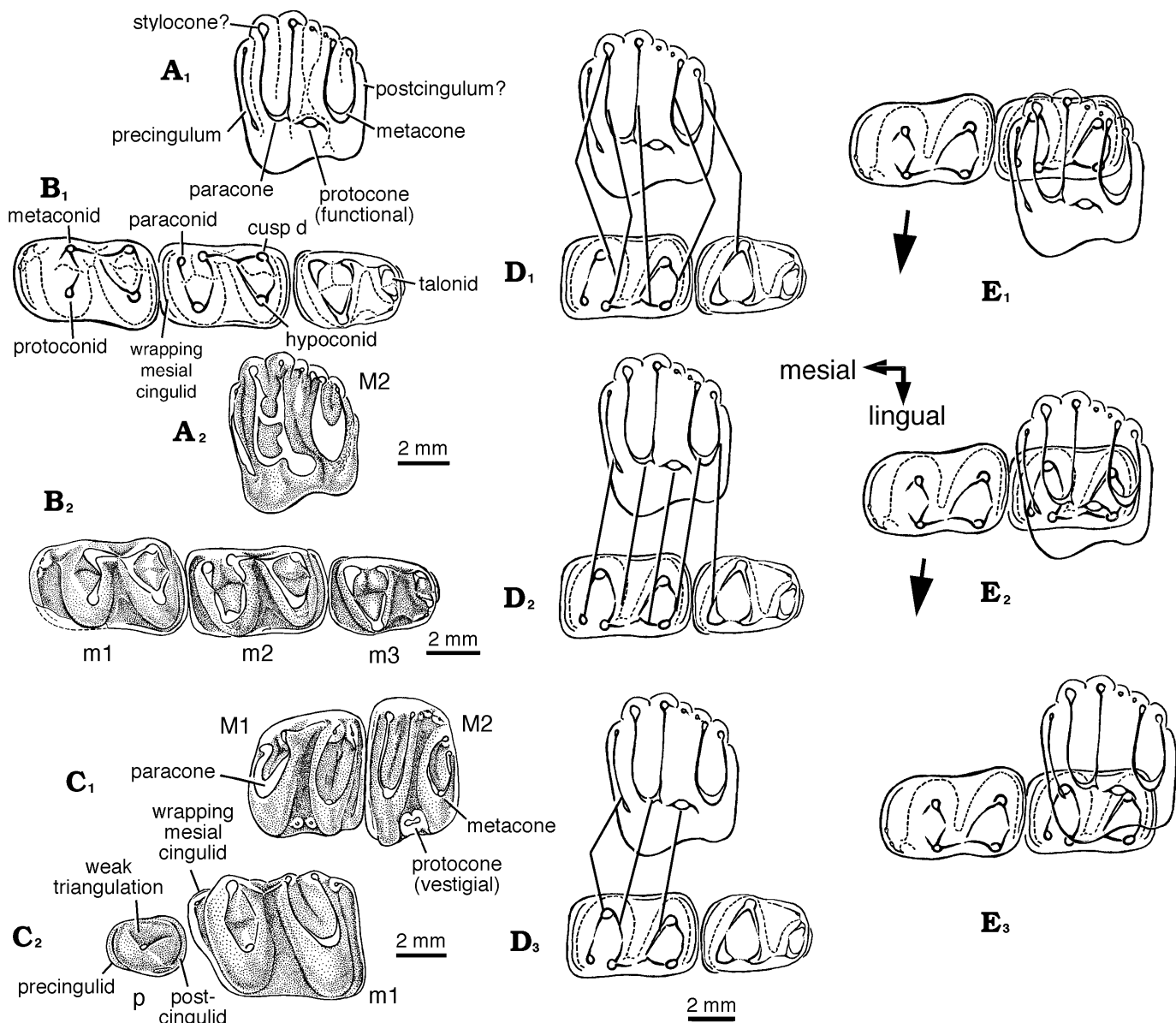


Fig. 4. Putative homologies of molar features among toothed monotremes, occlusal views; mesial is to the left in all the drawings. **A.** *Monotrematum*, the geologically oldest upper molar known for monotremes (left upper molar shown). Outline restoration for M2 (A₁); the same in stipple drawing (A₂). **B.** *Steropodon*, the geologically oldest lower molars known for monotremes (left lower molars shown). Diagrammatic drawing (B₁); the same in stippled drawing (B₂). **C.** *Obdurodon dicksoni*. Left upper molars (C₁); left lower ultimate premolar and first molar (C₂). **D.** Hypothetical occlusal relationship of the upper and lower molars for basal monotremes; hypothetical models of upper molar (reversed crown view of right M2 of *Monotrematum*) and lower molars (crown view of *Steropodon*). Hypothetical contacting relations between the upper and the lower structures at the beginning of occlusion (D₁); contacting relations near the mid-point of occlusion (analogous to the centric occlusion in the boreosphenidan mammals with the “pestle-to-mortar” occlusion (D₂); contacting relations near of the end of the occlusal cycle (D₃). The matching of the upper and the lower molar models is based on the similarity in the lowers between *Steropodon* and *Obdurodon dicksoni* and the similarity in the uppers of *Monotrematum* and *O. dicksoni*. **E.** Three stages (E₁–E₃) showing the sequence of upper-to-lower occlusion, in correspondence with D₁–D₃, as the lower molars moved across the transversely wider upper molar. Arrows denote direction of movement of the lower molars. Relative positions of the overlapping upper and lower molars of E₁, E₂, and E₃ correspond to the contact points of the upper and lower structures labelled in D₁–D₃. See text for explanation. All original drawings, based on: **A**, photos of Pascual *et al.* (1992a, b) reversed; **B**, a cast of the holotype, reversed; **C**, SEM photos of Archer *et al.* (1993), with premolar reversed from the right side to be consistent with the left m1; **D** and **E** originals.

Crucial to the hypothesis of a dual origin for mammals with tribosphenic molars (Luo, Cifelli, and Kielan-Jaworowska 2001) is the strength of the separate placements for australosphenidans (southern) and boreosphenidans (northern) mammals on the mammalian tree. If we enforce the col-

lapse of either Australosphenida or Boreosphenida (but not the collapse of both simultaneously), the resultant suboptimal trees would only swap the closest sister-taxon of either group. The more inclusive clades in which australosphenidans and boreosphenidans separately nested are still supported. The

separation of the australosphenidans from any of the boreosphenidans is maintained in the alternative suboptimal trees. The results from nonparametric tests (almost all permutations, see Appendix 2) are consistent with the hypothesis of separate origins for the two groups.

Separate placements of the southern tribosphenic mammals from the earliest known marsupials and placentals (and presumed relatives with tribosphenic molars) suggest that characteristics related to the tribosphenic molar pattern were homoplastic features in the evolution of Mesozoic mammals. Assuming a monophyletic Australosphenida, as supported by the analyses herein, it remains debatable as to whether the common ancestor of the group (as currently defined) had fully tribosphenic molars. We do not consider the toothed monotremes to have typical tribosphenic molars (see Kielan-Jaworowska et al. 1987). This is not, however, incompatible with the hypothesis that monotremes are closely related to taxa in which a recognizable tribosphenic pattern is present. Within the context of our phylogeny, two alternative scenarios could explain the evolution of the highly derived molars of toothed monotremes; we consider them equally plausible based on the limited data at hand. The first, proposed by Kielan-Jaworowska et al. (1987), posits the derivation of the precociously specialized talonid of *Steropodon* and *Obdurodon* from a non-tribosphenic pattern. This hypothesis has been reviewed and discussed by many authors (Jenkins 1990; Luo, Cifelli, and Kielan-Jaworowska 2001; Pascual and Goin 1999, 2001) and repetition here is unnecessary.

A second scenario, implied by the nesting of monotremes within the australosphenidan clade (Figs. 1, 2), calls for the presence of fully tribosphenic molars in the common ancestor of the stem australosphenidans and Monotremata. By this interpretation, the absence of an upper molar protocone represents a loss that occurred late in the history of the group, presumably among the Tertiary ornithorhynchids. The geologically oldest upper molar of a monotreme is that of the Paleocene *Monotrematum sudamericum* (see Pascual et al. 1992a, b). *Monotrematum* has a functional cusp near the valley of the upper molar trigon, and closely appressed to the paracone and metacone (Fig. 4). The extensive apical wear on this cusp, as described by Pascual et al. (1992a, b), suggests that it had occlusal contact with the lower molar talonid. We infer that it had apical wear against the cristid obliqua and hypoconid on the rim of the talonid (Fig. 4C–E), although not within the compressed talonid basin. We propose that this upper molar cusp is a reduced equivalent of the protocone (Fig. 4). Based on this model, we infer that the apical wear on the cristid obliqua and hypoconid of *Steropodon* corresponds to the apical wear of a reduced protocone (= “valley cusp” as identified by Pascual et al. 1992a, b).

An identical cusp is also present on M2 of *Obdurodon*, although it is vestigial and split into two cusps on M1. Because this reduced protocone (valley cusp) is much lower than the adjacent paracone and metacone in *Obdurodon*, it did not occlude with the lower molar as in *Monotrematum*. We hypothesize that the absence of a functional protocone in

the upper teeth of *Obdurodon* and the deciduous teeth of living *Ornithorhynchus* represent a secondary condition, via an intermediate evolutionary stage equivalent to that seen in *Monotrematum* (Fig. 4). If *Monotrematum* had a lower molar similar to that of *Steropodon*, as suggested by Pascual et al. (1992a, b), or if *Steropodon* had an upper molar similar to that of *Monotrematum*, then all of the currently known occlusal features of monotremes can be explained by designating the small (yet still occlusal) “valley cusp” of *Monotrematum* as the homologue to the inferred protocone of tribosphenic australosphenidans (see Fig. 4C–E).

In *Monotrematum* and *Obdurodon*, the large paracone (cusp A) and metacone (cusp C) (*sensu* Hopson 1994), together with their hypertrophied crests, represent a complex that is functionally analogous to, and convergent with, similar structures on “lophiodont-like” upper molars of some perissodactyls and diprotodontid marsupials, or to “dilambdodont-like” upper molars of some placental insectivores. Neither *Steropodon* nor *Monotrematum* has the typical “pestle-to-mortar” occlusion because the former’s talonid is longitudinally compressed and the latter’s protocone (valley cusp) is reduced and closely appressed to the paracone and metacone. But their respective molar patterns could be derived from typical tribosphenic precursors of a hypothetical common ancestor shared by *Ausktribosphenos* and *Bishops*. Parallel evolution of lophiodont (nontribosphenic) dental patterns from a tribosphenic precursor has been extensively documented for numerous, independent lineages of Tertiary placentals and marsupials (e.g., Osborn 1907).

Trechnotheria (modified from McKenna 1975).—This clade is defined as the common ancestor of *Zhangheotherium* (and by extrapolation the monophyletic group of Spalacotheriidae, see Cifelli and Madsen 1999) and crown Theria, plus all of its descendants. The most prominent diagnostic character of this group is the presence of a hypertrophied postvallum/prevallid shearing mechanism (Crompton and Jenkins 1968; Crompton and Sita-Lumdsen 1970; Krebs 1971; Fox 1975; Hu et al. 1997, 1998; Cifelli and Madsen 1999). Related to the hypertrophy of the postvallum crest, an acute triangulation of cusps is prominently developed, especially on the upper molars, in spalacotheriids, dryolestids, paurodontids, *Amphitherium* (Mills 1964; Butler and Clemens 2001), and the therian crown group, although not so well developed in “peramurids” and some stem taxa of boreosphenidans such as *Pappotherium*. In some spalacotheriids, there is a slight gradient of triangulation according to tooth locus (Fox 1976; Cifelli and Madsen 1986, 1999); but nonetheless the triangulation is a distinctive feature of the entire molar series, far better developed than the variable triangulation of “obtuse-angle symmetrodonts” (see previous discussion).

Several petrosal features are synapomorphies of the trechnotherian clade (Hu et al. 1997): a large post-tympanic recess and a caudal tympanic process are present in *Zhangheotherium* (Hu et al. 1997), *Vincelestes* (Rougier et al. 1992), and marsupials (Clemens 1966; Wible 1990; Meng

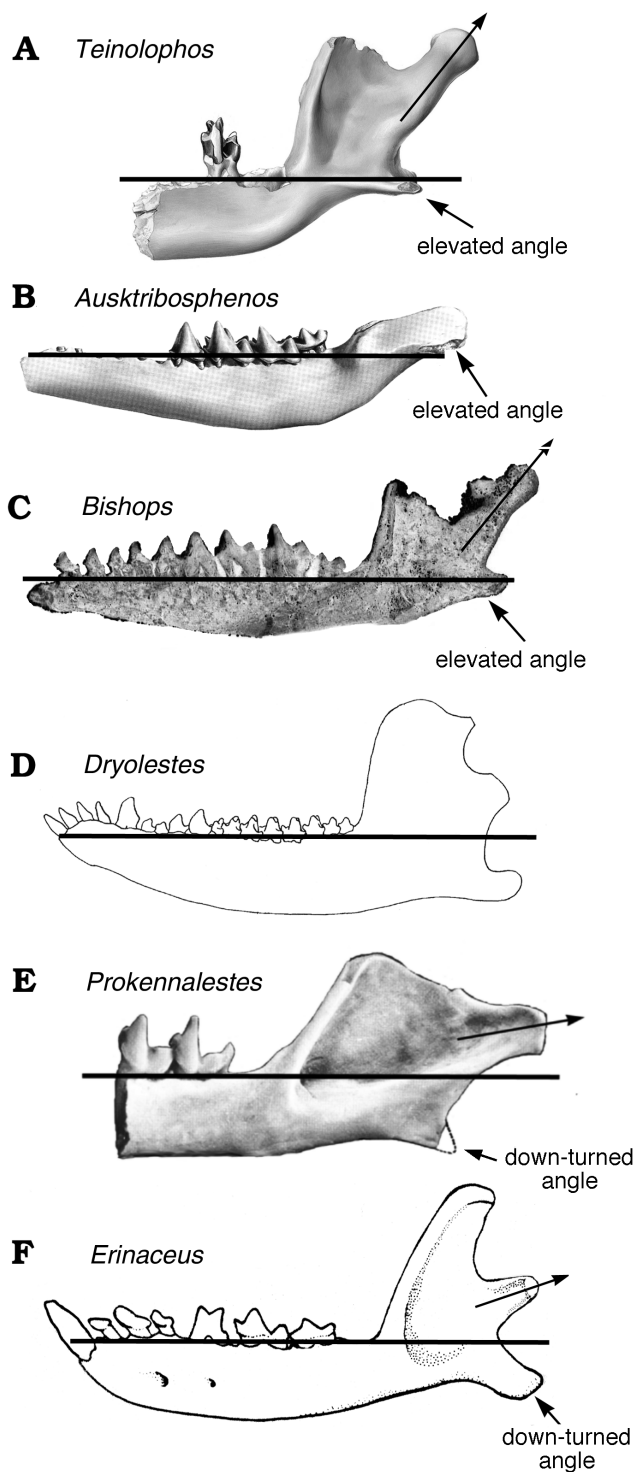


Fig. 5. Comparison of mandibular structures among australosphenidan and boreosphenidan mammals. A–C. Australosphenidans: The monotreme *Teinolophos* (A), *Ausktribosphenos* (B), *Bishops* (C). D–F. Boreosphenidans: *Dryolestes* (D), *Prokennalestes* (E), *Erinaceus europaeus* (F). Not to scale. The australosphenidans are characterized by a more vertically directed peduncle for the mandibular condyle, and a more elevated angular process (to the level of the dental alveolar line). By contrast, basal eutherians are characterized by a more posteriorly directed dentary peduncle and a down-turned angular process (Modified after: A, Rich, Vickers-Rich, et al. 2001; B, Rich et al. 1999; C, Rich, Flannery, et al. 2001; D, Martin 1999a; E, Kielan-Jaworowska and Dashzeveg 1989; F, Lawlor 1979).

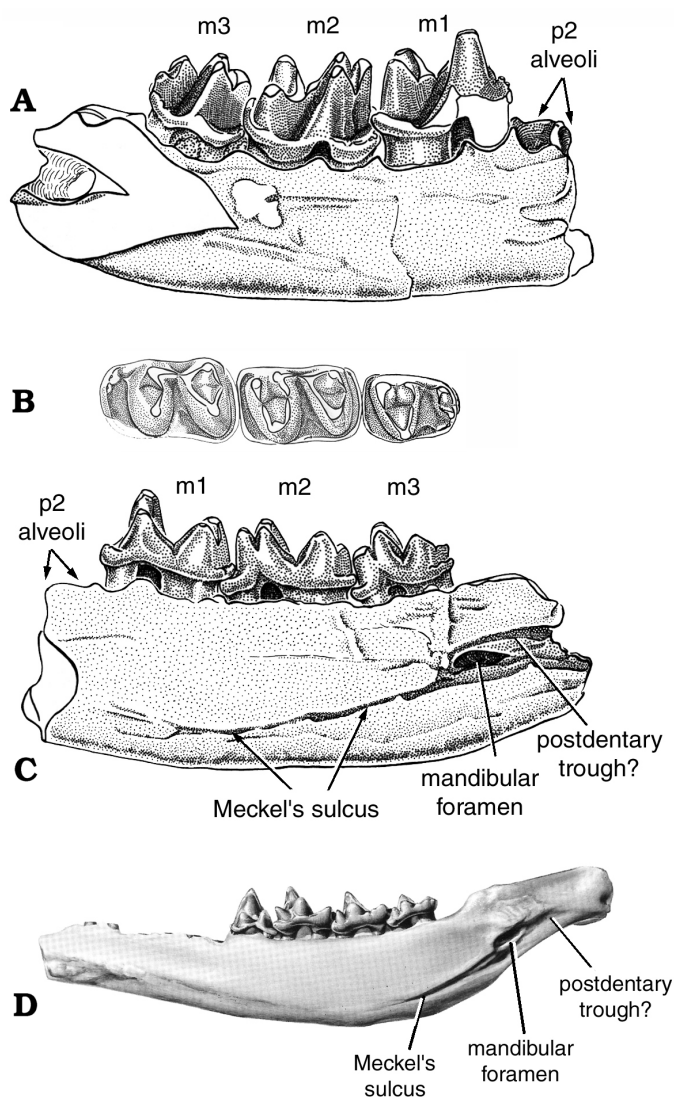


Fig. 6. Mandibular structure of the monotreme *Steropodon* (A–C), as compared to that of *Ausktribosphenos* (D). A. Lateral view (redrawn from a cast provided by Michael Archer). B. Dorsal view of dentition. C. Medial view: redrawn from cast, and the original photograph of Archer et al. 1995: fig. 1c). D. The mandible of *Ausktribosphenos* (from Rich et al. 1997).

and Fox 1995c), and in the earliest-known eutherian basi-crania (Kielan-Jaworowska 1981; McKenna et al. 2000; Wible et al. 2001). Where the petrosal is known, these apomorphies are absent in outgroups of Trechnotheria. In stem trechnotheres (Rougier et al. 1992; Hu et al. 1997), as well as crown therians (Clemens 1966; Kielan-Jaworowska 1981; MacPhee 1981; Wible and Hopson 1995), the epitympanic recess is bounded by a lateral wall formed by the squamosal. In contrast, the epitympanic recess is present but lacks a lateral wall of the squamosal in multituberculates and *Hadrocodium*, and is absent altogether in *Morganucodon* (Luo and Crompton 1994), *Ornithorhynchus*, and Triconodontidae (Rougier, Wible, and Hopson 1996); *Tachyglossus* is an exception (Kuhn 1971; Wible and Hopson 1995).

The trechnotherian clade is diagnosed by at least four unambiguous synapomorphies of the postcranial skeleton. On the scapula, the posterior part of the suprascapular fossa is relatively expanded and is far wider than the glenoid (and anterior) region, so that the fossa is fan-shaped or triangular in outline (Krebs 1991; Rougier 1993; Szalay 1994; Marshall and Sigogneau-Russell 1995; Hu et al. 1997; Muizon 1998). The suprascapular fossa is wider than the infrascapular fossa. In contrast, in the eutriconodont *Jeholodens*, cimolodontan multituberculates, and morganucodontids, the scapula has almost parallel dorsal and ventral borders, and the infrascapular fossa is wider than the suprascapular fossa (the latter only incipient in multituberculates, see Kielan-Jaworowska and Gambaryan 1994; Sereno and McKenna 1995). The second synapomorphy is the loss of the proximo-lateral process of the tibia, a primitive feature that is strongly developed and hook-like in cimolodontan multituberculates, monotremes, morganucodontids, and tritylodontids. A large proximo-lateral tibial process is also present in *Gobiconodon* and *Jeholodens*. The process is vestigial in *Zhangheotherium* (Hu et al. 1997, 1998), absent in *Henkelotherium* (Krebs 1991), *Vincelestes* (Rougier 1993), and the earliest known metatherian and eutherian skeletons (Kielan-Jaworowska 1977, 1978; Szalay and Trofimov 1996; Novacek et al. 1997; Muizon 1998). The third synapomorphy is on the humerus. The posterior aspect of its distal articulation for the radius is cylindrical (Hu et al. 1997, 1998), although its anterior aspect retains a primitive bulbous condyle. The fourth and potential synapomorphy is in the ankle joint. The sustentacular facet on the calcaneus, for the support of the astragalus, is oblique to the horizontal plane ($\leq 70^\circ$) as in *Vincelestes* and crown Theria (Szalay 1994; Horovitz 2000) (this feature is not preserved in *Zhangheotherium*). This contrasts with the plesiomorphic condition of a vertical (90°) orientation of this facet, as seen in cimolodontan multituberculates (Krause and Jenkins 1983; Kielan-Jaworowska and Gambaryan 1994), the eutriconodont *Jeholodens* (Ji et al. 1999), morganucodontids (Jenkins and Parrington 1976), and tritylodontids (Kühne 1956). The stem taxa of this clade are the spalacotheriids (Hu et al. 1997; Cifelli and Madsen 1999), known from the Cretaceous of Europe, Asia, and North America.

Cladotheria (*sensu* McKenna 1975).—This clade is defined as the common ancestor of dryolestids and living therians, plus all of its descendants. Spalacotheriidae constitute the sister-taxon to Cladotheria. The most prominent apomorphy of the dentition is the elevation of the talonid above the level of the cingulid on lower molars. The hypoconulid (an elevated version of cuspule d of *Kuehneotherium* and spalacotheriids) of the lower molar occludes between the paracone and metacone of the upper molar in dryolestids and paurodontids, as it does in living therians (Crompton 1971; Prothero 1981; Krebs 1991; Martin 1999a). A distinct wear surface is present on the hypoconulid (Krebs 1971; Ensom and Sigogneau-Russell 1998; Martin 1999a). In contrast, in non-cladotherian mammals such as spalacotheriids and kuehneotheriids, “talonid”

cuspule d (where present) is usually a part of the cingulid (Hu et al. 1998; Cifelli and Madsen 1999).

The second suite of characters deals with features on the angular process of the mandible. The angular process is posteriorly positioned, directly below the dentary condyle. The angle is not elevated as in australosphenidans (Fig. 5). The crest of the pterygoid shelf extends posteriorly along the ventral border of the mandible to reach the apex of the angular process. In contrast, in spalacotheriids, eutriconodonts, and all multituberculates, a distinctive angle is absent and the postero-ventral mandibular border is rounded. Where present, the pterygoid shelf on the medial side of the mandible extends continuously along the postero-ventral mandibular border toward the dentary condyle. In the stem taxa of mammals, such as *Sinoconodon*, *Morganucodon*, *Kuehneotherium*, and *Haramiyavia*, the angle is anteriorly positioned, below the anterior part of the coronoid process (not below the dentary condyle), and the pterygoid shelf is absent.

Prototribosphenida (*sensu* Rougier, Wible, and Hopson 1996).—This clade is defined as the common ancestor of *Vincelestes* and living therians, plus all of its descendants. The most important diagnostic features are in the inner ear. The bony cochlear canal contains a primary bony lamina (and even secondary bony lamina among the earliest-known metatherian and eutherian petrosals) that provides internal support for the coiled cochlear duct (*Vincelestes*, Rougier 1993; Rougier, Wible, and Hopson 1996; early marsupials, Meng and Fox 1995a; 1995c; early eutherians, Wible et al. 2001). The primary and secondary bony laminae are absent in monotremes (Zeller 1989; Luo and Ketten 1991; Fox and Meng 1997), multituberculates (Horum 1998a), and in such stem taxa as *Sinoconodon* (Luo et al. 1995), *Morganucodon* (Graybeal et al. 1989), *Haldanodon* (Lillgraven and Krusat 1991), and *Hadrocodium* (Luo, Crompton, and Sun 2001). Another character is the greater degree of coiling of the bony cochlear canal, which in Prototribosphenida is at least 270° . By contrast, in monotremes (herein considered to be part of Australosphenida), the bony cochlear canal is coiled less than 270° and lacks internal bony laminae for support of the membranous cochlear duct. Other outgroups do not have a coiled cochlear canal (although the canal may be curved to some degree), nor do they have any bony supporting structures for the basilar membrane within the canal. The perilymphatic duct of prototribosphenidans is completely enclosed within bone, and its endocranial foramen is separated from the fenestra cochlearis (Zeller 1987; Wible 1990; Rougier et al. 1992; Wible and Hopson 1993). Outside the Prototribosphenida, there is no separation of the perilymphatic foramen and the fenestra cochlearis in the immediate outgroups (*Zhangheotherium*, Hu et al. 1997; and some putative “symmetrodont” petrosals, Wible et al. 1995), or in the successively more distant outgroups.

Zatheria (*sensu* McKenna 1975).—This clade is defined as the common ancestor of *Peramus* and living marsupials and placentals, plus all of its descendants. *Peramus* is the basal

member of this clade. *Peramus*, like other “peramurids”, is known only by the dentition and mandible (Clemens and Mills 1971; Sigogneau-Russell 1999), and for this reason the diagnosis is necessarily restricted to dental features. This clade is diagnosed by the presence of wear within the talonid. In the earliest and most primitive members of this clade, the wear facet in the talonid, equivalent to facet 5 of Crompton (1971), extends onto the posterior face of the metaconid. As a result, a well-defined distal metacristid is present (Crompton 1971; Clemens and Mills 1971; Fox 1975; Sigogneau-Russell 1999). The distal metacristid is in alignment with the cristid obliqua, which extends anterolingually from the hypoconid (Fox 1975; Sigogneau-Russell 1999). This derived character is absent in the immediate and the successively more distant outgroups of Zatheria, including: *Vincelestes* (Rougier 1993; Sigogneau-Russell 1999), *Amphitherium* (Mills 1964; Butler and Clemens 2001), dryolestids (Krebs 1991; Martin 1999a), and spalacotheriids (Hu et al. 1998; Cifelli and Madsen 1999).

Boreosphenida (*sensu* Luo, Cifelli, and Kielan-Jaworowska 2001).—This group is defined as the common ancestor of *Kielantherium* and living marsupials and placentals, plus all of its descendants. The earliest-known taxa belonging to this clade, from the Berriasian (Sigogneau-Russell and Ensom 1994) and Valanginian (K.A. Kermack et al. 1965) of Britain and the Berriasian of Morocco (Sigogneau-Russell 1991a, 1992, 1994), are known by one or a few isolated teeth. *Kielantherium* is somewhat better represented, being known by a dentary and the lower molar series (Dashzeveg and Kielan-Jaworowska 1984). The diagnosis for this clade is therefore dependent on what is preserved in these basal yet very incomplete taxa.

An apomorphy of this group is that the upper molar preprotocrista extends labially beyond the paracone, into the stylar groove, as could be inferred from some incomplete taxa not included in this cladistic analysis (Fox 1972; Sigogneau-Russell 1994). The preprotocrista and preparacrista provide for double-rank prevallum/postvallid shearing (Kay and Hiimae 1974; Fox 1975; Crompton and Kielan-Jaworowska 1978; Cifelli 1993b; Averianov and Skutschas 1999). Basal members of Boreosphenida include a host of taxa represented by isolated teeth from the Aptian–Albian and Late Cretaceous of North America (e.g., Fox 1972, 1976, 1980, 1982; Butler 1978; Slaughter 1981; Clemens and Lillegraven 1986; Jacobs et al. 1989; Cifelli 1990c, 1990d, 1993b). There is disagreement as to whether some of these primitive boreosphenidans are referable to Metatheria on the one hand or Eutheria on the other. *Pappotherium*, for example, has been alternately considered as a stem eutherian (Slaughter 1971; Fox 1975), or a basal member of the therian crown group (Butler 1978; Kielan-Jaworowska, Eaton, and Bown 1979; Cifelli 1993b; Rougier et al. 1998). It is clear that these mammals are boreosphenidans and that they are more closely related to the therian crown group than any other zatherians. Beyond this, however, the phylogenetic relationships of these taxa cannot be resolved, owing to the fragmentary nature of the fossils upon

which they are based. Lacking a basis for defensible placement in a higher taxonomic group, these taxa are commonly termed “therians of metatherian–eutherian grade” (e.g., Patterson 1956; Kielan-Jaworowska, Eaton, and Bown 1979) or “tribotheres” (see review by Clemens and Lillegraven 1986).

In recent years, Mongolian Late Cretaceous *Deltatheridium* has assumed a prominent role in interpretation of the basal evolution of metatherians (Kielan-Jaworowska and Nessov 1990; Marshall and Kielan-Jaworowska 1992; Cifelli 1993b; Rougier et al. 1998). Its postcanine dental formula and the presence of an inflected angle that is associated with a continuous medial shelf on the mandible are apomorphies shared with marsupials. On the basis of these and other characters, *Deltatheridium* (and relatives, Deltatheroidea of Kielan-Jaworowska 1982) has been considered to be a metatherian (Kielan-Jaworowska and Nessov 1990; Marshall and Kielan-Jaworowska 1992; Rougier et al. 1998). However, Cifelli (1993b) has argued that *Deltatheridium* represents a basal boreosphenidan unrelated to marsupials, citing the lack of typical marsupial apomorphies (such as a labial postcingulid on lower molars) and the presence of numerous plesiomorphies (such as a distal metacristid). Our phylogeny that includes these and other dental characters (see Cifelli 1993b; Rougier et al. 1998) places *Deltatheridium* in a basal position with respect to both groups of living therians (Figs. 1, 2). Given the fact that our tree topologies separate *Deltatheridium* from Metatheria by only one or two nodes, and that the intervening taxa are very incompletely known, we regard the position of *Deltatheridium* as rather unstable. Newly-collected specimens of *Deltatheridium* currently under study (Rougier et al. 1998; Horovitz 2000) offer the promise of resolving the vexing problem of deltatheroidan relationships.

Our tally shows 20 published Early Cretaceous boreosphenidan genera (including eutherians and metatherians), distributed among Europe, Asia, and North America. Of these, stem boreosphenidans (11 genera) have been reported from all three major landmasses. Eutherians (five genera) are known from Asia and North America for this time interval; thus far, metatherians (four genera) of this age are restricted to North America (Kielan-Jaworowska and Cifelli 2001). The total number of Early Cretaceous boreosphenidans would be considerably higher (about 30) if published but unnamed taxa were included. Boreosphenidans of the Early Cretaceous are only known from the northern continents (Luo, Cifelli, and Kielan-Jaworowska 2001).

Crown-group Theria (Theria of Rowe 1988, 1993).—Several features of the dentition are diagnostic of crown Theria with respect to basal boreosphenidans. Related to the enlargement of entoconid and widening of the talonid basin, two separate wear facets 5 and 6 (following Crompton 1971; Crompton and Kielan-Jaworowska 1978) are differentiated within the talonid basin. The protocone is antero-posteriorly enlarged in correlation with the differentiation of wear facets 5 and 6 within the talonid basin. By contrast, the entoconid of

basal boreosphenidans, if present at all, is a miniscule structure and does not support separate and well differentiated facets on the lingual side of the talonid basin (e.g., *Kielantherium* and *Deltatheridium*, see Crompton and Kielan-Jaworowska 1978; Cifelli 1993b). The talonid is widened so that its width approaches that of the trigonid. The difference in width of trigonid and talonid is considerably less in the earliest-known taxa of crown Theria, than in the stem taxa of zatherians and basal boreosphenidans.

On upper molars of the therian crown group, the postprotocrista extends past the base of the metacone to form (in conjunction with the postmetacrista) a double-rank postvallum/prevallid shearing mechanism against the paracristid. On the trigonid of the lower molar, the distal metacristid is absent, as wear facet 5 (or its equivalent shearing surface) is reduced in size and no longer extends onto the posterior surface of the metaconid (Fox 1975; Crompton and Kielan-Jaworowska 1978; Cifelli 1993b). Both of these features are related to the hypertrophy and more vertical orientation of the postvallid surface of the trigonid in the earliest-known metatherians and eutherians, as compared to the sloping postvallid surface seen in basal boreosphenidans and successively more distant zatherians (Fox 1975; Sigogneau-Russell 1999) and “eupantotheres” (Krebs 1971). Due to these differences in the trigonid, the protocone can no longer shear against the posterior surface of the metaconid in the majority of crown Theria. The hypertrophied distal metacristid crest of more distantly related “peramurids” is usually absent in the therian crown clade, exceptions including some secondary reversals among Tertiary mammals.

The therian crown clade is strongly supported by some important features of the alisphenoid (Novacek 1986b; Zeller 1987; Maier 1987, 1989, 1993; Wible and Hopson 1993; Hopson and Rougier 1993; Rougier, Wible, and Hopson 1996). The alisphenoid is enlarged at the expense of the petrosal. The ascending process of the alisphenoid displaces the anterior lamina of the petrosal and the alisphenoid encircles the trigeminal nerve foramina. The ventral floor of the cavum epiptericum is formed by the alisphenoid (instead of the petrosal). In fossil and extant taxa of crown Theria for which the petrosal is known, this element lacks the broad lateral trough typical of *Vincelestes* and other outgroups. The ascending vascular canal for the arteria diploetica is entirely endocranial in the temporal region (Rougier, Wible, and Hopson 1996). At least one suite of postcranial characters is diagnostic for the crown group of therians: an astragalar head that is convex and that is wider than the astragalar neck (Horovitz 2000).

Unresolved problems of multituberculates

Relationships of multituberculates are controversial despite the facts that they are the most abundant and diverse Mesozoic mammals, and that their anatomy is the best studied. In an early scheme based on the premise of a polyphyletic origin of

mammals, multituberculates were classified together with tritylodontids (Simpson 1928, 1929a), permitting possible derivation of multituberculate dental specializations from those of tritylodontids. This scenario was based on the incomplete evidence then available, limited only to the rostrum and dentition. Upon the discovery of complete skulls of tritylodontids (Young 1940, 1947) and multituberculates (Simpson 1937), Watson (1942) and Young (1947) pointed out that tritylodontids lack the dentary–squamosal jaw hinge and retained the postdentary bones on the mandible. Since the studies of Watson (1942) and Young (1947), all students have agreed that tritylodontids are more primitive than mammals in all cranial and postcranial structures (Kühne 1956; Sues 1983; Sun and Li 1985), except for the dental replacement pattern. The multituberculate–tritylodontid hypothesis was abandoned by almost all students of cynodonts and multituberculates, including its original proponents (Simpson 1971), with exceptions of Tatarinov (1985), and Butler and MacIntyre (1994) who re-emphasized the dental similarities of multituberculates and tritylodontids. This hypothesis has had the least support, both historically and from contemporary parsimony phylogenies, and it will not be considered further here. The four current hypotheses on the relationships of multituberculates to other mammals are reviewed in the following sections.

(1) Multituberculate–monotreme sister-group hypothesis.—Kielan-Jaworowska (1971) showed similarities in braincase structure between multituberculates and monotremes. The sister-group hypothesis was first developed by Wible and Hopson (1993), on the basis of derived petrosal structures, and was supported by Meng and Wyss (1995), on features of the ear ossicles. As discussed by Rougier, Wible, and Novacek (1996b), extensive sampling and comparison of other cranial and postcranial features reveals that the shared similarities between multituberculates and monotremes are vastly outnumbered by conflicting features. The systematic characters supporting a multituberculate–monotreme relationship were included in our dataset. Nonetheless, the hypothesis of multituberculate–monotreme sister-groups is not corroborated by parsimony analyses of all morphological features available.

(2) Multituberculate–eutriconodont sister-group hypothesis.—Kielan-Jaworowska (1986) recognized two types of brain structure among Mesozoic mammals: the cryptomesencephalic type (large vermis, no dorsal midbrain exposure, and no cerebellar hemispheres) of Multituberculata and Eutriconodonta, *versus* the eumesencephalic type (wide cerebellar hemispheres, divided by a tentorium osseum from cerebrum, and large dorsal midbrain exposure), which apparently occurs primitively in *Morganucodon* and in some Cretaceous and extant therians (Kielan-Jaworowska 1997: fig. 1). If one were to construct a phylogeny based on the brain structure alone, Multituberculata and *Triconodon* (or some *Triconodon*-like forms) would be more closely related to each other than either taxon is to morganucodontids, or to living therians.

In multituberculates, the jugal is reduced and placed on the medial side of the zygomatic arch (Hopson et al. 1989; Wible

and Rougier 2000). It appears that, in monotremes and the eutriconodont *Jeholodens*, the jugal is placed on the medial side of the zygomatic arch, as in multituberculates. Another similarity of multituberculates, eutriconodonts, and monotremes concerns the foot structure. Metatarsal III is abducted 30° from the longitudinal axis of the tuber calcanei in multituberculates (Kielan-Jaworowska and Gambaryan 1994), *Jeholodens* (Ji et al. 1999), and monotremes, rather than parallel to it as in crown therians. Metatarsal V is offset from the cuboid and almost in contact with the distal end of the calcaneus in multituberculates and *Jeholodens* (see Kielan-Jaworowska 1997: fig. 3; and Ji et al. 1999: fig. 4). By contrast, metatarsal V, the cuboid, and the calcaneus are in alignment in morganucodontids (Jenkins and Parrington 1976) and crown Theria. In *Jeholodens*, a gap separates the distal margin of the calcaneus and metatarsal, as in the so-called Manda cynodont (Schaeffer 1941; Jenkins 1971; Szalay 1993b). In multituberculates and *Jeholodens*, there are no obvious facets on the distal margin of the calcaneus and proximal margin of metatarsal V, so it cannot be excluded that a small cartilage might have been also retained in the space between the offset metatarsal V and the cuboid. While multituberculates and triconodontids share a brain structure which is quite different from that of monotremes, the medially placed jugal on the zygoma, the offset of metatarsal V with respect to the distal cuboid, and the abduction of metatarsal III to the longitudinal axis of the foot are also present in monotremes. Support from these features for a multituberculate–triconodontid relationship is conditional, as it is contingent on a tree topology in which monotremes must be separated from multituberculates and eutriconodonts by some intervening clades.

(3) Multituberculate–Trechnotheria sister-group hypothesis (Theriiformes of Rowe 1988).—Multituberculates resemble trechnotherians (common ancestor of *Zhangheotherium* and crown Theria plus all its descendents) in several derived features of the postcranial skeleton (see Rowe 1986; Rowe and Greenwald 1987; Rowe 1988, 1993; Sereno and McKenna 1995; Hu et al. 1997). Of these, four synapomorphies for multituberculate and trechnotherians are unambiguous (Kielan-Jaworowska and Gambaryan 1994; Hu et al. 1997): spherical femoral head on a constricted neck, prominent greater trochanter that is vertically directed and separated from the shaft by a deep incisure, the high and laterally compressed tuber calcanei, and the complete overlap of astragalus and calcaneus.

The forelimb and pectoral girdle features used to support a multituberculate–trechnotherian relationship may be ambiguous (Gambaryan and Kielan-Jaworowska 1997; Rougier, Wible, and Novacek 1996b). The claviculo-interclavicle joint of multituberculates and trechnotherians is derived in being both pivotal and mobile; however, these characteristics are now known to have a wider distribution, as they are present in *Jeholodens* (Ji et al. 1999). The parasagittal stance of the forelimb is a variable feature among multituberculates (Gambaryan and Kielan-Jaworowska 1997; Kielan-Jaworowska 1998) and trechnotherians (Rougier, Wible, and Novacek

1996b). Moreover, it is also present in *Jeholodens* (Ji et al. 1999). Reduction of the procoracoid was used in support of Theriiformes (Rowe 1988), but the procoracoid is also absent in *Jeholodens* (Ji et al. 1999). Rougier, Wible, and Hopson (1996) suggested that several petrosal synapomorphies for the theriiform clade (multituberculates and the therian crown group) may be equivocal. One derived feature shared by theriiforms, the ellipsoidal fenestra vestibuli, is variable in crown Theria (MacIntyre 1972; Archibald 1979) and in multituberculates (Luo 1989; Meng 1992).

A variant of the Theriiformes hypothesis is that multituberculates may be the sister-taxon to “holotherians” (i.e., the clade of *Kuehneotherium* + monotremes + living therians) (see Miao 1991: fig. 1). Several studies have placed multituberculates in an unresolved trichotomy with living monotremes and living therians (Kemp 1983; Wible 1991; Rougier et al. 1992; Lillegraven and Hahn 1993). This is somewhat similar to the theriiform hypothesis, inasmuch as multituberculates are placed with crown Mammalia, but differs in that the position of multituberculates is not further resolved.

(4) Multituberculates–haramiyids hypothesis (the “Allotherian” hypothesis, Hahn 1989).—Haramiyids (known almost entirely by isolated teeth from the Late Triassic–Early Jurassic of Europe) have long been viewed only tentatively as mammals, and (assuming mammalian affinities) as possible relatives of Multituberculata. Beginning with Hahn (1973), a haramiyid–multituberculate relationship has been accepted by several specialists of the earliest-known multituberculates. This hypothesis is reflected in allocation of the two groups to Allotheria (Hahn et al. 1989; Sigogneau-Russell 1989b; Butler and MacIntyre 1994; Butler 2000). Because haramiyids are among the earliest known mammals, this hypothesis implies that the allotherian clade represents an early, divergent lineage of mammals. Indeed, McKenna (1987), Hahn et al. (1989), and Miao (1993) argued that the Allotheria are a sister-taxon to all other mammals. A somewhat similar proposal involves placement of multituberculates (or by extrapolation, allotherians in general) together with morganucodontids (Crompton and Sun 1985; Miao and Lillegraven 1986: fig. 2B), with the combined group being considered as a stem clade outside the living Mammalia (see Crompton and Sun 1985: fig. 8; also Hopson 1994: fig. 8). The allotherian hypothesis excludes multituberculates from the mammalian crown group, thereby differing significantly from interpretations that place multituberculates among crown mammals, or at the basal node of crown mammals.

Discovery by Jenkins et al. (1997) of the haramiyid *Haramiyavia* (Late Triassic, Greenland) cast doubt on a haramiyid–multituberculate relationship. Study of dentaries and partial maxillae (the only such fossils known for Haramiyidae) led Jenkins et al. (1997) to conclude that *Haramiyavia* had orthal jaw movement during the power stroke, in contrast to the backward power stroke of multituberculates. *Haramiyavia* has a short masseteric fossa that does not extend below the last premolar, as it does in multituberculates. This indicates that the anterior insertion of the

masseter muscle in multituberculates (Gambaryan and Kielan-Jaworowska 1995) and the inferred backward power stroke did not occur in *Haramiyavia* (Jenkins et al. 1997). Jenkins et al. (1997) further showed that *Haramiyavia* retains the primitive postdentary trough for accommodating the middle ear bones. By contrast, these structures are entirely absent in uncontested multituberculates. Based on these differences, Jenkins et al. (1997) excluded Haramiyida from Allotheria. Our most parsimonious tree (Fig. 1) is consistent with the phylogenetic conclusion of Jenkins et al. (1997).

Butler (2000) reviewed the allotherian groups, including *Haramiyavia*, the haramiyid *Thomasia*, and other haramiyid-like forms. He argued that all haramiyids (including *Haramiyavia*) show a common pattern of posteriorly directed power stroke, despite the fact that *Haramiyavia* lacks an anterior-inserted masseter muscle. Based solely on dental evidence, Butler (2000) assigned *Haramiyavia* and other haramiyid-like forms to the order Haramiyida, which he placed together with Multituberculata in Allotheria. He further concluded that Allotheria separated from other stem clades of Mammaliaformes (such as *Morganucodon*) even before mammaliaforms developed a shearing dentition and transverse jaw movement.

The allotherian hypothesis rests on the strength of a large number of recognizable systematic characters of the multiple-rows and multi-cusped teeth of haramiyidans and multituberculates and their inferred posteriorly directed power stroke during occlusion (Appendix 1: characters 85 through 92). However, if haramiyidans (including *Haramiyavia*) and multituberculates are united in one clade, then the highly derived dentition and the very primitive postdentary trough of the dentary in *Haramiyavia* would have discordant distributions among multituberculates and *Haramiyavia*, as pointed out by Jenkins et al. (1997). At least one of these conflicting character complexes (derived teeth *versus* primitive mandible) must be homoplastic. The weakness of the allotherian hypothesis is its requirement of some difficult evolutionary scenarios. The attachment of postdentary bones to the mandible must have secondarily evolved in *Haramiyavia*, as a reversal from an ancestor with a typical mammalian middle ear; alternatively, separation of postdentary from dentary bones in multituberculates occurred independent of a similar transformation in other mammals. If *Haramiyavia* is part of a clade that also includes multituberculates, homoplastic evolution of the rounded posteroventral margin of the mandible within Allotheria is also implied (our data suggest two other origins of this state, one among Spalacotheriidae and the other in eutriconodonts). Last but not least, if multituberculates are grouped with haramiyidans and placed outside the mammalian crown group, then the similarities in a great number of postcranial characters of multituberculates and trechnotherians must be convergent.

Discussion on multituberculate relationships.—The evolutionary origins of multituberculates and their relationships to other mammals are difficult to interpret for three reasons. The

first is that multituberculates and haramiyids have an extraordinary mosaic of derived and primitive features in different parts of their dentition and skeleton. Regardless of which known mammalian or cynodont group is favored as their sister-taxon, it is inevitable that some significant structures would have gone through conspicuous convergence or evolutionary reversal, or both. For example, the derived features of the cryptomesencephalic brain would have to be considered as convergence if multituberculates are related to haramiyids, or to monotremes, or to trechnotherians. The multi-rows and multicuspate cheek teeth would have to represent a convergence of multituberculates to haramiyids, if multituberculates are related to triconodontids, monotremes, or trechnotherians (or crown Theria). The mobile sterno-clavicle joint of multituberculates would have to be convergent with the similar condition seen in eutriconodonts and “therians” if multituberculates are related to monotremes, or if they are placed outside the mammalian crown group. The derived foot structures, such as calcaneal tubercle and peroneal process, would have to be convergent to trechnotherians if multituberculates are related to either monotremes or to eutriconodonts, or if they are placed outside the mammalian crown group. The monotreme–multituberculate and theriiform hypotheses both require that the multiple-row cusp pattern of multituberculates evolved from an ancestor having a triangulate molar cusp pattern. Each of the hypotheses for multituberculate relationships requires an enormous number of convergences and reversals among well-established anatomical characters or character complexes. Such conflicting patterns are the main source of the seemingly irreconcilable disagreement among those who have studied multituberculate interrelationships.

Second, multituberculates have many unique dental and mandibular features specialized for herbivory. Without an immediate outgroup that provides plausible structural antecedent conditions to the highly transformed dental features of multituberculates, it is very difficult to establish an evolutionary scenario that derives the multituberculate dentition from the dental patterns seen among known mammals—and, for that matter, among any of the non-mammalian cynodonts except tritylodontids. The difficulty in assessing the affinities of multituberculates, with their large number of highly specialized features associated with herbivory, is part of the general problem involving placement of “long-branch” clades in systematics. There are other controversial cases about the position of highly specialized herbivores, such as traversodontids and tritylodontids among advanced cynodonts (Crompton 1972b; Hopson and Barghusen 1986; Hopson 1991; *versus* Kemp 1982, 1988), and anomodonts (including dicynodonts) among noncynodont therapsids (Rowe 1986, 1988; *versus* Hopson and Barghusen 1986; Hopson 1991).

The third difficulty in interpreting multituberculate relationships is the lack of a good fossil record of the earliest taxa. A possible record from the late Triassic, reported by Hahn et al. (1987), has not been generally accepted (Butler 2000; Kielan-Jaworowska and Hurum 2001). Putative multituberculates have also been mentioned as occurring in the

Middle Jurassic (Bathonian of England), based on isolated teeth currently under study by P. M. Butler (see Butler 2000: p. 336; and Freeman 1976, 1979). As the first uncontested multituberculates are from the Late Jurassic (Kimmeridgian), their first fossil records occur long after those of other groups of early mammals, such as *Sinoconodon*, morganucodontids, and kuehneotheriids.

This study, like any effort to reconstruct the relationships of multituberculates, is also confronted with these difficulties and ambiguities. Herein we present two alternative placements for Allotheria (including Multituberculata) in mammalian phylogeny. The hypotheses differ radically in placement for the group. However, given the size of the data set, the difference in tree lengths is small, and for this reason we do not favor one interpretation over the other.

(1) The clade of Multituberculata and Trechnotheria (spalacotheriids + living therians) (modified from Theriiformes of Rowe 1988; Sereno and McKenna 1995; McKenna and Bell 1997).—This clade is defined as the common ancestor of multituberculates and living therians, plus all of its descendants (Fig. 1). Monotremes and other Australosphenida are explicitly excluded from this clade; so are eutriconodonts. The clade is primarily supported by diagnostic features of the hind limb: the spherical femoral head on a constricted neck, the prominent and vertically directed greater trochanter, separated from the shaft by a deep incisure; the high and laterally compressed tuber calcanei, and the complete overlap of the astragalus and calcaneus. Some additional basicranial (Rougier, Wible, and Hopson 1996) and postcranial features (Rowe 1993) may also support this clade, but they are contingent on the positions of other mammalian outgroups with respect to the putative clade including Allotheria and Trechnotheria.

(2) Allotherian (*Haramiyavia* + multituberculates) clade as a basal mammalian lineage.—Taking into account the evidence supporting a relationship between haramiyids and multituberculates (Hahn 1973; Hahn et al. 1989; Sigogneau-Russell 1989b; Butler and MacIntyre 1994; Butler 2000), as well as the widely-held view that the allotherians lie outside the mammalian crown group (Crompton and Sun 1985; McKenna 1987; Hahn et al. 1989; Miao 1991, 1993; Hopson 1994; Butler and MacIntyre 1994; Kielan-Jaworowska 1997; Butler 2000), we imposed a topological constraint that excludes the allotherian clade from that including the living mammals, and retained only those trees that are compatible with this topological constraint. The suboptimal phylogeny under this constraint of allotherians is presented in Fig. 2.

The constrained search (with the allotherian clade outside the mammalian crown-group) yielded shortest trees (942 steps for fundamental trees) that are 7 steps (>1%) longer than the shortest trees (935 steps for the fundamental trees) produced by unconstrained searches (more discussion below). The difference is also small if strict consensus trees are compared: 939 steps for basal placement of allotherians, outside the crown Mammalia (topology in Fig. 2), *versus* 944 steps for placement of multituberculates as sister taxon to trechno-

therians while *Haramiyavia* is excluded from Mammalia (topology in Fig. 1). This is a small difference between these two contrasting tree topologies (placement of Allotheria outside *versus* multituberculates within the crown group and being separated from haramiyids). The nonparametric tests (Templeton 1983; Swofford 2000) show that the difference is not significant between these alternative placements: 1) Multituberculata as the sister-taxon to trechnotherians (Fig. 1), or 2) both haramiyids and multituberculates being excluded from the mammalian crown-group (e.g., Butler 2000) (Fig. 2). Given the results of our analyses, the most parsimonious phylogenetic position of multituberculates as the sister-taxon to trechnotherians is still preferable, but weak. Also, it is very difficult to support the placement of haramiyids (as represented by *Haramiyavia*) within the mammalian crown group: on this issue our results are partially consistent with the argument by Butler (2000).

This alternative phylogeny (Fig. 2) has one putative clade that can be defined as the common ancestor of allotherians, eutriconodonts, and living mammals, plus all of its descendants. Excluded from this clade are the successively more distant *Hadrocodium*, *Haldanodon*, morganucodontids, and *Sinoconodon*. This clade can be diagnosed by derived features of mandible: the mandibular angle is absent (except for *Haramiyavia*) or reduced (some australosphenidans), reversal for this character is implied for “eupantotheres” and boreosphenidans; and the separation of the middle ear ossicles from the dentary (reversed in *Haramiyavia*). Derived features of the pectoral girdle also provide support for this clade: enlargement of the supraspinous fossa of the scapula, a mobile acromion-clavicle articulation, and a mobile and pivotal claviculo-interclavicle joint (reversed in living monotremes).

Relationships of eutriconodonts

Like multituberculates, eutriconodonts have been alternatively placed within or outside crown Mammalia. The hypothesis of Rowe (1988) places *Gobiconodon* and *Triconodon* within the mammalian crown group. Study of petrosal features by Rougier, Wible, and Hopson (1996) supports the placement of eutriconodonts within crown Mammalia, possibly even in a monophyletic clade of theriiforms (multituberculates + trechnotherians).

The placement of triconodontids as a part of the mammalian crown group can be supported by some equivocal synapomorphies of the petrosal (Rougier, Wible, and Hopson 1996: 37). A possible synapomorphy is the anterior position of the TMJ with respect to the fenestra vestibuli. A more recent study shows that the anterior position of the TMJ is present in the fossil ornithorhynchid *Obdurodon* (Musser and Archer 1998), in the echidna *Tachyglossus*, and in the stem mammal *Hadrocodium* (Luo, Crompton, and Sun 2001). The basal condition of monotremes as a whole is an anteriorly placed TMJ (Luo, Crompton, and Sun 2001); the posterior position of the TMJ with respect to the fenestra vestibuli in the living *Ornitho-*

rhynchus anatinus is secondary (Musser and Archer 1998). This feature is also polymorphic among Multituberculata (Kielan-Jaworowska and Hurum 1997). Thus the anterior position of the TMJ relative to the fenestra vestibuli may be a synapomorphy at a more inclusive level within mammals, including monotremes and *Hadrocodium* (Luo, Crompton, and Sun 2001). The implication of this broader distribution is that the anterior position of the TMJ may not be a synapomorphy supporting inclusion of eutriconodonts in Theriiformes.

In recent phylogenetic analyses that included postcranial characters, both *Gobiconodon* (see Hu et al. 1997) and the eutriconodont *Jeholodens* were placed outside the mammalian crown group (see Ji et al. 1999; Rowe 1999). *Gobiconodon* and *Jeholodens* were resolved into clades that are successively closer to the mammalian crown group (Ji et al. 1999). The support for this tree topology is mostly from the postcranial skeleton. Both *Gobiconodon* and *Jeholodens* (but especially the latter) lack a large number of the derived characters of the vertebral column and the pelvis that unite *Ornithorhynchus* with the living therians. By extrapolation, eutriconodonts can be excluded from the mammalian crown group due to the lack of these synapomorphies of living mammals. However, the study on *Jeholodens* (Ji et al. 1999) did not include some of the previously sampled basicranial characters, and differed from earlier studies (e.g., Rowe 1988; Rougier, Wible, and Hopson 1996) in taxonomic sampling of eutriconodonts. Therefore, competing hypotheses on the position of eutriconodonts with respect to the mammalian crown group may be attributable in part to the difference in sampling of anatomical features, and in part to differences in the selection of taxa.

The dataset of this study includes all anatomical features sampled by recent studies of the basicranium (e.g., Wible et al. 1995; Rougier, Wible, and Hopson 1996; Luo, Crompton, and Sun 2001), dentition, and postcranium (e.g., Ji et al. 1999). Taxonomic coverage of Eutriconodonta is broader than previous studies, with *Gobiconodon*, *Amphilestes*, *Jeholodens*, *Triacodon*, and *Priacodon* being included. The strictly parsimony analysis (Fig. 1) unambiguously places eutriconodonts within the mammalian crown group, between australosphenidans (including monotremes) and multituberculates, as in Rowe (1988). This is clearly the preferred position for eutriconodonts, given our dataset.

However, the alternative placement of eutriconodonts as sister-taxon to crown mammals (as advocated by Ji et al. 1999; Rowe 1999) remains viable (though less likely), because nonparametric tests showed that it cannot be rejected on a statistical basis. In the constrained search that resulted in placement of multituberculates outside the mammalian crown group, the eutriconodonts are placed outside crown Mammalia as well (without any constraint on eutriconodonts themselves). The alternative placement of eutriconodonts out of the mammalian crown group (Fig. 2) differs in only five or six steps from their placement within the mammalian crown group (Fig. 1) (Appendix 2).

How does this latter sub-optimal topology, obtained by a constrained search, compare with the preferred tree to-

pology? The nonparametric test shows that the difference between these two topologies (eutriconodonts within *versus* outside the mammalian crown group) is not significant ($p < 0.6222$ for comparison of the consensus trees, or $p < 0.4823$ for comparison of the fundamental trees), a result that is consistent with the small difference in number of steps between these two contrasting tree topologies (Appendix 2). Given our dataset, the placement of eutriconodonts within the mammalian crown group is weakly supported, though preferable only on the basis of strict parsimony.

Monophyly of eutriconodonts.—Our analysis groups eutriconodonts into a monophyletic clade (preferred tree in Fig. 1). However, we emphasize that an adequate test of eutriconodont monophyly must incorporate broader taxonomic sampling (to include all reasonably well-represented genera) than was possible in this study. Central to the issue of relationships among eutriconodonts is a suite of problems relating to “amphilestids”.

The concept of Eutriconodonta, with a fundamental division into “Amphilestidae” and Triconodontidae, was largely based on Simpson’s (1925a, b, 1928, 1929a) landmark studies of the limited Middle to Late Jurassic fossils available in the 1920s. Simpson recognized the Amphilestinae and Triconodontinae as subfamilies within Triconodontidae. In the classic division of eutriconodonts (*sensu* K.A. Kermack et al. 1973; = triconodonts of Simpson 1928), “amphilestids” were distinguished from triconodontids by their more symmetrical, molarized premolars; and by the size differential among primary cusps of the lower molars, with cusp a being much taller than cusps b and c. Correspondingly, triconodontids were characterized as having lower premolars with a more asymmetrical profile and cusp a being more recurved; and molars with cusp a “nearly or quite” (Simpson 1928, 1929a) equal to cusps b and c. These features need to be re-evaluated in lieu of the diversity of other mammals with a triconodont molar pattern, such as morganucodontids and *Sinoconodon*, all of which were discovered long after Simpson’s classic work.

Later studies have provided support for monophyly of Triconodontidae, based on well-established synapomorphies. Patterson (1951, 1956) recognized that the tongue-in-groove interlocking mechanism between molars (as seen in Early Cretaceous *Astroconodon*) is a unique character. Patterson and Olson (1961) also suggested that absence of the anterolingual cingular cuspule e on lower molars could be a defining feature of Triconodontidae. These diagnostic features are applicable to a wide diversity of triconodontids discovered in the last three decades (Fox 1969, 1976; Jenkins and Crompton 1979; Sigogneau-Russell 1995; Cifelli and Madsen 1998; Cifelli et al. 1998, 1999). Triconodontids form a robust clade supported by 1) nearly equal heights of molar cusps, 2) reduction or absence of anterior and internal cuspule e, and 3) an anterior embayment or groove on main cusp b for interlocking of molars. A recent cladistic analysis of dental and mandibular features of eutriconodonts and

other mammals supports monophyly of the traditional group Triconodontidae, which, in turn, are the sister-taxon to *Jeholodens* (Ji et al. 1999). Study of the basicranium, though necessarily limited in taxonomic sampling, also supports monophyly of the group (Rougier, Wible, and Hopson 1996).

“Amphilestidae”, however, are problematic. The traditional concept of this group is based on four genera, each represented only by parts of the lower dentition and dentary (for *Amphilestes* and *Phascolotherium*). Most known features appear to be plesiomorphic (though at various levels; see below). As a result, both the putative monophyly of “amphilestids”, and their phylogenetic proximity to Triconodontidae, are open to debate. Early Cretaceous *Gobiconodon*, known by much more complete materials, has an “amphilestid-like” lower dentition, and has been referred to this group (see review by Kielan-Jaworowska and Dashzeveg 1998). In some respects, however, *Gobiconodon* appears to be rather specialized, and it has been referred to its own family or subfamily (see Chow and Rich 1984; Jenkins and Schaff 1988; Kielan-Jaworowska and Dashzeveg 1998; Godefroit and Guo 1999). As we regard “Amphilestidae” as a paraphyletic grade and treat its included taxa individually in the analyses and relevant discussion, taxonomic placement of *Gobiconodon* is largely moot in the present context; we include it among “amphilestids” for linguistic convenience. However, given the poor knowledge of other “amphilestids”, the presence of certain apomorphies in *Gobiconodon*, and the lack of a defensible basis for “amphilestid” monophyly, we stress that *Gobiconodon* cannot be simply taken as exemplar for the “Amphilestidae”.

Simpson’s (1928, 1929a) main diagnostic characters for “amphilestids” have proven to be plesiomorphies shared by the more distantly related morganucodontids and *Siniconodon*. In fact, Simpson (1928: 70) had already recognized that the main distinguishing characters for this group were “clearly primitive characters lost in the more highly specialized Triconodontinae”. Patterson and Olson (1961) were the first to question a close relationship of “amphilestids” to triconodontids; similar skepticism was subsequently expressed by K.A. Kermack (1967b). Mills (1971) recognized that the wear facets were very similar in “amphilestids” and the “obtuse-angled symmetrodonts”, such as *Kuehneotherium* and *Tinodon*. He even advocated removal of “amphilestids” from “Triconodonta” and suggested that they should be placed instead with “obtuse-angle symmetrodonts”. This view has not been widely accepted. In a recent study, Kielan-Jaworowska and Dashzeveg (1998) showed that *Gobiconodon* and the “obtuse-angled symmetrodonts” share some similarities in wear facets of the upper molars, in a posteriorly increasing cusp triangulation of the upper molar series, and in the interlocking mechanism of lower molars (a feature that is also present in other “amphilestids” and the morganucodontid *Dinnetherium*). The dental similarities (especially the gradient of increasing triangulation in posterior molars) of the “obtuse-angle symmetrodonts” to *Gobiconodon* have discordant distributions with respect to the mandibular structures of the respective taxa, and can be used for the diagnosis of neither

“amphilestids” nor “symmetrodonts” (refer to the relevant discussion on problems with “obtuse-angle symmetrodonts”).

Monophyly of Eutriconodonta was weakly supported by our strict parsimony analysis (Fig. 1). In the constrained search whereby multituberculates were forced to the outside of the mammalian crown group, eutriconodonts collapse as a clade and become a paraphyletic group (Fig. 2). The taxa included “amphilestids”, *Amphilestes* and *Gobiconodon*, consistently appear as separately placed branches, rather than a monophyletic grouping, in all searches. Given these results, we provisionally maintain eutriconodonts as a clade, with “amphilestids” representing a basal, paraphyletic grade of Eutriconodonta. Nonparametric tests show that the topology in which eutriconodonts are a clade (Fig. 1) is not significantly different from the topology in which they are paraphyletic (Fig. 2) (Appendix 2).

Concluding remarks

Our estimates of Mesozoic mammal phylogeny at the familial or subordinal levels are summarized in Figs. 1 and 2. The analyses on which these hypotheses are based includes sampling of the entire range of Mesozoic mammal diversity (43 clades), as reflected by their respective dental specializations. Because temporal and biogeographic distributions of early mammals are documented mostly by dental fossils, a comprehensive phylogeny that includes the “dental” clades may help to provide a phylogenetic framework for studying chronological and biogeographic patterns in early mammal evolution. However, most anatomical features for many “dental clades” are unknown, and thus are necessarily coded as “missing” in our dataset. A weakness inherent to inclusion of these missing data is that the positions of the more incomplete fossil taxa tend to be less well resolved in the strict consensus (see discussions by Rowe 1988, 1993; Novacek 1992a; Simmons 1993), or to have a weaker statistical support, everything else being equal. This presents a dilemma for any study including comprehensive taxonomic coverage of incomplete fossil taxa, and ours is no exception.

The vast taxonomic diversity of Mesozoic mammal groups and their enormous scope of anatomical evolution present a great challenge for building a taxonomically comprehensive phylogeny from parsimonious analyses of a single “super-matrix” that combines characters from different anatomical areas (dentitions, mandibles, crania, and postcranial skeletons). Definition of highly transformed characters can be controversial. The dataset (Appendix 1) represents the best we can manage to gather to this date. We expect that future discoveries of new fossils may help to fill in the blank areas of the dataset, and to lead to new questions in Mesozoic mammal evolution. We also expect that this dataset will be critically re-evaluated and corrected by other researchers and by ourselves. This dataset will grow and will be modified as the knowledge of Mesozoic mammals accumulates. Such is the nature of our science.

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Addendum

While this paper was in press, one relevant paper appeared (Sigogneau-Russell et al. 2001) and one was in press (Rauhut et al. in press); adequate discussion here is impossible, and we confine ourselves to a brief commentary.

Sigogneau-Russell et al. (2001) supported the sister-taxon relationship of *Ausktribosphenos* and toothed monotremes, as implied in Luo et al. (2001) and explicitly stated in our present paper, but they presented a variant version of the “dual origin hypothesis” by excluding *Ambondro* from Australosphenida. These authors considered only two characters diagnosing Australosphenida (lingual molar cingulid and angulation of premolar cusps). We note that Boreosphenida and Australosphenida differ in many more ways, including apomorphic characters at 4–6 nodes of our earlier work (Luo et al. 2001: fig. 1) and 6–10 nodes herein (Figs. 1, 2). Their suggestion that a lingual cingulid is plesiomorphic was based on an eclectic and incomplete sampling of taxa and variants (e.g., polymorphisms in certain specimens of *Palaeoxonodon*). As for the other character, Sigogneau-Russell et al. (2001) failed to make the important distinction between molariform appearance and cusp angulation: the main cusps a, b, c are not triangulated on the mediolaterally compressed

p5 in *Peramus*, differing fundamentally from the ultimate lower premolar in Australosphenida.

Given the abysmal record of early Gondwanan mammals, the discovery of a Jurassic mammal from South America (Rauhut et al. in press) provides an astonishingly timely test of the hypothesis on dual origin of tribosphenic mammals. Phylogenetic analysis based on a data matrix modified from that of Luo et al. (2001) and including the new taxon yielded a tree (Rauhut et al. in press: fig. 3) with virtually identical topology to that originally obtained by us (Luo et al. 2001: fig. 1), providing corroborative support for the “dual origin” hypothesis.

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Appendix 1

Character description and systematic distribution

(Justification for selection of taxa in the main text)

Mandible (26 characters)

1. Postdentary trough (behind the tooth row):

(0) Present: *Probainognathus*, tritylodontids, tritheledontids, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Kuehneotherium*, *Shuotherium*, *Ausktribosphenos*, *Bishops* (incomplete, but its anterior part is visible), *Steropodon* (based upon the cast and published photos, we provisionally interpret that *Steropodon* has preserved the anterior part of the postdentary trough and its associated mandibular canal opening; but it lacks medial ridge overhanging the trough), *Haramiyavia*;

(1) Absent: *Hadrocodium*, *Teinolophos*, *Obdurodon*, *Ornithorhynchus*, *Gobiconodon*, *Amphilestes*, *Jeholodens*, *Priacodon*, *Triaracodon*, “plagiaulacidans”, cimolodontans, *Tinodon*, *Zhangheotherium*, *Dryolestes*, *Henkelotherium*, *Amphitherium*, *Vincelestes*, *Peramus*, *Kielantherium*, *Deltatheridium*, *Asiatherium*, *Didelphis*, *Pucadelphys*, *Erinaceus*, *Prokennalestes*, *Montanalestes*, *Asioryctes*;

(?) Not preserved: *Adelobasileus*, *Ambondro*, *Aegialodon*, *Kokopellia*, *Pappotherium*.

2. Separate scars for surangular—prearticular in Meckel’s groove and the postdentary trough:

(0) Present: *Probainognathus*, tritylodontids, tritheledontids, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Kuehneotherium*, *Shuotherium*, *Ausktribosphenos*;

(1) Absent: *Hadrocodium*, *Shuotherium*, *Ausktribosphenos*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Ornithorhynchus*, *Gobiconodon*, *Amphilestes*, *Jeholodens*, *Priacodon*, *Triaracodon*, “plagiaulacidans”, cimolodontans, *Tinodon*, *Zhangheotherium*, *Peramus*, *Dryolestes*, *Henkelotherium*, *Amphitherium*, *Vincelestes*, *Kielantherium*, *Deltatheridium*, *Asiatherium*, *Didelphis*, *Kokopellia*, *Pucadelphys*, *Erinaceus*, *Prokennalestes*, *Montanalestes*, *Asioryctes*;

(?) Not preserved: *Adelobasileus*, *Ambondro*, *Bishops*, *Steropodon*, *Haramiyavia*, *Aegialodon*, *Pappotherium*.

3. Overhanging medial ridge above the postdentary trough (behind the tooth row):

(0) Present: *Probainognathus*, tritylodontids, tritheledontids, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Kuehneotherium*, *Haramiyavia*;

(1) Absent: *Hadrocodium*, *Shuotherium*, *Ausktribosphenos*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Ornithorhynchus*, *Gobiconodon*, *Amphilestes*, *Jeholodens*, *Priacodon*, *Triaracodon*, “plagiaulacidans”, cimolodontans, *Tinodon*, *Zhangheotherium*, *Peramus*, *Dryolestes*, *Henkelotherium*, *Amphitherium*, *Vincelestes*, *Kielantherium*, *Deltatheridium*, *Asiatherium*, *Didelphis*, *Pucadelphys*, *Erinaceus*, *Prokennalestes*, *Montanalestes*, *Asioryctes*;

(?) Not preserved: *Adelobasileus*, *Ambondro*, *Bishops*, *Kokopellia*, *Aegialodon*, *Pappotherium*.

4. Curvature of Meckel’s groove (under the tooth row) in adult (*sensu* Luo 1994):

(0) Present and parallel to the ventral border of mandible: *Probainognathus*, tritylodontids, tritheledontids, *Sinoconodon*, *Haldanodon*, *Gobiconodon*, *Jeholodens*, *Priacodon*, *Triaracodon*, *Haramiyavia*, *Steropodon*, *Zhangheotherium*, *Henkelotherium*, *Dryolestes*, *Kielantherium*, *Prokennalestes*;

(1) Present and convergent to the ventral border of mandible: *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Kuehneotherium*, *Amphilestes*, *Tinodon*, *Shuotherium*, *Ausktribosphenos*, *Amphitherium*, *Peramus*;

(?) Unknown or not preserved: *Adelobasileus*, *Aegialodon*, *Pappotherium*; not applicable: *Hadrocodium*, *Ambondro*, *Bishops*, *Teinolophos*, *Obdurodon*, *Ornithorhynchus*, “plagiaulacidans”, cimolodontans, *Vincelestes*, *Erinaceus*, *Montanalestes*, *Asioryctes*, *Deltatheridium*, *Asiatherium*, *Didelphis*, *Kokopellia*, *Pucadelphys*.

5. Degree of development of Meckel’s groove in adults:

(0) Well developed: *Probainognathus*, tritylodontids, tritheledontids, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Kuehneotherium*, *Shuotherium*, *Ausktribosphenos*, *Steropodon*, *Haramiyavia*;

(1) Weakly developed: *Hadrocodium*, *Bishops*, *Gobiconodon*, *Amphilestes*, *Jeholodens*, *Priacodon*, *Triaracodon*, *Tinodon*, *Zhangheotherium*, *Peramus*, *Dryolestes*, *Henkelotherium*, *Amphitherium*, *Kielantherium*, *Asia-*

therium, *Kokopellia*, *Pucadelphys*, *Prokennalestes*;

(2) Vestigial or absent: *Teinolophos*, *Obdurodon*, *Ornithorhynchus*, “plagiaulacidans”, cimolodontans, *Vincelestes*, *Deltatheridium*, *Didelphis*, *Erinaceus*, *Montanalestes*, *Asioryctes*;

(?) Unknown or not preserved: *Adelobasileus*, *Aegialodon*, *Pappotherium*, *Ambondro*.

6. Mandibular symphysis:

(0) Fused: *Probainognathus*, tritylodontids;

(1) Unfused: tritheledontids, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Kuehneotherium*, *Haldanodon*, *Gobiconodon*, *Amphilestes*, *Jeholodens*, *Priacodon*, *Triaracodon*, “plagiaulacidans”, cimolodontans, *Vincelestes*, *Dryolestes*, *Henkelotherium*, *Amphitherium*, *Peramus*, *Kielantherium*, *Deltatheridium*, *Didelphis*, *Kokopellia*, *Pucadelphys*, *Erinaceus*, *Asioryctes*, *Prokennalestes*;

(2) Unfused and reduced: *Hadrocodium*, *Obdurodon*, *Ornithorhynchus*, *Zhangheotherium*;

(?) Not preserved: *Adelobasileus*, *Tinodon*, *Shuotherium*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Haramiyavia*, *Aegialodon*, *Kielantherium*, *Asiatherium*, *Pappotherium*, *Montanalestes*.

7. Groove for the replacement dental lamina (Crompton and Luo 1993; Luo 1994):

(0) Present: *Probainognathus*, tritheledontids (Crompton and Luo 1993), *Sinoconodon*, *Morganucodon* (based on Parrington 1973, 1978), *Megazostrodon* (visible in Gow 1986a: fig. 16);

(1) Absent: tritylodontids, *Dinnetherium*, *Haldanodon*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Ornithorhynchus*, *Gobiconodon*, *Amphilestes*, *Jeholodens*, *Priacodon*, *Triaracodon*, *Haramiyavia*, “plagiaulacidans”, cimolodontans, *Tinodon*, *Zhangheotherium*, *Peramus*, *Dryolestes*, *Henkelotherium*, *Amphitherium*, *Vincelestes*, *Kielantherium*, *Deltatheridium*, *Asiatherium*, *Didelphis*, *Kokopellia*, *Pucadelphys*, *Pappotherium*, *Erinaceus*, *Asioryctes*, *Prokennalestes*, *Montanalestes*;

(?) Not preserved: *Adelobasileus*, *Aegialodon*, *Hadrocodium* (not exposed).

8. Angular process of the dentary—presence versus absence:

(0) Present: *Probainognathus*, tritylodontids, tritheledontids, *Sinoconodon*, *Morganucodon*, *Haldanodon*, *Dryolestes*, *Henkelotherium*, *Amphitherium*, *Peramus*, *Vincelestes*, *Kielantherium*, *Prokennalestes*, *Erinaceus*;

(1) Reduced or weakly developed: *Megazostrodon* (Gow 1986a termed the process as the pseudo-angular process, we considered it to be a reduced angular process), *Dinnetherium* (Jenkins et al. 1983 termed the process as the pseudo-angular process; Hopson 1994 and; Kielan-Jaworowska 1997 considered this to be a true angular process of reduced size; see also Gambaryan and Kielan-Jaworowska 1995), *Kuehneotherium*, *Haramiyavia*, *Obdurodon* (a small but distinctive angle according to Musser and Archer 1998);

(2) Present and transversely flaring: *Bishops*, *Ausktribosphenos*, *Teinolophos* (note on *Ausktribosphenos*: the angular process is transversely flaring. Although the angular process was not described for the holotype of *Ausktribosphenos* in Rich et al. (1997), the second specimen photographed by Rich et al. (1999) has an angle that is identical to the transversely flaring angular process of *Teinolophos*; see Rich et al. (1999) and Rich, Vickers-Rich, et al. (2001). This is different from character state 4);

(3) Present and slightly inflected: *Hadrocodium*, *Asioryctes*, *Montanalestes* (but see discussion in Averianov and Kielan-Jaworowska 1999);

(4) Present, strongly inflected, and continuing anteriorly as a mandibular shelf: *Deltatheridium*, *Asiatherium*, *Kokopellia*, *Pucadelphys*, *Didelphis*;

(5) Absent: *Shuotherium*, *Ornithorhynchus*, *Gobiconodon*, *Amphilestes*, *Jeholodens*, *Priacodon*, *Triaracodon*, “plagiaulacidans”, cimolodontans, *Tinodon*, *Zhangheotherium*;

(?) Not preserved: *Adelobasileus*, *Ambondro*, *Steropodon*, *Aegialodon*, *Pappotherium*.

9. Angular process of the dentary—anteroposterior position relative to the dentary condyle:

(0) An anterior position (the angular process is below the main body of the coronoid process, separated widely from the dentary condyle): *Probainognathus*, tritylodontids, tritheledontids, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Kuehneotherium*, *Ausktribosphenos*, *Bishops*, *Teinolophos*, *Obdurodon* (Archer et al. 1993), *Haramiyavia*;

(1) A posterior position (the angular process is positioned at the same level at the posterior end of the coronoid process; either close to or directly under the dentary condyle): *Peramus*, *Dryolestes*, *Henkelotherium*, *Amphitherium*, *Vincelestes*, *Kielantherium*, *Deltatheridium*, *Asiatherium*, *Didelphis*, *Pucadelphys*, *Erinaceus*, *Prokennalestes*, *Montanalestes*, *Asioryctes*; (?) Not applicable: *Adelobasileus*, *Gobiconodon*, *Amphilestes*, *Jeholodens*, *Priacodon*, *Trioracodon*, *Shuotherium*, *Ornithorhynchus*, “plagiaulacidans”, cimolodontans, *Tinodon*, *Zhangheotherium*; not preserved: *Ambondro*, *Steropodon*, *Kokopellia*, *Aegialodon*, *Pappotherium*.

Alternative character (not used in this analysis). Characters 8 and 9 can be merged to form one multi-state character (“Compound Angular Process”). This compound and multi-state character should be run in parsimony search algorithms as an ordered sequence for transformation (present \leftrightarrow weak \leftrightarrow absent; anterior *versus* posterior).

(0) Present and anterior, with internal fossa for the angular bone: *Probainognathus*, tritylodontids, tritheledontids, *Sinoconodon*, *Morganucodon*, *Hadrocodium*, *Haldanodon*;

(1) Present and anterior, but weakly developed: *Megazostrodon*, *Dinnetherium*, *Kuehneotherium*, *Haramiyavia*;

(2) Present and posterior: *Ausktribosphenos*, *Bishops*, *Teinolophos*, *Obdurodon* (Archer et al. 1993; Musser and Archer 1998), *Amphitherium*, *Vincelestes*, *Dryolestes*, *Henkelotherium*, *Peramus*, *Kielantherium*, *Prokennalestes*, *Montanalestes*, *Asioryctes*, *Erinaceus*;

(3) Present as a shelf, posterior, and inflected: *Deltatheridium*, *Pucadelphys*, *Didelphis*, *Asiatherium*, *Kokopellia*;

(4) Absent: *Gobiconodon*, *Amphilestes*, *Jeholodens*, *Priacodon*, *Trioracodon*, *Shuotherium*, *Ornithorhynchus*, “plagiaulacidans”, cimolodontans, *Zhangheotherium*;

(?) Not preserved: *Steropodon*, *Ambondro*, *Tinodon*, *Aegialodon*, *Pappotherium*.

10. Angular process of the dentary—vertical elevation relative to the molar alveolar line:

(0) Angular process is low, at or near the level of the ventral border of the mandibular horizontal ramus: *Probainognathus*, tritylodontids, tritheledontids, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Kuehneotherium*, *Haramiyavia*, *Peramus*, *Dryolestes*, *Henkelotherium*, *Amphitherium*, *Vincelestes*, *Kielantherium*, *Deltatheridium*, *Asiatherium*, *Didelphis*, *Pucadelphys*, *Erinaceus*, *Prokennalestes*, *Montanalestes*, *Asioryctes*;

(1) Angular process is high, at or near the level of molar alveolar line (and far above the ventral border of the mandibular horizontal ramus): *Ausktribosphenos*, *Bishops*, *Teinolophos*, *Obdurodon* (the angle is level with the imaginary alveolar line);

(?) Not applicable: *Gobiconodon*, *Amphilestes*, *Jeholodens*, *Priacodon*, *Trioracodon*, *Shuotherium*, *Ornithorhynchus*, “plagiaulacidans”, cimolodontans, *Tinodon*, *Zhangheotherium*; not preserved: *Adelobasileus*, *Ambondro*, *Steropodon*, *Kokopellia*, *Aegialodon*, *Pappotherium*.

11. Coronoid (or its attachment scar) in adults:

(0) Present: *Probainognathus*, tritylodontids, tritheledontids, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Kuehneotherium*, *Shuotherium* (preserved as a partial scar, as illustrated by Chow and Rich 1982), *Ausktribosphenos*, *Teinolophos*, *Gobiconodon*, *Tinodon*, *Zhangheotherium*, *Peramus*, *Dryolestes*, *Henkelotherium*, *Amphitherium*, *Vincelestes*, *Kielantherium*, *Prokennalestes*, *Montanalestes*;

(1) Absent: *Obdurodon* (following Archer et al. 1993), *Ornithorhynchus*, *Amphilestes*, *Priacodon*, *Trioracodon*, cimolodontans, *Deltatheridium*, *Didelphis*, *Asiatherium*, *Kokopellia*, *Pucadelphys*, *Asioryctes*, *Erinaceus*; (0/1 polymorphic) “plagiaulacidans” (present {0} for *Kuehneodon*, Hahn 1977a, but absent {1} in other “plagiaulacidans”);

(?) Not visible: *Hadrocodium*, *Haramiyavia*; not preserved: *Ambondro*, *Bishops*, *Steropodon*, *Jeholodens*, *Aegialodon*, *Pappotherium*.

12. Mandibular foramen (posterior opening of the mandibular canal) for the inferior alveolar nerve and vessels:

(0) Located within the postdentary trough (the depression around the foramen is a part of Meckel’s sulcus-postdentary trough): *Probainognathus*, tritylodontids, tritheledontids, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Kuehneotherium*, *Shuotherium*, *Ausktribosphenos*, *Bishops*, *Steropodon* (canal is present, its aperture is shown in Archer et al. 1985: fig. 1c), *Haramiyavia*;

(1) The foramen is not associated with either postdentary trough or the Meckel’s groove: *Hadrocodium*, *Teinolophos*, *Obdurodon* (Archer et al. 1993), *Ornithorhynchus*, *Gobiconodon*, *Amphilestes*, *Jeholodens*, *Priacodon*, *Trioracodon*, “plagiaulacidans”, cimolodontans, *Tinodon*, *Zhangheotherium*, *Peramus*, *Dryolestes*, *Henkelotherium*, *Amphitherium*, *Vinceles-*

tes, *Kielantherium*, *Erinaceus*, *Deltatheridium*, *Asiatherium*, *Didelphis*, *Pucadelphys*, *Prokennalestes*, *Montanalestes*, *Asioryctes*;

(?) Not preserved: *Adelobasileus*, *Ambondro*, *Kokopellia*, *Aegialodon*, *Pappotherium*.

13. Medial concavity (fossa) for the reflected lamina of the angular bone on the medial side of the dentary angular process (Crompton and Luo 1993):

(0) Medial concavity (excavated fossa) for the angular bone on the mandibular angular process: *Probainognathus*, tritylodontids, tritheledontids, *Sinoconodon*, *Morganucodon*, *Dinnetherium*, *Megazostrodon* (based on Gow 1986a), *Haldanodon*, *Kuehneotherium*;

(1) Angular region has no fossa for the angular bone: *Hadrocodium*, *Gobiconodon*, *Amphilestes*, *Jeholodens*, *Trioracodon*, *Shuotherium*, *Ornithorhynchus*, *Obdurodon*, “plagiaulacidans”, cimolodontans, *Tinodon*, *Zhangheotherium*, *Peramus*, *Ausktribosphenos*, *Bishops*, *Teinolophos*, *Dryolestes*, *Henkelotherium*, *Amphitherium*, *Vincelestes*, *Kielantherium*, *Deltatheridium*, *Asiatherium*, *Didelphis*, *Pucadelphys*, *Erinaceus*, *Asioryctes*, *Prokennalestes*, *Montanalestes*, *Pappotherium*;

(?) Not preserved: *Adelobasileus*, *Ambondro*, *Steropodon*, *Haramiyavia*, *Kokopellia*, *Aegialodon*, *Pappotherium*.

14. The splenial as a separate element (as indicated by its scar on the dentary) in adult:

(0) Present: *Probainognathus*, tritylodontids, tritheledontids, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Kuehneotherium*, *Zhangheotherium*;

(1) Absent: *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Ornithorhynchus*, *Gobiconodon*, *Amphilestes*, *Jeholodens*, *Priacodon*, *Trioracodon*, “plagiaulacidans”, cimolodontans, *Dryolestes*, *Henkelotherium* (although Krebs 1991 identified a structure as the splenial scar, this is really a part of Meckel’s groove, and we consider the splenial scar to be absent), *Amphitherium*, *Peramus*, *Vincelestes*, *Kielantherium*, *Deltatheridium*, *Asiatherium*, *Didelphis*, *Kokopellia*, *Pucadelphys*, *Erinaceus*, *Asioryctes*, *Prokennalestes*, *Montanalestes*;

(?) Not preserved: *Hadrocodium*, *Adelobasileus*; unknown: *Haramiyavia*, *Tinodon*, *Aegialodon*, *Pappotherium*.

15. Relationship of the surangular to the craniomandibular joint (CMJ) (CMJ is made of several bones in stem groups of mammals, whereas temporomandibular joint (TMJ) is the medical and veterinary anatomical term applicable to living mammals, in which the jaw hinge is made only of the temporal (squamosal) bone and the dentary. CMJ and TMJ are used interchangeably in this paper as appropriate to the circumstances used in manuscript) (Rowe 1988):

(0) Participates in CMJ either as a separate bone, or fused with the articular: *Probainognathus*, tritylodontids, tritheledontids, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Haldanodon*;

(1) Surangular as bony element is lost in adults: *Obdurodon*, *Ornithorhynchus*, “plagiaulacidans”, cimolodontans, *Asiatherium*, *Didelphis*, *Pucadelphys*, *Erinaceus*, *Asioryctes*;

(?) Unknown: *Adelobasileus*, *Dinnetherium*, *Hadrocodium*, *Kuehneotherium*, *Ambondro*, *Shuotherium*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Gobiconodon*, *Amphilestes*, *Jeholodens*, *Trioracodon*, *Priacodon*, *Haramiyavia*, *Tinodon*, *Zhangheotherium*, *Peramus*, *Dryolestes*, *Henkelotherium*, *Amphitherium*, *Vincelestes*, *Kielantherium*, *Deltatheridium*, *Kokopellia*, *Prokennalestes*, *Montanalestes*, *Aegialodon*, *Pappotherium*.

16. The pterygoid fossa on the medial side of the mandible (Gambaryan and Kielan-Jaworowska 1995):

(0) Absent: *Probainognathus*, tritylodontids, tritheledontids, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Hadrocodium*, *Kuehneotherium*, *Shuotherium*, *Ausktribosphenos*, *Bishops*, *Teinolophos*;

(1) Present: *Haldanodon* (a small pterygoid fossa is present although different from those of other taxa, see the discussion by Krusat 1980: 41, fig. 10), *Gobiconodon* (shown by Kielan-Jaworowska and Dashzeveg 1998), *Amphilestes*, *Priacodon*, *Trioracodon*, *Obdurodon* (Archer et al. 1993), *Ornithorhynchus*, “plagiaulacidans”, cimolodontans, *Tinodon*, *Zhangheotherium*, *Peramus*, *Dryolestes*, *Henkelotherium*, *Amphitherium*, *Vincelestes*, *Kielantherium*, *Deltatheridium*, *Asiatherium*, *Kokopellia* (inferred from the crushed structure in the back of jaw), *Didelphis*, *Pucadelphys*, *Erinaceus*, *Prokennalestes*, *Asioryctes*, *Montanalestes*;

(?) Not preserved: *Adelobasileus*, *Jeholodens*, *Ambondro*, *Steropodon*, *Haramiyavia*, *Aegialodon*, *Pappotherium*.

17. The medial pterygoid ridge (shelf) along the ventral border of the coronoid part of the mandible (character definition *sensu* Miao 1988):

(0) Absent: *Probainognathus*, tritylodontids, tritheledontids, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Haldanodon* (this character may be coded as “absent 0”, the ventral ridge of Krusat’s pterygoid fossa

is also the ridge that overhangs the postdentary trough, and differs from the typical pterygoid ridge of other more derived mammals), *Hadrocodium*, *Kuehneotherium*, *Shuotherium*, *Ausktribosphenos*, *Bishops*, *Teinolophos*, “plagiaulacidans”, cimolodontans;

(1) Present: *Obdurodon* (Archer et al. 1993) *Ornithorhynchus*, *Peramus*, *Vincelestes*, *Dryolestes*, *Henkelotherium*, *Amphitherium*, *Kielantherium*, *Deltatheridium*, *Asiatherium*, *Didelphis*, *Pucadelphys*, *Erinaceus*, *Prokennalestes*, *Montanalestes*, *Asioryctes*;

(2) Pterygoid shelf present and reaching the dentary condyle via a low crest: *Gobicodon*, *Amphilestes*, *Jeholodens*, *Priacodon*, *Triaracodon*, *Tinodon*, *Zhangheotherium*;

(?) Not preserved: *Ambondro*, *Steropodon*, *Kokopellia*, *Pappotherium*; unknown: *Haramiyavia*, *Aegialodon*, *Pappotherium*.

18. The ventral border of the masseteric fossa:

(0) Absent: *Probainognathus*, tritylodontids, tritheledontids, *Sinoconodon*, *Morganucodon*, *Megazostrodon* (*Megazostrodon* has a shallow masseteric fossa but lacks a distinctive ventral ridge, Gow 1986a), *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Kuehneotherium*, *Shuotherium*, *Haramiyavia*;

(1) Present as a low and broad crest: *Tinodon*, *Vincelestes*, *Kielantherium*, *Deltatheridium*, *Asiatherium*, *Didelphis*, *Kokopellia*, *Pucadelphys*, *Erinaceus*, *Prokennalestes*, *Montanalestes*, *Asioryctes*;

(2) Present as a well-defined and thin crest: *Ausktribosphenos*, *Bishops*, *Teinolophos*, *Obdurodon* (Archer et al. 1993), *Ornithorhynchus*, *Gobicodon*, *Amphilestes* (based on verbal description in Simpson 1928) *Priacodon*, *Triaracodon*, “plagiaulacidans”, cimolodontans, *Zhangheotherium*, *Amphitherium*, *Peramus* (from description by Simpson 1928), *Dryolestes*, *Henkelotherium*;

(?) Not exposed: *Jeholodens*; not preserved: *Adelobasileus*, *Ambondro*, *Steropodon*, *Aegialodon*, *Pappotherium*.

19. Crest of the masseteric fossa along the anterior border of the coronoid process:

(0) Absent or weakly developed: *Probainognathus*, tritylodontids, tritheledontids, *Sinoconodon*, *Morganucodon*, *Megazostrodon* (*Megazostrodon* has a shallow masseteric fossa but lacks a distinctive ridge, Gow 1986a), *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Kuehneotherium*, *Haramiyavia*;

(1) Present: *Gobicodon*, *Jeholodens* (based on impression), *Priacodon*, *Triaracodon*, “plagiaulacidans”, cimolodontans, *Zhangheotherium*, *Peramus* (from description by Simpson 1928), *Dryolestes*, *Henkelotherium*, *Amphitherium*, *Vincelestes*, *Kielantherium*, *Deltatheridium*, *Asiatherium*, *Didelphis*, *Kokopellia*, *Pucadelphys*, *Erinaceus*;

(2) Present and laterally flaring: *Ausktribosphenos*, *Bishops*, *Teinolophos*, *Obdurodon*, *Ornithorhynchus* (in the Tertiary ornithorhynchids the anterior border of the masseteric fossa is hypertrophied, such that the masseteric fossa forms a deep concavity, or even a pocket), *Prokennalestes*, *Montanalestes*, *Asioryctes*;

(?) Not preserved: *Adelobasileus*, *Shuotherium*, *Ambondro*, *Steropodon*, *Amphilestes* (preserved but not exposed), *Tinodon*, *Aegialodon*, *Pappotherium*.

20. Anteroventral extension of the masseteric fossa:

(0) Below the ultimate molar or posterior to it: *Probainognathus*, tritylodontids, tritheledontids, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Kuehneotherium*, *Shuotherium*, *Ausktribosphenos*, *Bishops*, *Teinolophos*, *Obdurodon*, *Ornithorhynchus*, *Gobicodon*, *Jeholodens*, *Priacodon*, *Triaracodon*, *Haramiyavia*, *Tinodon*, *Zhangheotherium*, *Peramus*, *Dryolestes*, *Henkelotherium*, *Amphitherium*, *Vincelestes*, *Kielantherium*, *Deltatheridium*, *Asiatherium*, *Didelphis*, *Kokopellia*, *Pucadelphys*, *Erinaceus*, *Asioryctes*, *Prokennalestes*, *Montanalestes*;

(1) Anterior extension below the ultimate premolar: “plagiaulacidans”, cimolodontans;

(?) Not preserved: *Adelobasileus*, *Ambondro*, *Steropodon*, *Amphilestes*, *Aegialodon*, *Pappotherium*.

21. Orientation of the dentary peduncle and condyle:

(0) Dentary peduncle is posteriorly directed: *Probainognathus*, tritylodontids, tritheledontids (dentary lateral ridge contacting the squamosal but lacking a distinctive condyle), *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Kuehneotherium*, *Haramiyavia*, *Tinodon*, *Deltatheridium*, *Asiatherium* (its condyle is broken but peduncle is posteriorly directed), *Didelphis*, *Pucadelphys*, *Erinaceus*, *Asioryctes*, *Prokennalestes*, *Montanalestes*;

(1) Dentary condyle is continuous with the semicircular posterior margin of the dentary; condyle is facing up due to the upturning of the posteriormost part of the dentary: *Gobicodon*, *Amphilestes*, *Jeholodens*, *Priacodon*, *Triaracodon*, *Zhangheotherium*, *Peramus*, *Dryolestes*, *Henkelotherium*, *Amphitherium*, *Vincelestes* (the peduncle is upturned, *Vincelestes* is tentatively design-

nated as character state “1” but unlike “eutricodonts” and spalacotheriids, *Vincelestes* lacks the semicircular posterior margin in the dentary);

(2) Dentary articulation extends vertically for the entire depth of the horizontal ramus of mandible; it is confluent with the horizontal ramus and lacks a peduncle; the dentary articulation is posteriorly directed: “plagiaulacidans”, cimolodontans;

(3) Vertically directed dentary peduncle: *Bishops*, *Teinolophos*, *Obdurodon*, *Ornithorhynchus*;

(?) Not preserved: *Steropodon*, *Kielantherium*, *Adelobasileus*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Kokopellia*, *Aegialodon*, *Pappotherium*.

22. Shape and relative size of the dentary articulation:

(0) Small and dorsoventrally compressed: tritheledontids (represented by the lateral ridge), *Megazostrodon*, *Hadrocodium*, *Kuehneotherium*;

(1) Condyle is massive and bulbous, transversely broad in its dorsal aspect: *Sinoconodon*, *Haldanodon*, *Bishops*, *Teinolophos*, *Obdurodon*, *Ornithorhynchus*, *Gobicodon*, *Amphilestes*, *Tinodon*, *Zhangheotherium*, *Amphitherium*, *Peramus*, *Dryolestes*, *Henkelotherium*, *Vincelestes*, *Deltatheridium*, *Didelphis*, *Pucadelphys*, *Erinaceus*, *Prokennalestes*, *Montanalestes*, *Asioryctes*;

(2) Condyle mediolaterally narrow and vertically deep, forming a broad arc in lateral outline, either ovoid or triangular in posterior view: *Dinnetherium*, *Priacodon*, *Triaracodon*, *Jeholodens*, “plagiaulacidans”, cimolodontans;

(0/1 polymorphic): *Morganucodon*;

(?) Not preserved: *Steropodon*, *Adelobasileus*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Haramiyavia*, *Kielantherium*, *Asiatherium*, *Kokopellia*, *Aegialodon*, *Pappotherium*; not applicable (no condyle on the dentary): *Probainognathus*, tritylodontids.

23. Ventral (inferior) border of the dentary peduncle (characters modified from Sues 1986: 254; Kielan-Jaworowska 1997: 258):

(0) Posteriorly tapering: *Probainognathus*, tritylodontids;

(1) Columnar and with lateral ridge: tritheledontids, *Sinoconodon*, *Morganucodon*, *Haldanodon*, *Hadrocodium*, *Kuehneotherium*, *Ausktribosphenos*, *Bishops*, *Teinolophos*, *Obdurodon*, *Ornithorhynchus*, *Haramiyavia* (after Jenkins et al. 1997);

(2) Ventrally flaring: *Megazostrodon* (angle of Gow 1986a), *Dinnetherium* (neomorphic angle of Jenkins et al. 1983; Jenkins 1984);

(3) Robust and short: *Peramus*, *Dryolestes*, *Henkelotherium*, *Amphitherium*, *Vincelestes*, *Deltatheridium*, *Didelphis*, *Pucadelphys*, *Erinaceus*, *Asioryctes*, *Prokennalestes*, *Montanalestes*;

(4) Ventral part of the peduncle and condyle becoming continuous with the ventral border of the mandible: *Gobicodon*, *Amphilestes*, *Jeholodens*, *Priacodon*, *Triaracodon*, *Tinodon*, *Zhangheotherium*, “plagiaulacidans” (peduncle absent, ventral border of mandible is directly graded into the dentary condyle), cimolodontans;

(?) Not preserved: *Adelobasileus*, *Shuotherium*, *Ambondro*, *Steropodon*, *Aegialodon*, *Kielantherium*, *Asiatherium*, *Kokopellia*, *Pappotherium*.

24. Position of the dentary condyle relative to the vertical level of postcanine alveoli:

(0) Below or about the same level as the postcanine alveoli: *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Kuehneotherium*, *Gobicodon*, *Amphilestes*, *Jeholodens*, *Priacodon*, *Triaracodon*, “plagiaulacidans”, *Peramus*;

(1) Above the level of the postcanine alveoli: *Ausktribosphenos*, *Bishops* (inferred from the preserved part of the mandible), *Teinolophos*, *Obdurodon* (Archer et al. 1993), *Ornithorhynchus*, *Haramiyavia*, *Tinodon*, *Zhangheotherium*, *Peramus*, *Dryolestes*, *Henkelotherium*, *Amphitherium*, *Vincelestes*, *Kielantherium*, *Deltatheridium*, *Didelphis*, *Asiatherium*, *Pucadelphys*, *Erinaceus*, *Prokennalestes*, *Montanalestes*, *Asioryctes*;

(0/1 polymorphic): cimolodontans (below the tooth row {0} for some taxa; same as or above the tooth row {1} for others);

(?) Not applicable: *Probainognathus*, tritylodontids, tritheledontids; not preserved: *Shuotherium*, *Ambondro*, *Steropodon*, *Aegialodon*, *Kokopellia*, *Pappotherium*.

25. Tilting of the coronoid process of the dentary (measured as the angle between the imaginary line of the anterior border of the coronoid process and the horizontal alveolar line of all molars) (modified from Prothero 1981):

(0) Coronoid process is strongly reclined and the coronoid angle is obtuse ($\geq 150^\circ$): *Probainognathus*, *Sinoconodon* (150°), *Morganucodon* (150°), *Kuehneotherium* (155°), *Shuotherium* (155°), *Zhangheotherium* (150°);

(1) Coronoid process less reclined (135° – 145°): *Megazostrodon* (140°), *Dinnetherium* (140°), *Haldanodon* (135°), *Gobicodon* (145°), *Jeholodens* (145°), *Priacodon* (135°), *Triaracodon* (135°), *Haramiyavia* (140°), “plagiaulacidans” (140°),

(2) Coronoid process less than vertical (115° – 125°): tritheledontids (125°), *Hadrocodium* (125°), *Teinolophos* (115°), *Obdurodon* (125°), *Ornithorhyn-*

chus (125°), *Ausktribosphenos*, *Bishops* (115°), *Amphilestes* (125°), *Dryolestes*, *Henkelotherium* (115°), *Amphitherium* (120°), *Vincelestes* (120°), *Peramus* (125°), *Prokennalestes* (120°);

(1/2) cimolodontans (with a range of variation of 130°–150°);

(3) Coronoid process is near vertical and the coronoid angle small (95–105°): tritylodontids (95°), *Tinodon* (90–100°), *Kielantherium* (100°), *Deltatheridium* (105°), *Didelphis* (105°), *Asiatherium*, *Kokopellia*, *Pucadelphys*, *Erinaceus* (100°), *Montanalestes* (~100°), *Asioryctes* (105°);

(?) Not preserved: *Adelobasileus*, *Ambondro*, *Steropodon*, *Aegialodon*, *Pappotherium*.

26. Alignment of the erupting ultimate molar (or postcanine) to the anterior margin of the dentary coronoid process (and near the coronoid scar if the scar is present):

(0) Ultimate functional molar erupts medial to the coronoid process: *Haldanodon*, *Probainognathus*, tritylodontids, tritheledontids, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Kuehneotherium*, *Gobiconodon*, *Amphilestes*, *Jeholodens*, *Priacodon*, *Trioracodon*, *Haramiyavia*, “plagiaulacidans”, cimolodontans;

(1) Ultimate functional molar erupting in alignment with the anterior margin of coronoid process: *Shuotherium*, *Steropodon*, *Ausktribosphenos*, *Bishops*, *Teinolophos*, *Obdurodon*, *Ornithorhynchus*, *Tinodon*, *Zhangheotherium*, *Peramus*, *Dryolestes*, *Henkelotherium*, *Amphitherium*, *Vincelestes*, *Kielantherium*, *Deltatheridium*, *Asiatherium*, *Didelphis*, *Kokopellia*, *Pucadelphys*, *Erinaceus*, *Asioryctes*, *Montanalestes*, *Prokennalestes*;

(?) Not preserved: *Adelobasileus*, *Ambondro*, *Aegialodon*, *Pappotherium*; not exposed: *Hadrocodium*.

Lower premolars (11 characters)

27. Ultimate lower premolar—symmetry of the main cusp a (= protoconid). This character is measured by the length ratio of the anterior and posterior cutting edges extending from cusp (included because the symmetry of premolar was used by Simpson 1925a, b, 1928 as systematic character):

(0) Asymmetrical (anterior edge of cusp a is more convex in outline than the posterior edge): *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Kuehneotherium*, *Jeholodens*, *Priacodon*, *Trioracodon*, *Peramus*, *Dryolestes*, *Henkelotherium*, *Amphitherium*, *Kielantherium*, *Pappotherium*, *Deltatheridium*, *Asiatherium*, *Kokopellia*, *Pucadelphys*, *Didelphis*;

(1) Symmetrical (anterior and posterior cutting edges are equal or subequal in length; neither edge is more convex or concave than the other in lateral profile): *Sinoconodon* (after Zhang et al. 1998), *Hadrocodium*, *Gobiconodon*, *Amphilestes*, *Shuotherium*, *Ambondro* (premolar is not complete, but the preserved part of the main cusp is symmetrical), *Ausktribosphenos*, *Bishops*, *Obdurodon* (Archer et al. 1993), *Tinodon*, *Zhangheotherium*, *Vincelestes*, *Erinaceus*, *Prokennalestes*, *Montanalestes*, *Asioryctes*;

(?) Not applicable: *Probainognathus*, tritylodontids, *Haramiyavia*, tritheledontids (premolar versus molar undifferentiated), *Ornithorhynchus*, “plagiaulacidans”, cimolodontans; not preserved: *Adelobasileus*, *Steropodon*, *Teinolophos*, *Aegialodon*.

28. The ultimate lower premolar—anterior cusp b (= paraconid) (absence or reduction of anterior cusp b tends to make the premolar to appear more asymmetrical. This character is included because the asymmetry of premolar was used by Simpson 1925a, b, 1928 as a systematic character.):

(0) Present (at least subequal to cusp c of the same tooth): *Sinoconodon*, *Morganucodon*, *Dinnetherium*, *Haldanodon*, *Shuotherium*, *Ausktribosphenos*, *Bishops*, *Obdurodon* (as illustrated by Musser and Archer 1998), *Jeholodens*, *Tinodon*, *Zhangheotherium*, *Dryolestes*, *Henkelotherium*, *Erinaceus*;

(1) Small (much smaller than cusp c of the same tooth), or vestigial to absent: *Megazostrodon*, *Hadrocodium*, *Kuehneotherium* (Kermack et al. 1968), *Gobiconodon*, *Amphilestes*, *Priacodon*, *Trioracodon*, *Amphitherium*, *Peramus*, *Vincelestes*, *Kielantherium*, *Deltatheridium*, *Asiatherium*, *Didelphis*, *Kokopellia*, *Pucadelphys*, *Pappotherium*, *Prokennalestes*, *Montanalestes*, *Asioryctes*;

(?) Not preserved: *Adelobasileus*, *Ambondro* (preservation incomplete), *Steropodon*, *Teinolophos*, *Aegialodon*; not applicable: *Probainognathus*, tritylodontids, tritheledontids, *Ornithorhynchus*, *Haramiyavia*, “plagiaulacidans”, cimolodontans.

29. Ultimate lower premolar—arrangement of principal cusp a, cusp b (if present) and cusp c (we assume the cusp to be c if there is only one cusp behind the main cusp a):

(0) Aligned straight or at a slight angle: *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Haldanodon* (following Hopson and Crompton 1969; Krusat 1980) *Hadrocodium*, *Kuehneotherium*, *Shuotherium*, *Gobiconodon*, *Amphilestes*, *Jeholodens*, *Priacodon*, *Trioracodon*, *Tinodon*, *Zhangheotherium*, *Dryolestes*, *Henkelotherium*, *Amphitherium*,

Peramus, *Vincelestes*, *Kielantherium*, *Pappotherium*, *Prokennalestes*, *Montanalestes*, *Asioryctes*, *Deltatheridium*, *Asiatherium*, *Didelphis*, *Kokopellia*, *Pucadelphys*;

(1) Distinctive triangulation: *Ambondro*, *Ausktribosphenos*, *Bishops*, *Obdurodon* (the SEM photo of Archer et al. 1993 shows the right ultimate premolar has a triangular pattern of the cusp a and its two crests), *Erinaceus*;

(2) Premolar with multicusp in longitudinal row(s): tritylodontids (assuming morphology of anterior postcanines), *Haramiyavia*,

(3) Premolar multicuspate and blade-like: “plagiaulacidans”, cimolodontans; (?) Not preserved: *Adelobasileus*, *Steropodon*, *Teinolophos*, *Aegialodon*; not applicable: *Probainognathus*, tritheledontids, *Ornithorhynchus*.

30. Ultimate lower premolar—posterior (distal) cingulid or cingular cuspule d (in addition to main cusp c):

(0) Absent: *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Kuehneotherium*, *Dryolestes*, *Henkelotherium*, *Amphitherium*, *Vincelestes*, *Kielantherium*, *Pappotherium*;

(1) Posterior cingular cusp present: *Shuotherium*, *Gobiconodon*, *Amphilestes*, *Jeholodens*, *Priacodon*, *Trioracodon*, *Tinodon*, *Zhangheotherium*, *Peramus*, *Deltatheridium*, *Asiatherium*, *Didelphis*, *Kokopellia*, *Pucadelphys*, *Erinaceus*, *Prokennalestes*, *Montanalestes*, *Asioryctes*;

(2) Presence of the continuous posterior (distal) cingulid: *Ambondro*, *Ausktribosphenos*, *Bishops*, *Obdurodon* (the last premolar has a continuous distal cingulid but lacks cusp d, Archer et al. 1993, SEM photo);

(?) Premolar not preserved: *Adelobasileus*, *Steropodon*, *Teinolophos*, *Aegialodon*; not applicable: *Probainognathus*, tritylodontids, tritheledontids, *Ornithorhynchus*, *Haramiyavia*, “plagiaulacidans”, cimolodontans.

31. Ultimate lower premolar—outline:

(0) Laterally compressed (or slightly angled): *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Kuehneotherium*, *Shuotherium*, *Gobiconodon*, *Amphilestes*, *Jeholodens*, *Priacodon*, *Trioracodon*, *Haramiyavia*, *Tinodon*, *Zhangheotherium*, *Vincelestes*, *Dryolestes*, *Henkelotherium*, *Amphitherium*, *Peramus*, *Kielantherium*, *Pappotherium*, *Prokennalestes*, *Montanalestes*, *Asioryctes*, *Deltatheridium*, *Asiatherium*, *Didelphis*, *Kokopellia*, *Pucadelphys*;

(1) Blade-like: “plagiaulacidans”, cimolodontans;

(2) Transversely wide: *Ambondro*, *Ausktribosphenos*, *Bishops*, *Obdurodon* (Archer et al. 1993), *Erinaceus*;

(?) Premolar not preserved: *Adelobasileus*, *Steropodon*, *Teinolophos*, *Aegialodon*; not applicable: *Probainognathus*, tritylodontids, tritheledontids, *Ornithorhynchus*.

32. Labial cingulid of the ultimate lower premolar:

(0) Absent or vestigial: *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Kuehneotherium*, *Amphilestes*, *Jeholodens*, *Priacodon*, *Trioracodon*, *Haramiyavia*, “plagiaulacidans” (the distal labial cusps of premolar are part of a reduced main cusp row, not on cingulid in nature), cimolodontans, *Tinodon*, *Zhangheotherium*, *Dryolestes*, *Amphitherium*, *Peramus*, *Vincelestes*, *Kielantherium*, *Deltatheridium*, *Asiatherium*, *Didelphis*, *Kokopellia*, *Pucadelphys*, *Pappotherium*, *Prokennalestes*, *Montanalestes*, *Asioryctes*, *Erinaceus*;

(1) Present (along more than half of the crown length): *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Obdurodon* (Archer et al. 1993), *Gobiconodon*;

(?) Not preserved: *Adelobasileus*, *Bishops*, *Steropodon*, *Teinolophos*, *Henkelotherium* (not exposed), *Aegialodon*; not applicable: *Probainognathus*, tritylodontids, tritheledontids, *Ornithorhynchus*.

33. Lower premolars lingual cingulid:

(0) Absent or vestigial: tritylodontids (coded from anterior postcanines), tritheledontids, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Kuehneotherium*, *Gobiconodon*, *Amphilestes*, *Jeholodens*, *Priacodon*, *Trioracodon*, *Haramiyavia*, “plagiaulacidans”, cimolodontans, *Tinodon*, *Zhangheotherium*, *Peramus*, *Henkelotherium*, *Vincelestes*, *Kielantherium*, *Deltatheridium*, *Asiatherium*, *Didelphis*, *Kokopellia*, *Pucadelphys*, *Pappotherium*, *Erinaceus*, *Prokennalestes*, *Asioryctes*;

(1) Present: *Haldanodon*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Obdurodon* (Archer et al. 1993), *Dryolestes*, *Amphitherium*, *Montanalestes*;

(?) Premolar not preserved: *Adelobasileus*, *Steropodon*, *Teinolophos*, *Aegialodon*; not applicable: *Probainognathus*, *Hadrocodium*, *Ornithorhynchus*.

34. Relative height of the primary cusp a to c of the ultimate lower premolar (measured as the height ratio of a and c from the bottom of the valley between the two adjacent cusps):

(0) Posterior cusp c is indistinctive: *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Kuehneotherium*, *Shuotherium*, *Tinodon*, *Zhangheotherium*, *Dryolestes*, *Peramus*, *Henkelo-*

therium, Amphitherium, Vincelestes, Kielantherium, Pappotherium, Erinaceus, Asioryctes, Montanalestes, Prokennalestes;

(1) Posterior cusp c is distinctive but less than 30% of primary cusp a: *Ambondro, Ausktribosphenos, Bishops, Gobiconodon* (~25%), *Amphilestes, Jeholodens* (~27%), *Deltatheridium, Asiatherium, Kokopellia, Pucadelphys, Didelphis*;

(2) Posterior cusp c and primary cusp a are equal or subequal in height (c is 40–100% of a): *Priacodon, Trioracodon*;

(?) Not preserved: *Adelobasileus, Steropodon, Teinolophos, Aegialodon*; Not applicable: *Probainognathus*, tritylodontids, tritheledontids, *Obdurodon* (Archer et al. 1993), *Ornithorhynchus, Haramiyavia*, “plagiaulacidans”, cimolodontans.

35. Ultimate upper premolar—functional protocone (character applicable to mammals with reversed triangulation of molar cusps):

(0) Absent: *Kuehneotherium, Zhangheotherium, Peramus, Dryolestes, Henkelotherium, Vincelestes, Deltatheridium, Asiatherium, Didelphis, Pucadelphys*;

(1) Present: *Erinaceus, Asioryctes, Prokennalestes*;

(?) Not preserved: *Adelobasileus, Shuotherium, Ambondro, Ausktribosphenos, Bishops, Steropodon, Teinolophos, Amphitherium, Kielantherium, Kokopellia, Pappotherium, Aegialodon, Montanalestes*; not applicable: *Probainognathus*, tritylodontids, tritheledontids, *Sinoconodon, Megazostrodon, Morganucodon, Dinnetherium, Haldanodon, Hadrocodium, Obdurodon, Ornithorhynchus, Gobiconodon, Amphilestes, Priacodon, Trioracodon, Jeholodens, Haramiyavia*, “plagiaulacidans”, cimolodontans, *Aegialodon*.

36. The penultimate lower premolar—anterior cusp b (= paraconid):

(0) Vestigial (much smaller than cusp c of the same tooth) to absent: *Sinoconodon, Shuotherium, Obdurodon* (Archer et al. 1993), *Gobiconodon, Amphilestes, Priacodon, Trioracodon, Jeholodens, Tinodon, Zhangheotherium, Amphitherium, Dryolestes, Henkelotherium, Peramus, Vincelestes, Kielantherium, Deltatheridium, Asiatherium, Didelphis, Kokopellia, Pucadelphys, Prokennalestes, Montanalestes, Asioryctes, Erinaceus*;

(1) Distinctive: *Morganucodon, Megazostrodon, Dinnetherium, Haldanodon, Ausktribosphenos, Bishops*;

(2) Multicusped row(s): tritylodontids (assuming some of the postcanines are homologous to premolars), *Haramiyavia*, “plagiaulacidans”, cimolodontans;

(?) Not preserved: *Adelobasileus, Kuehneotherium* (indeterminate from isolated premolars), *Ambondro, Steropodon, Teinolophos, Aegialodon, Pappotherium*; not applicable: *Probainognathus*, tritheledontids, *Hadrocodium* (tooth absent), *Ornithorhynchus*.

37. Penultimate lower premolar—arrangement of principal cusp a, cusp b (if present), and cusp c (we assume the cusp to be c if there is only one cusp behind the main cusp a):

(0) Cusps in straight alignment (for tooth with a single cusp, the anterior and posterior crests from the main cusp are in alignment): *Sinoconodon, Megazostrodon, Morganucodon, Dinnetherium, Haldanodon, Shuotherium, Obdurodon* (Archer et al. 1993), *Gobiconodon, Amphilestes, Priacodon, Trioracodon, Jeholodens, Tinodon, Zhangheotherium, Amphitherium, Dryolestes, Henkelotherium, Peramus, Vincelestes, Kielantherium, Deltatheridium, Asiatherium, Didelphis, Kokopellia, Pucadelphys, Prokennalestes, Montanalestes, Asioryctes, Erinaceus*;

(1) Cusps in triangulation: *Ausktribosphenos, Bishops*;

(2) Premolar with multiple cusps in longitudinal row(s): tritylodontids (assuming morphology of anterior postcanines), *Haramiyavia*, “plagiaulacidans”;

(?) Not preserved: *Adelobasileus, Kuehneotherium* (indeterminate from isolated premolars), *Ambondro, Steropodon, Teinolophos, Aegialodon, Pappotherium*; not applicable: *Probainognathus*, tritheledontids, *Hadrocodium, Ornithorhynchus*, cimolodontans (reduced, and peg-like p3).

Molar morphology (55 characters)

38. Alignment of main cusps of the posterior lower molar(s) (m3 or more posterior if present) {Note: this character differs from character 39 based on the following justification. In *Tinodon* (Crompton and Jenkins 1967) the cusps on m1 are hardly triangulated but the posterior molar cusps are distinctively triangulated. There clearly is a gradient of increasing triangulation of molar cusps in the obtuse-angle symmetrodont *Gobiotheriodon* from Mongolia (Averianov in press); Parrington (1978: 202) noted that cusps of some anterior molars of *Kuehneotherium* are linear, but posterior lower molars cusps are triangulated; therefore molar cusp triangulation may not be applicable to all lower molars in the same taxon, especially among “obtuse-angle” symmetrodonts. Here we split these characters between m1

{character 39} and more posterior molars (m3 or more posterior, character 38) to reflect this gradient of triangulation; coding these separately may influence the placement of the taxa with the gradient}:

(0) Single longitudinal row: *Probainognathus*, tritheledontids (on undifferentiated postcanines), *Sinoconodon, Morganucodon, Megazostrodon, Dinnetherium, Haldanodon, Hadrocodium, Amphilestes, Gobiconodon* (Kielan-Jaworowska and Dashzev 1998 show that *Gobiconodon* lacks a triangulate pattern on m3), *Jeholodens, Priacodon, Trioracodon*;

(1) Obtuse angle ($\geq 95^\circ$): *Kuehneotherium, Tinodon*;

(2) Acute angle ($\leq 90^\circ$): *Shuotherium, Ambondro, Ausktribosphenos, Bishops, Steropodon, Teinolophos, Obdurodon* (Archer et al. 1993), *Zhangheotherium, Amphitherium, Peramus, Dryolestes, Henkelotherium, Vincelestes, Aegialodon, Kielantherium, Deltatheridium, Asiatherium, Didelphis, Kokopellia, Pucadelphys, Pappotherium, Erinaceus, Asioryctes, Prokennalestes, Montanalestes*;

(3) Multiple longitudinal multicuspate rows: tritylodontids, *Haramiyavia*, “plagiaulacidans”, cimolodontans;

(?) Not preserved: *Adelobasileus*; not applicable: *Ornithorhynchus*.

39. Alignment of main cusps of the anterior lower molar (m1) (see justification on character 38 and the note below):

(0) Single longitudinal row: *Probainognathus*, tritheledontids (on undifferentiated postcanines), *Adelobasileus, Sinoconodon, Morganucodon, Megazostrodon, Dinnetherium, Haldanodon, Hadrocodium, Gobiconodon, Amphilestes, Jeholodens, Priacodon, Trioracodon, Kuehneotherium* (the anterior molars with linear alignment, see Parrington 1971, Parrington 1978: 202), *Tinodon* (anterior molars with straight alignment, see Crompton and Jenkins 1967);

(1) Acute angle: *Shuotherium, Ambondro, Ausktribosphenos, Bishops, Steropodon, Teinolophos, Obdurodon* (Archer et al. 1993), *Zhangheotherium, Peramus, Dryolestes, Henkelotherium, Amphitherium, Vincelestes, Aegialodon, Kielantherium, Deltatheridium, Asiatherium, Didelphis, Kokopellia, Pucadelphys, Pappotherium, Erinaceus, Asioryctes, Montanalestes, Prokennalestes*;

(2) Multiple longitudinal rows: tritylodontids, *Haramiyavia*, “plagiaulacidans”, cimolodontans;

(?) Not applicable: *Ornithorhynchus*.

Note: an alternative treatment would be to combine characters 38 and 39, and to code *Kuehneotherium, Tinodon* and other obtuse-angle symmetrodonts as polymorphic (little triangulated anterior molar versus triangulated posterior molars) for the combined character; but this would be less preferable because it would result in the loss of systematic information that may help to resolve the highly heterogeneous “obtuse-angle symmetrodonts”. The combined character from 38 and 39 would have to be run as ordered in algorithms.

40. Postvallum/prevallid shearing (angle of the main trigonoid shear facets):

(0) Absent: *Morganucodon, Megazostrodon, Dinnetherium, Haldanodon, Hadrocodium, Gobiconodon, Amphilestes, Jeholodens, Priacodon, Trioracodon*;

(1) Present, weakly developed, slightly oblique: *Kuehneotherium, Tinodon, Shuotherium, Dryolestes, Henkelotherium, Vincelestes, Amphitherium, Aegialodon, Kielantherium*;

(2) Present, strongly developed, and more transverse: *Ambondro, Ausktribosphenos, Bishops, Steropodon, Teinolophos, Obdurodon* (Archer et al. 1993), *Zhangheotherium, Peramus, Deltatheridium, Asiatherium, Didelphis, Kokopellia, Pucadelphys, Pappotherium, Erinaceus, Asioryctes, Montanalestes, Prokennalestes*;

(?) Not preserved: *Adelobasileus*; not applicable: *Probainognathus*, tritylodontids, tritheledontids, *Sinoconodon, Haramiyavia*, “plagiaulacidans”, cimolodontans; homology uncertain: *Ornithorhynchus*.

41. Development of postprotocrista on the upper molar for double rank postvallum shear (applicable to molars with reversed triangulation of molar cusps) (from Cifelli 1993b):

(0) Postprotocrista is short and does not extend labially beyond metacone: *Kuehneotherium, Shuotherium, Zhangheotherium, Peramus, Dryolestes, Henkelotherium, Vincelestes, Kielantherium, Pappotherium, Deltatheridium*;

(1) Postprotocrista is long and extends labially beyond metacone: *Asiatherium, Didelphis, Kokopellia, Pucadelphys, Erinaceus, Asioryctes, Prokennalestes*;

(?) Not preserved: *Ambondro, Ausktribosphenos, Bishops, Steropodon, Teinolophos, Amphitherium, Aegialodon, Montanalestes*; not applicable: *Probainognathus*, tritylodontids, tritheledontids, *Adelobasileus, Sinoconodon, Megazostrodon, Morganucodon, Dinnetherium, Haldanodon, Hadrocodium, Obdurodon, Ornithorhynchus, Haramiyavia*, “plagiaulacidans”, cimolodontans, *Gobiconodon, Amphilestes, Jeholodens, Priacodon, Trioracodon, Dryolestes*.

42. Precise opposition of the upper and lower molars (either one-to-one, or occluding at the opposing embrasure or talonid):

(0) Absence of precise opposition of upper and lower molars: *Probainognathus*, tritheledontids, *Sinoconodon*;

(1) Present (either one-to-one, or occluding at the opposing embrasure or talonid): *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon* (Archer et al. 1993), *Ornithorhynchus*, *Gobiconodon*, *Amphilestes*, *Jeholodens*, *Priacodon*, *Triaracodon*, *Tinodon*, *Zhangheotherium*, *Peramus*, *Dryolestes*, *Henkelotherium*, *Amphitherium*, *Vincelestes*, *Aegialodon* (based on the inference of Crompton 1971), *Kielantherium*, *Deltatheridium*, *Asiatherium*, *Didelphis*, *Kokopellia*, *Pucadelphys*, *Pappotherium*, *Erinaceus*, *Prokennalestes*, *Montanalestes*, *Asioryctes*;

(2) Present: one lower molar sequentially contacts more than one upper molars: tritylodontids, *Haramiyavia* (following interpretation of Butler 2000), “plagiaulacidans”, cimolodontans.

(?) Not preserved: *Adelobasileus*.

43. Relationships between the cusps of the opposing upper and lower molars:

(0) Absent: *Probainognathus*, tritheledontids, *Sinoconodon*;

(1) Present, lower primary cusp a occludes in the groove between upper cusps A, B: *Morganucodon*, *Dinnetherium*, *Haldanodon*, *Amphilestes*, *Jeholodens*, *Priacodon*, *Triaracodon*;

(2) Present, lower main cusp a occludes in front of upper cusp B and into the embrasure between the opposing and preceding upper teeth: *Megazostrodon*, *Hadrocodium*, *Kuehneotherium*, *Gobiconodon*, *Amphilestes*, *Tinodon*, *Zhangheotherium*;

(3) Present, parts of the talonid occluding with the lingual face (or any part) of the upper molar: *Ausktribosphenos*, *Ambondro*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon* (Archer et al. 1993), *Peramus*, *Dryolestes*, *Henkelotherium*, *Amphitherium*, *Vincelestes*, *Aegialodon* (based on the inference of Crompton 1971), *Kielantherium*, *Deltatheridium*, *Asiatherium*, *Didelphis*, *Kokopellia*, *Pucadelphys*, *Pappotherium*, *Erinaceus*, *Prokennalestes*, *Montanalestes*, *Asioryctes*;

(4) Lower multicuspate rows alternately occlude between the upper multicuspate rows: tritylodontids, *Haramiyavia*, “plagiaulacidans”, cimolodontans;

(?) Not preserved: *Adelobasileus*; not applicable: *Shuotherium* (Note: *Shuotherium* has only cuspule d posterior to the trigonid; occlusion of the anterior pseudo-talonid to the upper molar is not homologous to tribosphenic therians; see relevant coding of *Shuotherium*'s mesial and anterior occlusal feature in character 55. In a far less justifiable alternative, *Shuotherium* could be coded 3 for this feature); uncertain occlusal relationships (of deciduous teeth): *Ornithorhynchus*.

44. Relative height of the primary cusp a (protoconid) to cusp c (metaconid) of the anterior lower molars (measured as the height ratio of a and c from the bottom of the valley between the two adjacent cusps, on m1):

(0) Posterior cusp c is less than 40% of the primary cusp a (protoconid): *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Hadrocodium*, *Kuehneotherium*, *Tinodon*, *Shuotherium*, *Gobiconodon* (~25%), *Amphilestes*, *Jeholodens* (~27%), *Zhangheotherium*, *Peramus*, *Amphitherium*, *Vincelestes*, *Kielantherium*, *Kokopellia*, *Prokennalestes*, *Montanalestes*, *Asioryctes*, *Erinaceus*;

(1) Posterior cusp c and primary cusp a are equal or subequal in height (c is 50–100% of a): *Priacodon*, *Triaracodon*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon* (Archer et al. 1993), *Dryolestes*, *Henkelotherium*, *Pappotherium*, *Deltatheridium*, *Asiatherium*, *Didelphis*, *Pucadelphys*;

(?) Not applicable: *Probainognathus*, tritylodontids, tritheledontids, *Haldanodon*, *Haramiyavia*, “plagiaulacidans”, cimolodontans, *Ornithorhynchus*. Incomplete: *Adelobasileus*, *Aegialodon*.

45. Relative size/height of the anterior cusp b (paraconid) to posterior cusp c (metaconid) (based on m2):

(0) c taller than b: *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Hadrocodium*, *Ausktribosphenos*, *Bishops*, *Dryolestes*, *Henkelotherium*, *Amphitherium*, *Pappotherium*, *Pucadelphys*, *Prokennalestes*, *Asioryctes*, *Erinaceus*;

(1) b taller than c: *Dinnetherium*, *Haldanodon*, *Kuehneotherium*, *Peramus*, *Vincelestes*, *Kielantherium*, *Deltatheridium*, *Didelphis*;

(2) b and c are more or less equal in height: *Tinodon*, *Shuotherium*, *Steropodon*, *Teinolophos*, *Obdurodon* (Archer et al. 1993), *Gobiconodon*, *Amphilestes*, *Jeholodens*, *Priacodon*, *Triaracodon*, *Zhangheotherium*, *Asiatherium*, *Kokopellia*, *Montanalestes*.

(?) Incomplete: *Adelobasileus*, *Ambondro* (cusps b and c are not complete, thus this character is coded ?), *Aegialodon*; not applicable: *Probainognathus*, tritylodontids, tritheledontids, *Haramiyavia*, “plagiaulacidans”, cimolodontans, *Ornithorhynchus*.

46. Elevation of the cingulid base of paraconid (cusp b) relative to the cingulid base of metaconid (cusp c) on the lower molars:

(0) Absent: *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Kuehneotherium*, *Shuotherium*, *Gobiconodon*, *Amphilestes*, *Jeholodens*, *Priacodon*, *Triaracodon*, *Tinodon*, *Zhangheotherium*, *Dryolestes*, *Henkelotherium*, *Amphitherium*, *Vincelestes*, *Peramus*, *Kielantherium*, *Aegialodon*, *Deltatheridium*, *Asiatherium*, *Didelphis*, *Pucadelphys*, *Kokopellia*, *Pappotherium*, *Erinaceus*, *Asioryctes*, *Montanalestes*; *Prokennalestes*;

(1) Present: *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Ornithorhynchus* (based on deciduous teeth);

(?) Not preserved: *Adelobasileus*, not applicable: *Probainognathus*, tritylodontids, tritheledontids, *Haramiyavia*, “plagiaulacidans”, cimolodontans.

47. The cristid obliqua (*sensu* Fox 1975: defined as the oblique crest anterior to, and connected with, a labialmost cusp on the talonid heel, the leading edge of facet 3): presence *versus* absence and orientation (applicable only to the molar with at least a hypoconid on the talonid or a distal cingulid cuspule):

(0) Absent: *Kuehneotherium*, *Shuotherium*, *Tinodon*, *Zhangheotherium*, *Dryolestes*, *Henkelotherium*, *Vincelestes* (Rougier 1993; Sigogneau-Russell 1999);

(1) Present, and oriented lingual of the metaconid-protoconid notch: *Amphitherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Pappotherium*, *Prokennalestes*, *Montanalestes*, *Asioryctes*;

(2) Present, hypertrophied, and directed to posterior (distal) part of metaconid: *Steropodon*, *Teinolophos*, *Obdurodon* (Archer et al. 1993);

(3) Present, short and pointed anteriorly between the metaconid-protoconid notch and the protoconid (labial of the notch): *Ambondro*, *Ausktribosphenos*, *Bishops*, *Asiatherium*, *Didelphis*, *Kokopellia* (pointed directly at the notch), *Pucadelphys*, *Erinaceus*;

(?) Not applicable: *Probainognathus*, tritylodontids, tritheledontids, *Adelobasileus*, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Ornithorhynchus*, *Gobiconodon*, *Amphilestes*, *Jeholodens*, *Priacodon*, *Triaracodon*, *Haramiyavia*, “plagiaulacidans”, cimolodontans.

48. Lower molar—medial and longitudinal crest (= “pre-entocristid” or “pre-hypoconulid”) on the talonid heel (only applicable to taxa with talonid or at least cusp d):

(0) Talonid (or cusp d) lacks medial and longitudinal crest: *Kuehneotherium*, *Shuotherium*, *Tinodon*, *Zhangheotherium*, *Dryolestes*, *Henkelotherium*, *Amphitherium*, *Vincelestes*, *Peramus*;

(1) Medialmost cristid (“pre-entoconid cristid”) of talonid in alignment with the metaconid or with the postmetacristid if the latter is present (the postmetacristid defined as the posterior crest of metaconid that is parallel to the lingual border of the crown), but widely separated from the latter: *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Asiatherium*, *Didelphis*, *Kokopellia*, *Pucadelphys*, *Pappotherium*, *Erinaceus*, *Prokennalestes*, *Montanalestes*, *Asioryctes*;

(2) Medialmost cristid of talonid (“prehypoconulid”) cristid, based on cusp designation of Kielan-Jaworowska et al. 1987) is hypertrophied and in alignment with the postmetacristid and abuts the latter by a V-shaped notch: *Steropodon*, *Teinolophos*, *Obdurodon* (Archer et al. 1993);

(3) “Pre-entocristid” crest is offset from the metaconid (and postmetacristid if present), and the “pre-entocristid” extends anterolingually past the base of the metaconid: *Ambondro* (best developed on m2, Flynn et al. 1999: fig. 3c), *Ausktribosphenos* (we designate the medialmost of the three cristids in its talonid basin as the pre-entocristid, other internal ridges are considered to be wear features, as proposed by 1997; 1999), *Bishops*;

(?) Not preserved: *Adelobasileus*; not applicable: *Probainognathus*, tritylodontids, tritheledontids, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Gobiconodon*, *Amphilestes*, *Jeholodens*, *Priacodon*, *Triaracodon*, *Ornithorhynchus* (the area for “prehypoconulid” is heavily crenulated, but *Ornithorhynchus* may also be coded as state {2}), *Haramiyavia*, “plagiaulacidans”, cimolodontans.

49. Labial curvature of the primary cusp a of lower molars (at the base level) relative to the curvature of cusps b and c:

(0) Cusp a and cusps b, c have the same degree of bulging: *Adelobasileus*, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Gobiconodon*, *Amphilestes*, *Jeholodens*, *Priacodon*, *Triaracodon*;

(1) Cusp a is far more bulging than cusps b, c (“bulging” of Mills 1971; “tri-angulation” of cusps on posterior molars of Kielan-Jaworowska and Dashzeveg 1998): *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon* (Archer et al. 1993), *Tinodon*, *Zhangheotherium*, *Vincelestes*, *Dryolestes*, *Henkelotherium*, *Amphitherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Asiatherium*, *Didelphis*, *Kokopellia*, *Pucadelphys*, *Pappotherium*, *Erinaceus*, *Prokennalestes*, *Montanalestes*, *Asioryctes*;

(?) Not applicable: *Probainognathus*, tritylodontids, tritheledontids, *Ornithorhynchus*, *Haramiyavia*, “plagiaulacidans”, cimolodontans.

50. Labial curvature of the main cusps A, B, C at the level of the cusp valley of the penultimate and ultimate upper molars (see Mills 1971: 53; Kielan-Jaworowska and Dashzeveg 1998):

(0) Cusps A, B, and C have about the same degree of curvature: *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Jeholodens*, *Priacodon*, *Triaracodon*;

(1) Cusp A is slightly concave (or far less convex than either cusp B or cusp C): *Kuehneotherium*, *Shuotherium*, *Gobiconodon*, *Tinodon* (based on *Eurylambda*), *Zhangheotherium*, *Dryolestes*, *Henkelotherium*, *Amphitherium*, *Vincelestes*, *Peramus*, *Kielantherium*, *Deltatheridium*, *Asiatherium*, *Didelphis*, *Kokopellia*, *Pucadelphys*, *Pappotherium*, *Erinaceus*, *Prokennalestes*, *Montanalestes*, *Asioryctes*;

(?) Not applicable: *Probainognathus*, tritylodontids, tritheledontids, *Obdurodon* (Archer et al. 1993), *Ornithorhynchus*, *Haramiyavia*, “plagiaulacidans”, cimolodontans; not preserved: *Adelobasileus*, *Amphilestes*, *Ambondro*, *Ausktribosphenos*, *Steropodon*, *Teinolophos*, *Aegialodon*.

51. Labiolingual compression of the primary functional cusps of the lower molars (at the level of the cusp base but above the cingulid):

(0) Absent: *Probainognathus*, tritylodontids, tritheledontids, *Adelobasileus*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Ornithorhynchus*, *Haramiyavia*, “plagiaulacidans”, cimolodontans, *Peramus*, *Dryolestes*, *Henkelotherium*, *Amphitherium*, *Peramus*, *Vincelestes*, *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Asiatherium*, *Didelphis*, *Kokopellia*, *Pucadelphys*, *Pappotherium*, *Erinaceus*, *Asioryctes*, *Prokennalestes*, *Montanalestes*;

(1) Present: *Sinoconodon*, *Megazostrodon*, *Morganucodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Gobiconodon*, *Amphilestes*, *Jeholodens*, *Priacodon*, *Triaracodon*.

52. Posterior lingual cingulid of the lower molars:

(0) Absent or weak: *Probainognathus*, tritylodontids, tritheledontids, *Sinoconodon*, *Adelobasileus*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon* (Archer et al. 1993), *Jeholodens*, *Haramiyavia*, “plagiaulacidans”, cimolodontans, *Peramus*, *Dryolestes*, *Henkelotherium*, *Amphitherium*, *Vincelestes*, *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Asiatherium*, *Didelphis*, *Kokopellia*, *Pucadelphys*, *Pappotherium*, *Erinaceus*, *Prokennalestes*, *Montanalestes*, *Asioryctes*;

(1) Distinctive: *Kuehneotherium*, *Shuotherium*, *Gobiconodon*, *Amphilestes*, *Priacodon*, *Triaracodon*, *Tinodon*, *Zhangheotherium*;

(2) Strongly developed, crenulated with distinctive cusplines (such as the kuehnecone): *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Haldanodon* (assuming the homology of cusp g of *Haldanodon* to the kuehnecone of *Morganucodon*, Krusat 1980; this cuspline is labelled as “c” by Butler 1997);

(?) Not exposed: *Hadrocodium*; not applicable: *Ornithorhynchus*.

53. Anterior internal (mesiolingual) cingular cuspline (e) on the lower molars:

(0) Present: *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Kuehneotherium*, *Shuotherium* (we consider one of the cusplines on the rim of the pseudotalonid to be homologous to cuspline e), *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon* (Archer et al. 1993), *Gobiconodon*, *Amphilestes*, *Tinodon*, *Zhangheotherium*, *Peramus*, *Aegialodon*;

(1) Absent: *Jeholodens*, *Priacodon*, *Dryolestes*, *Henkelotherium*, *Amphitherium*, *Vincelestes*, *Asiatherium*, *Didelphis*, *Kokopellia*, *Pucadelphys*, *Pappotherium*, *Erinaceus*, *Asioryctes*, *Prokennalestes*, *Montanalestes*;

(0/1) *Sinoconodon* (this feature is variable in the molars of *Sinoconodon*, see Zhang et al. 1998, therefore coded polymorphic), *Kielantherium* (absent on m1 {state 1}, present on m2–3 {state 0}), *Deltatheridium*, *Triaracodon* (the feature is variable in this taxon);

(?) Not applicable: *Probainognathus*, tritylodontids, tritheledontids, *Adelobasileus*, *Ornithorhynchus*, *Haramiyavia*, “plagiaulacidans”, cimolodontans.

54. Anterior and labial (mesiolabial) cingular cuspline (f):

(0) Absent: *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Haldanodon*, *Hadrocodium*, *Jeholodens*, *Priacodon*, *Triaracodon*, *Zhangheotherium*, *Dryolestes*, *Vincelestes*;

(1) Present: *Dinnetherium*, *Kuehneotherium*, *Tinodon*, *Shuotherium* (we assume that the single cusp in *Shuotherium kermacki* Sigogneau-Russell 1998 is homologous to the anterior labial cingulid cuspline f, whereas one of the two cusps in the “pseudo-talonid” of *Shuotherium dongi* is homologous to cuspline f), *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Gobiconodon*, *Amphilestes*, *Amphitherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Asiatherium*, *Didelphis* (*Didelphis* may have a series of minute and individualized cusplines, but no continuous mesial cingulid), *Kokopellia*, *Pucadelphys*, *Pappotherium*, *Prokennalestes*, *Montanalestes*, *Asioryctes*, *Erinaceus* (*Erinaceus* has a very reduced cuspline on the discontinuous mesial cingulid);

(?) Not preserved: *Adelobasileus*, *Henkelotherium* (not exposed); not applicable (homology uncertain): *Probainognathus*, tritylodontids, tritheledontids, *Ornithorhynchus*, *Haramiyavia*, “plagiaulacidans”, cimolodontans.

55. Mesial transverse cingulid above the gum:

(0) Absent: *Probainognathus*, tritylodontids, tritheledontids, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Hadrocodium*, *Kuehneotherium*, *Gobiconodon*, *Amphilestes*, *Triaracodon*, *Jeholodens*, *Priacodon*, *Triaracodon*, *Haramiyavia*, “plagiaulacidans”, cimolodontans, *Tinodon*, *Zhangheotherium*, *Peramus*, *Dryolestes*, *Henkelotherium*, *Amphitherium*, *Vincelestes*;

(1) Present below the trigonid but weak and discontinuous (as individual cusplines e, or f, or both, but e and f are not connected): *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Asiatherium*, *Didelphis*, *Kokopellia*, *Pucadelphys*, *Pappotherium*, *Erinaceus*, *Asioryctes*, *Prokennalestes*, *Montanalestes*;

(2) Present in a continuous shelf below the trigonid (with no relations to protoconid and paraconid), and without occlusal function: *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon* (Archer et al. 1993), *Ornithorhynchus* (coded from the deciduous premolars, Simpson 1929b);

(3) Cingular area present, and has occlusal contact with the upper molar: *Shuotherium* (we assume the homology of the “pseudo-talonid” of *Shuotherium* to the mesial transverse cingulids of other mammals); *Haldanodon* (we note that *Haldanodon* is similar to *Shuotherium* in possessing an anterior shelf area with occlusal contact to the upper molar, but *Haldanodon* differs from *Shuotherium* in that the former’s shelf is connected to cusp b (paraconid), see Butler 1997 and references cited therein).

(?) Not preserved: *Adelobasileus*.

56. Cingulid shelf wrapping around the anterointernal corner of the molar to extend to the lingual side of the trigonid below the paraconid:

(0) Absent: *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Hadrocodium*, *Kuehneotherium*, *Gobiconodon*, *Triaracodon*, *Jeholodens*, *Priacodon*, *Amphilestes*, *Tinodon*, *Zhangheotherium*, *Peramus*, *Dryolestes*, *Henkelotherium*, *Amphitherium*, *Vincelestes*, *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Asiatherium*, *Didelphis*, *Kokopellia*, *Pucadelphys*, *Pappotherium*, *Erinaceus*, *Asioryctes*, *Prokennalestes*, *Montanalestes*;

(1) Present, weakly developed, and its lingual part without occlusal function to upper molars: *Steropodon*, *Teinolophos*, *Obdurodon* (Archer et al. 1993);

(2) Present, strongly developed, and its lingual part without occlusal function to upper molars: *Ambondro*, *Ausktribosphenos*, *Bishops*;

(3) Present, weakly developed, and with occlusal function to the upper molar: *Haldanodon*, *Shuotherium*;

(?) Not preserved: *Adelobasileus*; not applicable: *Probainognathus*, tritylodontids, tritheledontids, *Ornithorhynchus*, *Haramiyavia*, “plagiaulacidans”, cimolodontans.

57. Postcingulid (distal transverse cingulid) on the lower molars:

(0) Absent: *Probainognathus*, tritylodontids, tritheledontids, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Kuehneotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Gobiconodon* (confirmed on all three known species), *Amphilestes*, *Priacodon*, *Triaracodon*, *Jeholodens*, *Haramiyavia*, “plagiaulacidans”, cimolodontans, *Tinodon*, *Zhangheotherium*, *Peramus*, *Dryolestes*, *Henkelotherium*, *Amphitherium*, *Vincelestes*, *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Pappotherium*, *Erinaceus*, *Prokennalestes*, *Montanalestes*, *Asioryctes*;

(1) Present, oblique, and connected to hypoconulid: *Asiatherium*, *Didelphis*, *Kokopellia*, *Pucadelphys*;

(2) Present, horizontal above the gum level: *Shuotherium* (assuming the positional homology of the distal “cingulid” of this taxon to the postcingulid

of other therians), *Steropodon*, *Teinolophos*, *Obdurodon* (Archer et al. 1993), *Ornithorhynchus* (based on deciduous p2, Simpson 1929b);

(?) Not preserved: *Adelobasileus*.

58. Interlocking mechanism between two adjacent lower molars:

(0) Absent: *Probainognathus*, tritylodontids, tritheledontids, *Sinoconodon*, *Haldanodon*, *Hadrocodium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon* (Archer et al. 1993), *Ornithorhynchus*, *Haramiyavia*, “plagiaulacidans”, cimolodontans, *Zhangheotherium*, *Dryolestes*, *Henkelotherium*, *Vincelestes*;

(1) Present, posterior cingular cuspule d (or the base of the hypoconulid) of the preceding molar fits in between cingular cuspules e and f of the succeeding molar: *Dinnetherium*, *Kuehneotherium*, *Gobiconodon*, *Amphilestes*, *Tinodon*, *Peramus*, *Kielantherium*; or the base of the hypoconulid interlocks with a concave area between the irregular mesial cingulid cuspules in front of the paraconid: *Amphitherium*, *Deltatheridium* (present in some molars), *Asiatherium*, *Didelphis*, *Kokopellia*, *Pucadelphys*, *Aegialodon*, *Pappotherium*, *Erinaceus*, *Asioryctes*, *Prokennalestes*, *Montanalestes*;

(2) Present, posterior cingular cuspule d fits between cingular cuspule e and cusp b of the succeeding molar: *Morganucodon*, *Megazostrodon*;

(3) Present, posterior cingular cuspule d of the preceding molar fits into an embayment or vertical groove of the anterior aspect of cusp b the succeeding molar (without any involvement of distinctive cingular cuspules in interlocking): *Jeholodens*, *Priacodon*, *Trioracodon*;

(?) Not preserved: *Adelobasileus*.

59. Size ratio of the posterior lower molars:

(0) Last three postcanines forming a series of posteriorly decreasing size: penultimate molar is larger than the ultimate molar but smaller than the preceding molar (for a total of 5 molars: $m_3 \geq m_4 \geq m_5$; for a total of 4 molars: $m_2 \geq m_3 \geq m_4$, or for a total of 3 molars, $m_1 \geq m_2 \geq m_3$): *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Kuehneotherium*, *Shuotherium*, *Ausktribosphenos*, *Steropodon*, *Obdurodon*, *Haramiyavia* ($m_1 > m_2 > m_3$), “plagiaulacidans” ($m_1 > m_2$), cimolodontans ($m_1 > m_2$), *Gobiconodon*, *Amphilestes* ($m_3 \geq m_4 > m_5$), *Tinodon* ($m_2 > m_3 > m_4$), *Zhangheotherium*, *Peramus*, *Dryolestes* ($m_5 > m_6 > m_7$), *Henkelotherium*, *Amphitherium*, *Vincelestes*, *Kielantherium*, *Erinaceus*;

(1) Penultimate molar is the largest of molars ($m_1 \leq m_2 \leq m_3 > m_4$): *Sinoconodon*, *Bishops*, *Jeholodens* (based on the assessment that the erupting m_4 is small, and needs to be confirmed with future discovery of adult specimens), *Priacodon*, *Trioracodon*, *Deltatheridium*, *Didelphis* ($m_1 \leq m_2 \leq m_3 = m_4$), *Asiatherium*, *Kokopellia*, *Pucadelphys*.

(2) Ultimate molar the largest: *Prokennalestes*, *Montanalestes*, *Asioryctes*;

(?) Not preserved: *Adelobasileus*, *Ambondro* (incomplete preservation), *Aegialodon*, *Pappotherium*; not applicable: *Probainognathus*, tritylodontids, tritheledontids, *Teinolophos*, *Ornithorhynchus*.

60. Trigonid configuration on lower molars:

(0) Paraconid in anterolingual position and the paraconid-protoconid line forming an oblique angle to longitudinal axis of the tooth: *Kuehneotherium*, *Amphitherium*, *Peramus*, *Vincelestes*, *Kokopellia*, *Pucadelphys*, *Pappotherium*, *Asioryctes*, *Prokennalestes*, *Montanalestes*;

(1) Paraconid lingually positioned and the paraconid-protoconid line forming a more transverse triangle to the longitudinal axis of the tooth: *Shuotherium*, *Ambondro*, *Tinodon*, *Zhangheotherium*, *Dryolestes*, *Henkelotherium*, *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Asiatherium*, *Didelphis*, *Erinaceus*;

(2) Paraconid lingually positioned and appressed to the metaconid (“twinned”): *Ausktribosphenos*, *Bishops*, *Steropodon*, *Obdurodon* (Archer et al. 1993), *Teinolophos*, *Ornithorhynchus* (based the deciduous teeth described by Simpson 1929b);

(?) Not preserved: *Adelobasileus*; not applicable: *Probainognathus*, tritylodontids, tritheledontids, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Gobiconodon*, *Amphilestes*, *Jeholodens*, *Priacodon*, *Trioracodon*, *Haramiyavia*, “plagiaulacidans”, cimolodontans.

61. Orientation of the paracristid (crest between cusps a and b) relative to the longitudinal axis of the molars (from Hu et al. 1998). (This is separated from character 60 because of different distribution of the a–b crest among mammals with non-triangulated molars):

(0) Longitudinal orientation: tritheledontids, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Gobiconodon*, *Amphilestes*, *Jeholodens*, *Priacodon*, *Trioracodon*;

(1) Oblique: *Kuehneotherium*, *Tinodon*, *Shuotherium*, *Ambondro*, *Zhangheotherium*, *Peramus*, *Dryolestes*, *Henkelotherium*, *Amphitherium*, *Vincelestes*, *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Asiatherium*, *Didelphis*, *Kokopellia*, *Pucadelphys*, *Pappotherium*, *Erinaceus*, *Asioryctes*, *Prokennalestes*, *Montanalestes*;

(2) Nearly transverse: *Ausktribosphenos*, *Bishops*, *Steropodon*, *Obdurodon*, *Teinolophos*, *Ornithorhynchus* (coded from deciduous molars);

(?) Not applicable: *Probainognathus*, tritylodontids, *Haramiyavia*, “plagiaulacidans”, cimolodontans; not preserved: *Adelobasileus*.

62. Mesiolingual surface of paraconid on lower molars (applicable only to taxa with triangulation of molar cusps):

(0) Rounded: *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon* (the peculiar crest on the mesial face of the paraconid in *Obdurodon* connects to the precingulid and is assumed to be different from character state 1), *Ornithorhynchus*, *Tinodon*, *Zhangheotherium*, *Amphitherium*, *Dryolestes*, *Henkelotherium*, *Vincelestes*, *Kielantherium*, *Aegialodon*, *Deltatheridium*, *Pappotherium*, *Erinaceus*, *Asioryctes*, *Prokennalestes*, *Montanalestes*;

(1) Forming a keel: *Asiatherium*, *Didelphis*, *Kokopellia*, *Pucadelphys*;

(0/1) Polymorphic: *Peramus*;

(?) Not preserved: *Adelobasileus*; not applicable: *Probainognathus*, tritylodontids, tritheledontids, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Gobiconodon*, *Amphilestes*, *Jeholodens*, *Priacodon*, *Trioracodon*, *Haramiyavia*, “plagiaulacidans”, cimolodontans.

63. Molar (m_2) trigonid/talonid width ratio:

(0) Narrow (talonid $\leq 40\%$ of trigonid): *Kuehneotherium*, *Shuotherium*, *Tinodon*, *Zhangheotherium*, *Peramus*, *Dryolestes*, *Henkelotherium*, *Amphitherium*, *Vincelestes*, *Aegialodon*, *Kielantherium*;

(1) Wide (talonid is 40–70% of the trigonid in width): *Deltatheridium*, *Pappotherium*, *Asioryctes*, *Prokennalestes*, *Montanalestes*;

(2) Talonid is equal or wider than trigonid: *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon* (Archer et al. 1993), *Ornithorhynchus*, *Erinaceus*, *Asiatherium*, *Didelphis*, *Kokopellia*, *Pucadelphys*;

(?) Not applicable: *Probainognathus*, tritylodontids, tritheledontids, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Gobiconodon*, *Amphilestes*, *Jeholodens*, *Priacodon*, *Trioracodon*, *Ornithorhynchus*, *Haramiyavia*, “plagiaulacidans”, cimolodontans.

64. Lower molar hypoflexid (the labial embayment between trigonid part and the talonid or the posterior heel located between the protoconid and hypoconid above the cingulid level):

(0) Absent or shallow: *Kuehneotherium*, *Shuotherium*, *Tinodon*, *Zhangheotherium*, *Dryolestes*, *Amphitherium*, *Peramus*, *Vincelestes*;

(1) Deep (but less than 50% of the talonid width): *Aegialodon*, *Kielantherium*, *Ausktribosphenos*, *Bishops*, *Deltatheridium*, *Asiatherium*, *Didelphis*, *Kokopellia*, *Pucadelphys*, *Pappotherium*, *Erinaceus*, *Prokennalestes*, *Montanalestes*, *Asioryctes*;

(2) Very deep ($\geq 60\%$ of the width of the talonid): *Ambondro*, *Steropodon*, *Teinolophos*, *Obdurodon* (Archer et al. 1993), *Ornithorhynchus* (based on deciduous premolars described by Simpson 1929b);

(?) Not applicable: *Probainognathus*, tritylodontids, tritheledontids, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Gobiconodon*, *Amphilestes*, *Jeholodens*, *Priacodon*, *Trioracodon*, *Haramiyavia*, “plagiaulacidans”, cimolodontans; not exposed: *Henkelotherium*.

65. Morphology of the talonid (or posterior heel) of the molars:

(0) Absent: *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Gobiconodon*, *Amphilestes*, *Jeholodens*, *Priacodon*, *Trioracodon*;

(1) Present as an incipient heel or a cingulid, or cingular cuspule (d): *Kuehneotherium* (*sensu* Kermack et al. 1968), *Shuotherium* (this taxon retains a vestigial cingulid shelf posterior to the trigonid, which is positionally identical to the true talonid), *Tinodon*, *Zhangheotherium*;

(2) Present as a heel (with at least one functional cusp): *Dryolestes*, *Henkelotherium* (a large talonid heel but no basin), *Amphitherium*, *Vincelestes*, *Peramus*;

(3) Present as a transverse “V-shaped” basin with two functional cusps: *Steropodon*, *Teinolophos*, *Obdurodon* (Kermack et al. 1968), *Ornithorhynchus* (coded on the deciduous teeth, Simpson 1929b);

(4) Present as a functional basin, rimmed with 3 functional cusps (if the entoconid is vestigial, there is a functional crest to define the medial rim of the basin): *Ausktribosphenos*, *Bishops*, *Ambondro*, *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Asiatherium*, *Didelphis*, *Kokopellia*, *Pucadelphys*, *Pappotherium*, *Prokennalestes*, *Montanalestes*, *Asioryctes*, *Erinaceus*;

(?) Not preserved: *Adelobasileus*; not applicable: *Probainognathus*, tritylodontids, tritheledontids, *Haramiyavia*, “plagiaulacidans”, cimolodontans.

66. Hypoconulid (revised from Luo, Cifelli, and Kielan-Jaworowska 2001; we designate the distal cingulid cuspule d as the homolog to the hypoconulid in the teeth with linear alignment of main cusps; we assume

that the cusp to be the hypoconulid if there is only a single cusp on the talonid in the teeth with reversed triangulation):

(0) Present, but not elevated above the cingulid level: *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Gobiconodon*, *Amphilestes*, *Jeholodens*, *Priacodon*, *Trioracodon*, *Kuehneotherium*, *Tinodon*, *Zhangheotherium*;

(1) Present, elevated above the cingulid level, labially positioned: *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon* (Archer et al. 1993), *Ornithorhynchus*, *Amphitherium*, *Peramus*, *Vincelestes* (see Rougier 1993; Sigogneau-Russell 1999: fig. 7), *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Asiatherium*, *Didelphis*, *Kokopellia*, *Pucadelphys*, *Pappotherium*, *Prokennalestes*, *Montanalestes*, *Asioryctes*, *Erinaceus*;

(2) Present and larger, with occlusal contact to the upper molar (elevated above the cingulid level, lingually positioned): *Dryolestes*, *Henkelotherium*;

(?) Not preserved: *Adelobasileus*; not applicable: *Probainognathus*, tritylodontids, tritheledontids, *Haramiyavia*, "plagiaulacidans", cimolodontans.

67. Hypoconulid (= distal cusplule d, after Crompton 1971):

(0) Absent: *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Kuehneotherium*, *Shuotherium*, *Gobiconodon*, *Amphilestes*, *Jeholodens*, *Priacodon*, *Trioracodon*, *Tinodon*, *Zhangheotherium*, *Dryolestes*, *Henkelotherium*, *Amphitherium*, *Vincelestes*;

(1) Present, posterior, median and equal distant to entoconid and hypoconid: *Ambondro*, *Peramus*, *Aegialodon*, *Kielantherium*, *Deltatheridium* (median), *Kokopellia*, *Pappotherium*, *Prokennalestes*, *Montanalestes*, *Asioryctes*, *Erinaceus*;

(2) Present and placed on the lingual rim of the talonid basin: *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos* (assuming the homology by Kielan-Jaworowska et al. 1987), *Obdurodon* (Archer et al. 1993), *Ornithorhynchus* (coded on the deciduous teeth), *Asiatherium*, *Didelphis* (hypoconulid closer to entoconid than to hypoconid), *Pucadelphys*;

(?) Not preserved: *Adelobasileus*; not applicable: *Probainognathus*, tritylodontids, tritheledontids, *Haramiyavia*, "plagiaulacidans", cimolodontans.

68. Hypoconulid anteroposterior orientation: procumbent versus reclined (applicable to taxa with at least two cusps on the talonid):

(0) Cusp tip reclined and posterior wall of hypoconulid is slanted and overhanging the root: *Peramus*, *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Asiatherium*, *Didelphis*, *Kokopellia*, *Pucadelphys*, *Pappotherium*, *Prokennalestes*, *Montanalestes*, *Asioryctes*;

(1) Cusp tip procumbent and the posterior wall of the cusp is vertical: *Steropodon*, *Teinolophos* (assuming the homology by Kielan-Jaworowska et al. 1987), *Obdurodon* (Archer et al. 1993), *Ornithorhynchus* (coded on the deciduous teeth), *Erinaceus*;

(2) Cusp tip procumbent and the posterior wall is gibbous: *Ambondro*, *Ausktribosphenos*, *Bishops*,

(?) Not applicable: *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Kuehneotherium*, *Shuotherium*, *Gobiconodon*, *Amphilestes*, *Jeholodens*, *Priacodon*, *Trioracodon*, *Tinodon*, *Zhangheotherium*, *Dryolestes*, *Henkelotherium*, *Amphitherium*, *Vincelestes*, *Probainognathus*, tritylodontids, tritheledontids, *Haramiyavia*, "plagiaulacidans", cimolodontans; not preserved: *Adelobasileus*.

69. Hypoconulid labial postcingulid (shelf) on lower molars (non-homologous with postcingulid of character 57 because of different relationship to talonid cusps; applicable to taxa with identifiable hypoconid and hypoconulid only) (Cifelli 1993b):

(0) Absent: *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Ornithorhynchus*, *Peramus*, *Kielantherium*, *Aegialodon*, *Deltatheridium*, *Pappotherium*, *Erinaceus*, *Asioryctes*, *Prokennalestes*, *Montanalestes*;

(1) Present as a crest descending mesiolabially from apex of hypoconulid to base of hypoconid: *Asiatherium*, *Didelphis* (weak), *Kokopellia*, *Pucadelphys*;

(?) Not preserved: *Adelobasileus*; not applicable: *Probainognathus*, tritylodontids, tritheledontids, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Kuehneotherium*, *Shuotherium*, *Gobiconodon*, *Amphilestes*, *Jeholodens*, *Priacodon*, *Trioracodon*, *Haramiyavia*, "plagiaulacidans", cimolodontans, *Tinodon*, *Zhangheotherium*, *Amphitherium*, *Dryolestes*, *Henkelotherium*, *Vincelestes*.

70. Morphology of entoconid:

(0) Absent: *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Kuehneotherium*, *Shuotherium*, *Steropodon* (*sensu* Kielan-Jaworowska et al. 1987), *Teinolophos* (assuming the homology of Kielan-Jaworowska et al. 1987), *Obdurodon* (Archer et al. 1993), *Gobiconodon*, *Amphilestes*, *Jeholodens*, *Priacodon*, *Trioracodon*, *Tinodon*,

Zhangheotherium, *Peramus*, *Vincelestes*, *Dryolestes*, *Henkelotherium*, *Amphitherium*;

(1) Present: *Ambondro*, *Aegialodon*, *Asiatherium*, *Kokopellia*, *Pappotherium*, *Erinaceus*, *Prokennalestes*, *Montanalestes*, *Asioryctes*;

(2) Present and twinned with hypoconulid: *Ausktribosphenos*, *Bishops*, *Pucadelphys*, *Didelphis*;

(0/1 polymorphic): *Deltatheridium*, *Kielantherium* (character variable);

(?) Not preserved: *Adelobasileus*; not applicable: *Probainognathus*, tritylodontids, tritheledontids, *Ornithorhynchus*, *Haramiyavia*, "plagiaulacidans", cimolodontans.

71. Height of the entoconid as compared to other cusps of the talonid (character after Rougier et al. 1998) (applicable only to the taxa with triangulated molar cusps and a talonid or cusp d):

(0) Absent on the talonid: *Kuehneotherium*, *Shuotherium*, *Steropodon* (*sensu* Kielan-Jaworowska et al. 1987), *Teinolophos*, *Obdurodon*, *Tinodon*, *Zhangheotherium*, *Dryolestes*, *Peramus*, *Henkelotherium*, *Amphitherium*, *Vincelestes*;

(1) Lower than the hypoconulid (or even vestigial): *Ambondro*, *Aegialodon*;

(2) Subequal height as the hypoconulid: *Ausktribosphenos*, *Bishops*, *Asiatherium*, *Didelphis*, *Kokopellia*, *Pucadelphys*, *Pappotherium*, *Erinaceus*, *Prokennalestes*, *Montanalestes*, *Asioryctes*;

(0/1 polymorphic): *Deltatheridium*, *Kielantherium* (feature variable, but vestigial at best);

(?) Not preserved: *Adelobasileus*; not applicable: *Probainognathus*, tritylodontids, tritheledontids, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Ornithorhynchus*, *Gobiconodon*, *Amphilestes*, *Jeholodens*, *Priacodon*, *Trioracodon*, *Haramiyavia*, "plagiaulacidans", cimolodontans.

72. Alignment of the paraconid, metaconid, and entoconid on lower molars (applicable only to taxa with triangulation of trigonid cusps and entoconid present on talonid) (Clemens 1979a):

(0) Cusps not aligned: *Deltatheridium*, *Aegialodon*, *Kielantherium*, *Pappotherium*, *Asioryctes*, *Prokennalestes*, *Montanalestes*, *Erinaceus*;

(1) Cusps aligned: *Ambondro*, *Ausktribosphenos*, *Bishops*, *Asiatherium*, *Didelphis*, *Kokopellia*, *Pucadelphys*;

(?) Not preserved: *Adelobasileus*; not applicable: *Probainognathus*, tritylodontids, tritheledontids, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Kuehneotherium*, *Shuotherium*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Ornithorhynchus*, *Gobiconodon*, *Amphilestes*, *Jeholodens*, *Priacodon*, *Trioracodon*, *Haramiyavia*, "plagiaulacidans", cimolodontans, *Tinodon*, *Zhangheotherium*, *Peramus*, *Amphitherium*, *Dryolestes*, *Henkelotherium*, *Vincelestes*.

73. Aspect ratio in occlusal view (length versus width) of the functional talonid basin at the cingulid level (based on m2):

(0) Longer than wide (or narrows posteriorly): *Peramus*, *Vincelestes*, *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Kokopellia*, *Pappotherium*, *Prokennalestes*, *Montanalestes*, *Asioryctes*;

(1) Length equals width: *Ambondro*, *Asiatherium*, *Didelphis*, *Pucadelphys*, *Erinaceus*;

(2) Wider than long: *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Ornithorhynchus* (based on deciduous p2 as described by Simpson 1929b; and illustrated by Woodburne and Tedford 1975);

(?) Not preserved: *Adelobasileus*; not applicable: *Probainognathus*, tritylodontids, tritheledontids, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Kuehneotherium*, *Gobiconodon*, *Amphilestes*, *Jeholodens*, *Priacodon*, *Trioracodon*, *Shuotherium*, *Haramiyavia*, "plagiaulacidans", cimolodontans, *Tinodon*, *Zhangheotherium*; *Dryolestes*, *Henkelotherium*, *Amphitherium*.

74. Elevation of the talonid (measured as the height of hypoconid from the cingulid on the labial side of the crown) relative to the trigonid (measured as the height of protoconid from the cingulid) (applicable only to the teeth with reversed triangle):

(0) Hypoconulid/protoconid height ratio less than 20% (hypoconulid or cusp d is on the cingulid): *Kuehneotherium*, *Shuotherium*, *Tinodon*, *Zhangheotherium*;

(1) Hypoconulid/protoconid height ratio between 25% and 35% (talonid cusp elevated above the cingulid level): *Dryolestes* (~33%), *Henkelotherium* (~25%), *Peramus* (~25%), *Vincelestes* (35–40%), *Amphitherium* (~30%); *Kielantherium* (~37%), *Deltatheridium* (37%);

(2) Hypoconulid/protoconid height ratio between 40% and 50%: *Aegialodon* (~40%), *Pappotherium* (49%);

(3) Hypoconulid/protoconid height ratio between 50% and 60%: *Ambondro* (estimated ~57%), *Asiatherium*, *Didelphis* (~59%), *Kokopellia*, *Pucadel-*

phys, *Erinaceus* (56%), *Asioryctes* (~55%), *Prokennalestes* (average 57%), *Montanalestes* (~53%), *Teinolophos*;

(4) Hypoconid/protoconid height ratio between 60% and 70%: *Ausktribosphenos* (~61%) *Bishops* (~62%), *Steropodon* (67%), *Obdurodon* (~65%), *Ornithorhynchus* (subequal height);

(?) Not applicable: *Probainognathus*, tritylodontids, tritheledontids, *Adelobasileus*, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Gobiconodon*, *Amphilestes*, *Jeholodens*, *Priacodon*, *Triaracodon*, *Haramiyavia*, “plagiaulacidans”, cimolodontans.

75. Width of upper molar stylar shelf (the area labial to the paracone-metacone) (Prothero 1980; as modified by Hu et al. 1997, 1998):

(0) Absent: *Probainognathus*, tritheledontids, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Gobiconodon*, *Amphilestes*, *Jeholodens*, *Priacodon*, *Triaracodon*;

(1) Present and narrow: *Kuehneotherium*, *Tinodon* (based on *Eurylambda*), *Dryolestes*, *Henkelotherium*, *Amphitherium*;

(2) Present and broad: *Shuotherium*, *Obdurodon*, *Ornithorhynchus* (coded from deciduous teeth), *Zhangheotherium*, *Vincelestes*, *Asiatherium*, *Erinaceus*;

(3) Present, broad, and with a hypertrophied ectoflexus: *Peramus*, *Deltatheridium*, *Didelphis*, *Kokopellia*, *Pucadelphys*, *Pappotherium*, *Asioryctes*, *Prokennalestes*;

(?) Unknown: *Adelobasileus*, *Ausktribosphenos*, *Bishops*, *Ambondro*, *Steropodon*, *Teinolophos*, *Aegialodon*, *Kielantherium*, *Montanalestes*; not applicable: tritylodontids, *Haramiyavia*, “plagiaulacidans”, cimolodontans.

76. Morphology of labial cingulum of the upper molars:

(0) Absent or weak: *Probainognathus*, tritylodontids, *Sinoconodon*, *Hadrocodium*, *Haramiyavia*, “plagiaulacidans”, cimolodontans, *Dryolestes*, *Henkelotherium*;

(1) Distinctive cingulum, straight: *Haldanodon*, *Gobiconodon*, *Priacodon*, *Triaracodon*, *Kuehneotherium*, *Tinodon*, *Obdurodon* (Archer et al. 1993), *Ornithorhynchus* (deciduous teeth), *Zhangheotherium*, *Vincelestes*, *Peramus*, *Amphitherium*, *Asiatherium* (with slight ectoflexus), *Erinaceus*,

(2) Distinctive cingulum with strong ectoflexus (but without hypertrophied stylar cusps): *Shuotherium*, *Deltatheridium*, *Kokopellia*, *Asioryctes*;

(3) Wide cingulum with ectoflexus, plus individualized and hypertrophied stylar cusps: *Didelphis*, *Pappotherium*, *Prokennalestes*, *Pucadelphys*;

(4) Cingulum crenulated with distinctive and even-sized multiple cusps: tritheledontids, *Morganucodon*, *Megazostrodon*, *Dinnetherium*;

(0/1 polymorphic) *Jeholodens*;

(?) Not preserved: *Adelobasileus*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Amphilestes*, *Kielantherium*, *Aegialodon*, *Montanalestes*.

77. Upper molars with a functional lingual protocone or pseudoprotocone that grinds against a basin on the lowers:

(0) Absent: *Probainognathus*, tritylodontids, tritheledontids, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Hadrocodium*, *Kuehneotherium*, *Gobiconodon*, *Jeholodens*, *Priacodon*, *Triaracodon*, *Haramiyavia*, “plagiaulacidans”, cimolodontans, *Tinodon*, *Zhangheotherium*, *Dryolestes*, *Henkelotherium*, *Amphitherium*, *Peramus*, *Vincelestes* (has a lingual enlargement of the upper molar, but no functional cusp to fit into the any lower molar basin, Bonaparte and Rougier 1987; Rougier 1993);

(1) Present: *Haldanodon* (MCL of Kermack et al. 1987; cusp X of Krusat 1973, 1980; Butler 1997), *Shuotherium* (“pseudoprotocone” of Wang et al. 1998; Sigogneau-Russell 1998), *Deltatheridium*, *Asiatherium*, *Didelphis*, *Kokopellia*, *Pucadelphys*, *Pappotherium*, *Erinaceus*, *Asioryctes*, *Prokennalestes*;

(?) Not preserved: *Adelobasileus*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Amphilestes*, *Aegialodon*, *Kielantherium*, *Montanalestes*; uncertain: *Teinolophos*, *Obdurodon*, *Ornithorhynchus*.

78. Transverse width of the protocone on upper molars (applicable only to taxa with protocone present; M2 measured where possible):

(0) Narrow (distance from protocone apex to paracone apex less than 0.60 of total tooth width): *Pappotherium* (0.50), *Deltatheridium* (0.51), *Asiatherium*, *Kokopellia* (0.48), *Didelphis* (0.52), *Pucadelphys* (0.52);

(1) Strongly transverse (distance from protocone apex to paracone apex greater than 0.60 of total tooth width): *Prokennalestes* (0.62), *Asioryctes* (0.62), *Erinaceus* (0.67);

(?) Not preserved: *Adelobasileus*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Amphitherium*, *Kielantherium*, *Aegialodon*, *Montanalestes*; not applicable: *Probainognathus*, tritylodontids, tritheledontids, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Haldanodon* (Cusp MCL of K.A. Kermack et al. 1987 or Cusp x of Butler 1997 is a functional analogue to the protocone, but its shape and con-

necting crests are different, so that there is uncertainty in how to apply this character to *Haldanodon*), *Hadrocodium*, *Kuehneotherium*, *Shuotherium* (the pseudoprotocone is a functional analogue to the protocone, so that there is uncertainty in how to apply this character to *Shuotherium*), *Ornithorhynchus*, *Gobiconodon*, *Amphilestes*, *Jeholodens*, *Priacodon*, *Triaracodon*, *Haramiyavia*, “plagiaulacidans”, cimolodontans, *Tinodon*, *Zhangheotherium*, *Peramus*, *Dryolestes*, *Henkelotherium*, *Vincelestes*.

79. Anteroposterior development of the lingual region on the upper molars (applicable only to taxa with triangulation of molar cusps and an occluding lingual portion of the upper molar; for the taxa with conules, this is measured between the paracone and metacone; for those taxa without conules, this is measured as the length of the tooth labial to the base of paracone; M2 measured where possible):

(0) Narrow (anteroposterior distance medial to the paracone and metacone less than 0.30 of total tooth length): *Peramus*, *Vincelestes*, (distance between position of conules less than 0.30): *Deltatheridium* (0.29), *Pappotherium* (0.29);

(1) Moderate development (distance between position of conules = 0.31–0.50 of total tooth length): *Kokopellia* (0.50), *Asioryctes* (0.44), *Prokennalestes* (0.46);

(2) Long (distance between conules greater than 0.51 of total tooth length): *Asiatherium*, *Pucadelphys* (0.59), *Didelphis* (0.55), *Erinaceus* (lophate crown);

(?) Not preserved: *Adelobasileus*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Amphitherium*, *Kielantherium*, *Aegialodon*, *Montanalestes*; not applicable: *Probainognathus*, tritylodontids, tritheledontids, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Haldanodon* (The lingual portion of *shuotheriids* is a functional analogue to the protocone; so there is uncertainty in how to apply this character to *Shuotherium*), *Hadrocodium*, *Kuehneotherium*, *Shuotherium* (The lingual portion of docodont upper molar has different shape and connecting crests; so there is uncertainty in how to apply this character to *Shuotherium*), *Ornithorhynchus*, *Gobiconodon*, *Amphilestes*, *Jeholodens*, *Priacodon*, *Triaracodon*, *Haramiyavia*, “plagiaulacidans”, cimolodontans, *Tinodon* (this feature could not be measured in *Eurylambda*), *Zhangheotherium*, *Amphitherium*, *Dryolestes*, *Henkelotherium*.

80. Conules on the upper molars (character applicable to mammals with triangulation of molar cusps and a functional lingual cusp) (character after Rougier et al. 1998; also see discussion by Clemens and Lillegraven 1986; Cifelli 1993b):

(0) Absent: *Kuehneotherium*, *Shuotherium*, *Tinodon* (based on *Eurylambda*), *Zhangheotherium*, *Peramus*, *Dryolestes*, *Henkelotherium*, *Amphitherium*, *Vincelestes*, *Didelphis*;

(1) Present but weak and without cristae: *Deltatheridium*, *Pappotherium*, *Prokennalestes*;

(2) Conules distinctive, with cristae: *Asiatherium*, *Kokopellia*, *Pucadelphys*, *Erinaceus*, *Asioryctes*;

(?) Not preserved: *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Kielantherium*, *Aegialodon*, *Montanalestes*; not applicable: *Probainognathus*, tritylodontids, tritheledontids, *Adelobasileus*, *Sinoconodon*, *Megazostrodon*, *Morganucodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Obdurodon*, *Ornithorhynchus*, *Gobiconodon*, *Amphilestes*, *Jeholodens*, *Priacodon*, *Triaracodon*, *Haramiyavia*, “plagiaulacidans”, cimolodontans.

81. Relative height and size of the paracone (cusp B) and metacone of the upper molars (character after Rougier et al. 1998); also see discussion by Clemens and Lillegraven (1986) and Cifelli (1993a):

(0) Paracone higher and larger than metacone: *Kuehneotherium*, *Shuotherium*, *Tinodon*, *Zhangheotherium*, *Dryolestes*, *Henkelotherium*, *Amphitherium*, *Peramus*, *Vincelestes*, *Deltatheridium*, *Kokopellia*, *Pappotherium*, *Erinaceus*, *Asioryctes*, *Prokennalestes*,

(1) Metacone is higher and larger than paracone: *Asiatherium*, *Pucadelphys*, *Didelphis*;

(?) Not preserved: *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Amphilestes*, *Kielantherium*, *Aegialodon*, *Montanalestes*; not applicable: *Probainognathus*, tritylodontids, tritheledontids, *Adelobasileus*, *Sinoconodon*, *Megazostrodon*, *Morganucodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Obdurodon*, *Ornithorhynchus*, *Gobiconodon*, *Jeholodens*, *Priacodon*, *Triaracodon*, *Haramiyavia*, “plagiaulacidans”, cimolodontans.

82. Centrocrista between the paracone and metacone of upper molars (applicable only to taxa with well-developed metacone and distinctive wear facets 3 and 4):

(0) Straight: *Shuotherium*, *Peramus*, *Deltatheridium*, *Pappotherium*, *Erinaceus*, *Asioryctes*, *Prokennalestes*, *Kokopellia*;

(1) V-shaped, with labially directed postparacrista and premetacrista: *Asiatherium*, *Didelphis*, *Pucadelphys*;

(?) Not preserved: *Adelobasileus*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Amphitherium*, *Kielantherium*, *Aegialodon*, *Montanalestes*; not applicable: *Probainognathus*, tritylodontids, tritheledontids, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Kuehneotherium*, *Ornithorhynchus*, *Gobiconodon*, *Amphilestes*, *Jeholodens*, *Priacodon*, *Triaracodon*, *Haramiyavia*, “plagiaulacidans”, cimolodontans, *Tinodon*, *Zhangheotherium*, *Dryolestes*, *Henkelotherium*, *Vincelestes*.

83. Upper molars cuspule E (an enlarged version of E would be the metastyle, after Crompton 1971):

(0) Present: *Probainognathus*, trithledontids, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Kuehneotherium*, *Shuotherium*, *Gobiconodon*, *Jeholodens*, *Tinodon*, *Zhangheotherium*, *Dryolestes*, *Henkelotherium*, *Amphitherium*, *Peramus*, *Vincelestes*, *Deltatheridium*, *Asiatherium*, *Kokopellia*, *Pucadelphys*, *Didelphis*, *Erinaceus*, *Asioryctes*, *Prokennalestes*, *Pappotherium*;

(1) Absent: tritylodontids, *Priacodon*, *Triaracodon*, *Haramiyavia*, “plagiaulacidans”, cimolodontans;

(?) Not preserved: *Adelobasileus*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Amphilestes*, *Aegialodon*, *Kielantherium*, *Montanalestes*; not applicable: *Obdurodon*, *Ornithorhynchus*.

84. Upper molars interlock:

(0) Absent: *Probainognathus*, tritylodontids, trithledontids, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Kuehneotherium*, *Shuotherium*, *Obdurodon*, *Ornithorhynchus*, *Gobiconodon*, *Jeholodens*, *Haramiyavia*, “plagiaulacidans”, cimolodontans, *Tinodon* (based on *Eurylambda*) *Zhangheotherium*, *Dryolestes*, *Henkelotherium*, *Amphitherium*, *Peramus*, *Vincelestes*, *Deltatheridium*, *Asiatherium*, *Didelphis*, *Kokopellia*, *Pucadelphys*, *Pappotherium*, *Erinaceus*, *Asioryctes*, *Prokennalestes*;

(1) Tongue-in-groove interlock: *Priacodon*, *Triaracodon*;

(?) Not preserved: *Adelobasileus*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Amphilestes*, *Kielantherium*, *Aegialodon*, *Montanalestes*.

85. M1—number of cusps within the main functional straight cusp row (if there are multiple rows, the labial row is designated):

(0) Three main functioning cusps (or fewer) within a row: tritheledontids, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Gobiconodon*, *Amphilestes*, *Jeholodens*, *Priacodon*, *Triaracodon*;

(1) Four main functioning cusps or more: *Haramiyavia*, “plagiaulacidans”, cimolodontans;

(0/1 polymorphic) tritylodontids;

(?) Not preserved: *Adelobasileus*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Amphilestes*; not applicable (main cusps are not differentiated): *Probainognathus* (main cusps not aligned in row); *Kuehneotherium*, *Shuotherium*, *Obdurodon*, *Ornithorhynchus*, *Tinodon* (= *Eurylambda*) *Zhangheotherium*, *Peramus*, *Henkelotherium*, *Dryolestes*, *Vincelestes*, *Amphitherium*, *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Asiatherium*, *Kokopellia*, *Pucadelphys*, *Didelphis*, *Pappotherium*, *Erinaceus*, *Montanalestes*, *Prokennalestes*, *Asioryctes*.

86. Multi-cuspsate m1—number of cusps within the main functional straight multi-cusp row (if there are multiple rows, the labial row is designated):

(0) Three main functioning cusps (or fewer) within a row: tritheledontids, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Gobiconodon*, *Amphilestes*, *Jeholodens*, *Priacodon*, *Triaracodon*;

(1) Four main functioning cusps or more: *Haramiyavia*, “plagiaulacidans”, cimolodontans;

(0/1 polymorphic): tritylodontids (four cusps in a row {1} for *Oligokyphus*, Kühne 1956; Sues 1985; Luo and Sun 1993); three or fewer {0} for other derived tritylodontids);

(?) Not preserved: *Adelobasileus*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*; not applicable (main cusps are not differentiated): *Probainognathus*; (main cusps not aligned in multiple rows): *Kuehneotherium*, *Shuotherium*, *Obdurodon*, *Ornithorhynchus*, *Tinodon*, *Zhangheotherium*, *Vincelestes*, *Peramus*, *Dryolestes*, *Henkelotherium*, *Amphitherium*, *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Kokopellia*, *Pucadelphys*, *Didelphis*, *Pappotherium*, *Erinaceus*, *Montanalestes*, *Prokennalestes*, *Asioryctes*.

87. Outline of m1:

(0) Oval-shaped: *Probainognathus*, tritheledontids, *Adelobasileus*;

(1) Laterally compressed: *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Hadrocodium*, *Gobiconodon*, *Amphilestes*, *Jeholodens*, *Priacodon*, *Triaracodon*;

(2) Oblong with slight labial bulge: *Kuehneotherium*, *Tinodon* (see Crompton and Jenkins 1967);

(3) Oblong with a strong labial bulge: *Shuotherium*, *Ambondro*, *Vincelestes*, *Peramus*, *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Asiatherium*, *Kokopellia*, *Pucadelphys*, *Didelphis*, *Pappotherium*, *Montanalestes*, *Prokennalestes*, *Asioryctes*;

(4) Triangular or tear-drop shaped: *Zhangheotherium*, *Dryolestes*, *Henkelotherium* (near triangular), *Amphitherium*;

(5) Rectangular (or slightly rhomboidal): tritylodontids, *Haldanodon*, *Steropodon*, *Ausktribosphenos* (anterior part rhomboidal), *Bishops* (anterior part rhomboidal), *Teinolophos*, *Obdurodon*, *Ornithorhynchus*, *Haramiyavia*, “plagiaulacidans”, cimolodontans, *Erinaceus*.

88. Aspect ratio of M1:

(0) Laterally compressed: *Adelobasileus*, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Hadrocodium*, *Gobiconodon*, *Amphilestes*, *Jeholodens*, *Priacodon*, *Triaracodon*;

(1) Longer than transversely wide (oval-shaped or spindle shaped): *Probainognathus*, tritheledontids, *Kuehneotherium*, *Tinodon*, *Amphitherium*, *Peramus*, *Vincelestes*;

(2) Transversely wider than long (triangular outline): *Shuotherium* (the single upper molar from China has almost equal length to the width, Wang et al. 1998; *Shuotherium* upper molar from Bathonian of England is wider than long, Sigogneau-Russell 1998), *Zhangheotherium*, *Dryolestes*, *Henkelotherium*, *Deltatheridium*, *Asiatherium*, *Kokopellia*, *Pucadelphys*, *Didelphis*, *Pappotherium*, *Erinaceus*, *Asioryctes*, *Prokennalestes*;

(3) Transversely wide (dumbbell shaped): *Haldanodon*;

(4) Rectangular or nearly so: tritylodontids, *Obdurodon*, *Ornithorhynchus*, *Haramiyavia*, “plagiaulacidans”, cimolodontans;

(?) Not preserved: *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Aegialodon*, *Kielantherium*, *Montanalestes*.

89. Multi-cuspsate row in the upper molars: cusp height gradient within the individual longitudinal rows of cusps:

(0) Cusps in a row with more or less equal height: cimolodontans;

(1) Distal cusp highest, with a gradient of anteriorly decreasing height: *Haramiyavia*, “plagiaulacidans”;

(0/1 polymorphic): tritylodontids.

(?) Not preserved: *Adelobasileus*, *Kuehneotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Aegialodon*, *Kielantherium*; not applicable: *Probainognathus*, tritheledontids, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Shuotherium*, *Obdurodon*, *Ornithorhynchus*, *Gobiconodon*, *Amphilestes*, *Jeholodens*, *Priacodon*, *Triaracodon*, *Tinodon* (*Eurylambda*), *Zhangheotherium*, *Peramus*, *Dryolestes*, *Henkelotherium*, *Amphitherium*, *Vincelestes*, *Deltatheridium*, *Asiatherium*, *Kokopellia*, *Pucadelphys*, *Didelphis*, *Pappotherium*, *Erinaceus*, *Asioryctes*, *Prokennalestes*, *Montanalestes*.

90. Lower molars with multicuspsate rows—U-shaped ridge:

(0) U-shaped ridge (anterior crest) absent at the mesial end of lower molar with open valley-basin between longitudinal cusp rows: tritylodontids, cimolodontans;

(1) Presence of the U-shaped ridge (anterior crest) at mesial end of lower molar enclosing the valley-basin between longitudinal cusp rows: *Haramiyavia*, “plagiaulacidans”;

(?) Not applicable: *Probainognathus*, tritheledontids, *Adelobasileus*, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Kuehneotherium*, *Gobiconodon*, *Amphilestes*, *Jeholodens*, *Priacodon*, *Triaracodon*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Ornithorhynchus*, *Tinodon*, *Zhangheotherium*, *Peramus*, *Dryolestes*, *Henkelotherium*, *Amphitherium*, *Vincelestes*, *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Asiatherium*, *Kokopellia*, *Pucadelphys*, *Didelphis*, *Pappotherium*, *Erinaceus*, *Asioryctes*, *Prokennalestes*, *Montanalestes*.

91. Multicuspsate M2 with longitudinal multicuspsate rows—lingual offset with M1:

(0) Upper M2 lingually offset from M1 so that the lower m2 lingual row occludes the lingual side of the M2 upper labial row: tritylodontids (assuming the morphology of an undifferentiated postcanine), *Haramiyavia*;

(1) m2 labial row occludes to the labial side of the M2 labial row: “plagiaulacidans”, cimolodontans;

(?) Not preserved: *Adelobasileus*; not applicable: *Probainognathus*, tritheledontids, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Kuehneotherium*, *Gobiconodon*, *Amphilestes*, *Jeholodens*, *Priacodon*, *Trioracodon*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Ornithorhynchus*, *Tinodon*, *Zhangheotherium*, *Peramus*, *Dryolestes*, *Henkelotherium*, *Amphitherium*, *Vincelestes*, *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Asiatherium*, *Kokopellia*, *Pucadelphys*, *Didelphis*, *Pappotherium*, *Erinaceus*, *Asioryctes*, *Prokennalestes*, *Montanalestes*.

92. Multicusped lower molars: cusp height ratio within the labial longitudinal row:

(0) The first cusp (b1 by the designation of Butler 2000) is the highest so that the labial cusp row forms a series of decreasing height posteriorly: tritylodontids, cimolodontans;

(1) The second cusp (b2 by the designation of Jenkins et al. 1997; Butler 2000) is the highest: *Haramiyavia*, “plagiaulacidans”;

(?) Not preserved: *Adelobasileus*; not applicable: *Probainognathus*, tritheledontids, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Kuehneotherium*, *Gobiconodon*, *Amphilestes*, *Jeholodens*, *Priacodon*, *Trioracodon*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Ornithorhynchus*, *Tinodon*, *Zhangheotherium*, *Peramus*, *Dryolestes*, *Henkelotherium*, *Amphitherium*, *Vincelestes*, *Deltatheridium*, *Asiatherium*, *Kokopellia*, *Pucadelphys*, *Didelphis*, *Pappotherium*, *Erinaceus*, *Erinaceus*, *Asioryctes*, *Prokennalestes*, *Montanalestes*.

Molars wear pattern (12 characters)

93. Functional development of occlusal facets on individual molar cusps:

(0) Absent for lifetime: *Probainognathus*, tritheledontids, *Sinoconodon*;

(1) Absent at eruption but developed later by wearing of the crown: *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Kuehneotherium*, *Tinodon*, *Gobiconodon*, *Amphilestes*, *Jeholodens*, *Priacodon*, *Trioracodon*;

(2) Wear facets matches upon the eruption of teeth (inferred from the flat contact surface upon eruption): tritylodontids, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon* (Archer et al. 1993), *Haramiyavia*, “plagiaulacidans”, cimolodontans, *Zhangheotherium*, *Peramus*, *Dryolestes*, *Henkelotherium*, *Amphitherium*, *Vincelestes*, *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Asiatherium*, *Kokopellia*, *Pucadelphys*, *Didelphis*, *Pappotherium*, *Erinaceus*, *Prokennalestes*, *Montanalestes*, *Asioryctes*;

(?) Not preserved: *Adelobasileus*; not applicable: *Ornithorhynchus* (uncertain for juvenile teeth, not applicable to adult teeth).

94. Topographic relationship of wear facets to the main cusps:

(0) Wear facet absent or a simple longitudinal facet that extends the entire length of the crown: *Probainognathus*, tritheledontids, *Sinoconodon*;

(1) Lower cusps a, c support two different wear facets (facets 1 and 4) that contact the upper primary cusp A: *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Jeholodens*, *Priacodon*, *Trioracodon*;

(2) Lower cusps a, c support a single wear facet (4) that contacts the upper primary cusp B (this facet extends onto cusp A as wear continues, but facets 1 and 4 do not develop simultaneously in these taxa): *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon* (Archer et al. 1993), *Gobiconodon* (Kielan-Jaworowska and Dashzeveg 1998), *Amphilestes*, *Tinodon*, *Zhangheotherium*, *Peramus*, *Dryolestes*, *Henkelotherium*, *Amphitherium*, *Vincelestes*, *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Asiatherium*, *Kokopellia*, *Pucadelphys*, *Didelphis*, *Pappotherium*, *Erinaceus*, *Asioryctes*, *Prokennalestes*, *Montanalestes*;

(3) Multicusped series, each cusp may support 2 wear facets: tritylodontids; *Haramiyavia*, “plagiaulacidans”, cimolodontans;

(?) Not preserved: *Adelobasileus*; homology uncertain: *Ornithorhynchus*.

95. Development and orientation of the prevallum/postvallid shearing:

(0) Absent: *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Gobiconodon*, *Amphilestes*, *Jeholodens*, *Priacodon*, *Trioracodon*;

(1) Present and obtuse: *Kuehneotherium*, *Tinodon*, *Shuotherium*, *Ambondro*, *Peramus*, *Dryolestes*, *Henkelotherium*, *Amphitherium*, *Vincelestes*;

(2) Present, hypertrophied and transverse: *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Zhangheotherium*, *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Asiatherium*, *Kokopellia*, *Pucadelphys*, *Didelphis*, *Pappotherium*, *Prokennalestes*, *Montanalestes*, *Asioryctes*, *Erinaceus*;

(?) Not preserved: *Adelobasileus*; not applicable: *Probainognathus*, tritylodontids, tritheledontids, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Kuehneotherium*, *Shuotherium*, *Gobiconodon*, *Amphilestes*, *Jeholodens*, *Priacodon*, *Trioracodon*, *Haramiyavia*, “plagiaulacidans”, cimolodontans; homology uncertain: *Ornithorhynchus*.

96. Wear facet 1 (a single facet supported by cusp a and cusp c) and facet 2 (a single facet supported by cusp a and cusp b):

(0) Absent: *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Jeholodens*, *Priacodon*, *Trioracodon*;

(1) Present: *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon* (Archer et al. 1993), *Gobiconodon*, *Amphilestes*, *Tinodon*, *Zhangheotherium*, *Peramus*, *Dryolestes*, *Henkelotherium*, *Amphitherium*, *Vincelestes*, *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Asiatherium*, *Kokopellia*, *Pucadelphys*, *Didelphis*, *Pappotherium*, *Erinaceus*, *Asioryctes*, *Prokennalestes*, *Montanalestes*;

(?) Not preserved: *Adelobasileus*; not applicable: *Probainognathus*, tritylodontids, tritheledontids, *Haramiyavia*, “plagiaulacidans”, cimolodontans; homology uncertain: *Ornithorhynchus*.

97. Upper molars—development of facet 1 and preprotocrista on upper molar (applicable to molars with reversed triangulation of molar cusps) (modified from Cifelli 1993b):

(0) Facet 1 (prevallum crest) is short, and does not extend to the stylocone area: *Kuehneotherium*, *Shuotherium*, *Zhangheotherium*, *Dryolestes*, *Henkelotherium*, *Vincelestes*;

(1) Wear facet 1 extends beyond into the hook-like area near the stylocone: *Amphitherium*, *Peramus*;

(2) A long preprotocrista (below the paracone-stylocone crest) is added to the prevallum shear and extends labially beyond paracone: *Pappotherium*, *Deltatheridium*, *Asiatherium*, *Kokopellia*, *Pucadelphys*, *Didelphis*, *Erinaceus*, *Asioryctes*, *Prokennalestes*;

(?) Not preserved: *Adelobasileus*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Amphitherium*, *Aegialodon*, *Kielantherium*, *Montanalestes*; not applicable: *Probainognathus*, tritylodontids, tritheledontids, *Adelobasileus*, *Sinoconodon*, *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Amphilestes*, *Jeholodens*, *Gobiconodon*, *Obdurodon*, *Ornithorhynchus*, *Haramiyavia*, “plagiaulacidans”, cimolodontans, *Dryolestes*.

98. Differentiation of wear facet 3 (on the anterolabial aspect of talonid) and facet 4 (on the posterolabial aspect of the talonid):

(0) Absent: *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Kuehneotherium*, *Shuotherium*, *Gobiconodon*, *Amphilestes*, *Jeholodens*, *Priacodon*, *Trioracodon*, *Morganucodon*, *Zhangheotherium*, *Vincelestes*, *Dryolestes*, *Henkelotherium*;

(1) Present: *Ambondro*, *Ausktribosphenos*, *Bishops*, *Amphitherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Asiatherium*, *Kokopellia*, *Pucadelphys*, *Didelphis*, *Pappotherium*, *Asioryctes*, *Prokennalestes*, *Montanalestes*, *Erinaceus*;

(2) Facets 3 and 4 hypertrophied on the flanks of the strongly V-shaped talonid: *Steropodon*, *Teinolophos*, *Obdurodon*, *Ornithorhynchus* (Archer et al. 1993);

(?) Not preserved: *Adelobasileus*; not applicable: *Probainognathus*, tritylodontids, tritheledontids, *Haramiyavia*, “plagiaulacidans”, cimolodontans.

99. Orientation of facet 4 (on the posterior aspect of the hypoconid):

(0) Present and oblique to long axis of the tooth: *Amphitherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Asiatherium*, *Kokopellia*, *Pucadelphys*, *Didelphis*, *Pappotherium*, *Asioryctes*, *Prokennalestes*, *Montanalestes*;

(1) Present and forming a more transverse angle to long axis of the tooth: *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon* (Archer et al. 1993), *Erinaceus*;

(?) Not preserved: *Adelobasileus*; not applicable: *Probainognathus*, tritylodontids, tritheledontids, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Kuehneotherium*, *Shuotherium*, *Ornithorhynchus*, *Gobiconodon*, *Amphilestes*, *Jeholodens*, *Priacodon*, *Trioracodon*, *Haramiyavia*, “plagiaulacidans”, cimolodontans, *Tinodon*, *Zhangheotherium*, *Dryolestes*, *Henkelotherium*, *Vincelestes*.

100. Morphology of the posterolateral aspect of the talonid (the labial face of the hypoconid, applicable to the taxa with fully basined talonids):

(0) Gently rounded: *Ambondro*, *Peramus*, *Dryolestes*, *Henkelotherium*, *Amphitherium*, *Vincelestes*, *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Asiatherium*, *Kokopellia*, *Pucadelphys*, *Didelphis*, *Pappotherium*, *Prokennalestes*, *Montanalestes*, *Asioryctes*;

(1) Angular: *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon* (Archer et al. 1993), *Erinaceus*;

(?) Not preserved: *Adelobasileus*; not applicable: *Probainognathus*, tritylodontids, tritheledontids, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Kuehneotherium*, *Shuotherium*, *Gobiconodon*, *Amphilestes*, *Jeholodens*, *Priacodon*, *Trioracodon*, *Haramiyavia*, “plagiaulacidans”, cimolodontans; homology uncertain: *Ornithorhynchus*.

miyavia, "plagiaulacidans", cimolodontans, *Tinodon*, *Zhangheotherium*; homology uncertain (on the deciduous teeth): *Ornithorhynchus*.

101. Wear pattern on the talonid:

(0) Absent: *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Kuehneotherium*, *Shuotherium*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Gobiconodon*, *Amphilestes*, *Jeholodens*, *Priacodon*, *Trioracodon*, *Tinodon*, *Zhangheotherium*, *Dryolestes*, *Henkelotherium*, *Amphitherium*, *Peramus*, *Vincelestes*;

(1) Present: *Ambondro*, *Ausktribosphenos*, *Bishops*, *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Asiatherium*, *Kokopellia*, *Pucadelphys*, *Didelphis*, *Pappotherium*, *Erinaceus*, *Asioryctes*, *Prokennalestes*, *Montanalestes*;

(?) Not preserved: *Adelobasileus*, not applicable: *Probainognathus*, tritylodontids, tritheledontids, *Haramiyavia*, "plagiaulacidans", cimolodontans; homology uncertain: *Ornithorhynchus*.

102. Development of the distal metacristid (applicable only to taxa with triangulation of molar cusps):

(0) Distal metacristid present: *Kuehneotherium*, *Tinodon*, *Ambondro*, *Zhangheotherium*, *Amphitherium*, *Peramus*, *Vincelestes* (Sigogneau-Russell 1999: fig. 7), *Aegialodon*, *Kielantherium*, *Deltatheridium*;

(1) Distal metacristid absent: *Shuotherium*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Ornithorhynchus*, *Dryolestes*, *Henkelotherium*, *Asiatherium*, *Kokopellia*, *Pucadelphys*, *Didelphis*, *Pappotherium*, *Erinaceus*, *Asioryctes*, *Prokennalestes*, *Montanalestes*;

(?) Not preserved: *Adelobasileus*, not applicable: *Probainognathus*, tritylodontids, tritheledontids, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Haramiyavia*, "plagiaulacidans", cimolodontans, *Gobiconodon*, *Amphilestes*, *Jeholodens*, *Priacodon*, *Trioracodon*.

103. Differentiation of wear facets 5 and 6 on the labial face of entoconid:

(0) Absent: *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Kuehneotherium*, *Shuotherium*, *Steropodon*, *Teinolophos*, *Obdurodon* (Archer et al. 1993), *Gobiconodon*, *Amphilestes*, *Jeholodens*, *Priacodon*, *Trioracodon*, *Tinodon*, *Zhangheotherium*, *Peramus*, *Dryolestes*, *Henkelotherium*, *Amphitherium*, *Vincelestes*, *Aegialodon*, *Kielantherium*, *Deltatheridium*;

(1) Present: *Ambondro*, *Ausktribosphenos* (the areas in the talonid basin corresponding to facets 5 and 6 have multiple ridges and differ from boreosphenidans), *Bishops* (talonid basin corresponding to facets 5 and 6 has fewer ridges), *Asiatherium*, *Kokopellia*, *Pucadelphys*, *Didelphis*, *Pappotherium*, *Erinaceus*, *Asioryctes*, *Prokennalestes*, *Montanalestes*;

(?) Not preserved: *Adelobasileus*; not applicable: *Probainognathus*, tritylodontids, tritheledontids, *Haramiyavia*, "plagiaulacidans", cimolodontans; homology uncertain: *Ornithorhynchus*.

104. Surficial features on the occluding surfaces of facets 5 and 6 in the talonid (only applicable to taxa with triangulation of molar cusps):

(0) Smooth surface on the talonid (or on cusp d): *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Steropodon*, *Teinolophos*, *Obdurodon* (Archer et al. 1993), *Tinodon*, *Zhangheotherium*, *Peramus*, *Dryolestes*, *Henkelotherium*, *Amphitherium*, *Vincelestes*, *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Asiatherium*, *Kokopellia*, *Pucadelphys*, *Didelphis*, *Pappotherium*, *Erinaceus*, *Asioryctes*, *Prokennalestes*, *Montanalestes*;

(1) Multiple ridges within talonid basin: *Ausktribosphenos* (the areas in talonid basin corresponding to facets 5 and 6 have multiple ridges and differ from the northern tribosphenidans), *Bishops* (talonid basin has fewer ridges);

(?) Not preserved: *Adelobasileus*; not applicable: *Probainognathus*, tritylodontids, tritheledontids, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Haldanodon* (the posterior part of the tooth is not homologous to the tribosphenic talonid, so *Haldanodon* is coded "?"); *Hadrocodium*, *Ornithorhynchus*, *Gobiconodon*, *Amphilestes*, *Jeholodens*, *Priacodon*, *Trioracodon*, *Haramiyavia*, "plagiaulacidans", cimolodontans.

Other dental features (14 characters)

105. Number of lower incisors:

(0) Three or more: *Probainognathus*, tritheledontids, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Amphilestes*, *Jeholodens*, *Priacodon*, *Haramiyavia*, *Zhangheotherium*, *Dryolestes*, *Amphitherium*, *Peramus*, *Deltatheridium*, *Kokopellia*, *Pucadelphys*, *Didelphis*, *Asioryctes*, *Prokennalestes*;

(1) Two or fewer: tritylodontids, *Obdurodon*, *Ornithorhynchus*, *Gobiconodon*, "plagiaulacidans", cimolodontans, *Vincelestes*, *Erinaceus*;

(?) Not preserved: *Adelobasileus*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Trioracodon*,

Tinodon, *Henkelotherium*, *Aegialodon*, *Kielantherium*, *Pappotherium*, *Asiatherium*, *Montanalestes*.

106. Upper canine, presence versus absence, and size:

(0) Upper canine present and large: *Probainognathus*, tritheledontids, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Priacodon*, *Trioracodon*, *Dryolestes*, *Henkelotherium*, *Vincelestes*, *Deltatheridium*, *Asiatherium*, *Kokopellia*, *Pucadelphys*, *Didelphis*, *Asioryctes*;

(1) Present and small: *Gobiconodon*, *Jeholodens*, *Haramiyavia*, *Zhangheotherium*, *Erinaceus*;

(2) Absent: tritylodontids, *Obdurodon*, *Ornithorhynchus*, cimolodontans; (1/2 polymorphic): "plagiaulacidans" (present {1} in *Kuehneodon*, *Pinheirodon*; absent {2} in other "plagiaulacidans");

(?) Not preserved: *Adelobasileus*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Amphilestes*, *Tinodon*, *Peramus*, *Amphitherium*, *Aegialodon*, *Kielantherium*, *Pappotherium*, *Montanalestes*, *Prokennalestes*.

107. Lower canine size, presence versus absence:

(0) Present and large: *Probainognathus*, tritheledontids, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Amphilestes* (present, large, two-rooted), *Priacodon*, *Trioracodon*, *Peramus*, *Dryolestes*, *Henkelotherium*, *Amphitherium*, *Vincelestes*, *Kielantherium*, *Deltatheridium*, *Kokopellia*, *Pucadelphys*, *Didelphis*, *Asioryctes*, *Prokennalestes*;

(1) Present and small: *Gobiconodon*, *Jeholodens*, *Haramiyavia*, *Tinodon* (based on description by Simpson 1929a), *Zhangheotherium*, *Erinaceus*;

(2) Absent: tritylodontids, *Obdurodon*, *Ornithorhynchus*, "plagiaulacidans", cimolodontans;

(?) Not preserved: *Adelobasileus*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Asiatherium*, *Aegialodon*, *Pappotherium*, *Montanalestes*.

108. Total number of the lower premolars:

(0) Five or more: *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Kuehneotherium* (at least five, after Kermack et al. 1968), *Bishops*, *Amphitherium* (following Simpson 1928), *Peramus* (Butler and Clemens 2001; modified from Clemens and Mills 1971), *Prokennalestes*, *Montanalestes*;

(1) Four premolars: *Gobiconodon* (after Kielan-Jaworowska and Dashzeveg 1998; Jenkins and Crompton 1979 identified 3 to 4 premolars), *Amphilestes*, *Trioracodon*, *Haramiyavia*, *Dryolestes*, *Henkelotherium*, *Kielantherium*, *Asioryctes*;

(2) Three: *Haldanodon*, *Priacodon*, *Tinodon*, *Zhangheotherium* (revised from Hu et al. 1997, 1998), *Deltatheridium*, *Asiatherium*, *Kokopellia*, *Pucadelphys*, *Didelphis*;

(1/2 polymorphic) "plagiaulacidans" (either 3 or 4 premolars);

(3) Two or fewer: *Sinoconodon*, *Hadrocodium*, *Obdurodon*, *Ornithorhynchus*, *Jeholodens*, cimolodontans, *Vincelestes*, *Erinaceus*;

(?) Not applicable (premolars not differentiated): *Probainognathus*, tritylodontids, tritheledontids; not preserved: *Adelobasileus*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Steropodon*, *Teinolophos*, *Aegialodon*, *Pappotherium*.

109. Diastema separating P1 from P2 (Rougier et al. 1998):

(0) Absent: *Probainognathus*, tritheledontids, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Gobiconodon*, *Priacodon*, *Trioracodon*, *Peramus*, *Dryolestes*, *Vincelestes*, *Asioryctes*, *Erinaceus*;

(1) Present: *Sinoconodon*, *Jeholodens*, *Henkelotherium*, *Asiatherium*, *Deltatheridium*, *Pucadelphys*, *Didelphis*;

(?) Not applicable: tritylodontids, *Hadrocodium*, "plagiaulacidans", cimolodontans, *Obdurodon*, *Ornithorhynchus*; not preserved: *Ausktribosphenos*, *Bishops*, *Adelobasileus*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Steropodon*, *Teinolophos*, *Haramiyavia*, *Amphilestes*, *Tinodon*, *Zhangheotherium*, *Amphitherium*, *Kielantherium*, *Aegialodon*, *Pappotherium*, *Kokopellia*, *Prokennalestes*, *Montanalestes*.

110. Number of lower molars or molariform postcanines:

(0) 6 or more: *Kuehneotherium* (following Mills 1984), *Zhangheotherium*, *Dryolestes*, *Henkelotherium*, *Amphitherium*;

(1) 4 to 5 molars (or molariforms): *Sinoconodon* (= molariform loci, Zhang et al. 1998), *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Tinodon*, *Shuotherium* (*sensu* Chow and Rich 1982), *Gobiconodon* (= molariform loci, see Jenkins and Schaff 1988), *Amphilestes*, *Jeholodens*, *Priacodon*, *Kielantherium*, *Deltatheridium*, *Asiatherium*, *Kokopellia*, *Pucadelphys*, *Didelphis*;

(2) 3 molars or fewer: *Hadrocodium*, *Ausktribosphenos*, *Bishops* (based on Rich, Flannery, et al. 2001), *Steropodon*, *Obdurodon* (Archer et al. 1993), *Ornithorhynchus* (based on milk teeth, Simpson 1929b), *Trioracodon*,

Haramiyavia, *Vincelestes*, *Peramus*, *Erinaceus*, *Asioryctes*, *Prokennalestes*, *Montanalestes*;

(3) 2 molars: “plagiaulacidans”, cimolodontans;

(0/1 polymorphic): tritylodontids;

(?) Uncertain (postcanines undifferentiated): *Probainognathus*, tritheledontids; incompletely preserved (missing the posterior molar{s}): *Ambondro*, *Steropodon*, *Teinolophos*, *Aegialodon*, *Pappotherium*.

111. Lower postcanine roots:

(0) Root division is incipient or incomplete: *Probainognathus*, tritheledontids. See below on the polymorphic character states: *Sinoconodon* is polymorphic in this character (some of its postcanines have poorly divided roots, Luo 1994, but a small number of taxa have divided roots, but *Essonodon* has developed multiple roots; an alternative coding for cimolodontans as a whole is 1/2 polymorphic), *Tinodon*, *Zhangheotherium*, *Peramus*, *Dryolestes*, *Henkelotherium*, *Amphitherium*, *Vincelestes*, *Aegialodon*, *Kielantherium*, *Asiatherium*, *Kokopellia*, *Pucadelphys*, *Didelphis*, *Deltatheridium*, *Pappotherium*, *Erinaceus*, *Asioryctes*, *Prokennalestes*, *Montanalestes*;

(1) Roots are divided: *Megazostrodon*, *Morganucodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Gobiconodon*, *Amphilestes*, *Jeholodens*, *Priacodon*, *Trioracodon*, *Haramiyavia*, “plagiaulacidans”, cimolodontans (the majority of taxa have divided roots, but *Essonodon* has developed multiple roots; an alternative coding for cimolodontans as a whole is 1/2 polymorphic), *Tinodon*, *Zhangheotherium*, *Peramus*, *Dryolestes*, *Henkelotherium*, *Amphitherium*, *Vincelestes*, *Aegialodon*, *Kielantherium*, *Asiatherium*, *Kokopellia*, *Pucadelphys*, *Didelphis*, *Deltatheridium*, *Pappotherium*, *Erinaceus*, *Asioryctes*, *Prokennalestes*, *Montanalestes*;

(2) Multiple roots (more than three): *Obdurodon*, *Ornithorhynchus* (in deciduous teeth, and the replacement horny pads);

(0/1) polymorphic: *Sinoconodon*, *Kuehneotherium*;

(1/2) polymorphic: tritylodontids (most lower postcanines have multiple roots, but *Bienotheroides* has only two roots for the lower postcanines);

(?) Not preserved: *Adelobasileus*.

112. Replacement of the incisors and canines:

(0) Alternating and multiple replacement: *Probainognathus*, tritheledontids, *Sinoconodon*;

(1) Diphodont replacement or none: *Morganucodon*, *Haldanodon*, *Trioracodon*, “plagiaulacidans”, cimolodontans (Greenwald 1988), *Zhangheotherium*, *Dryolestes*, *Didelphis* (no replacement), *Erinaceus*;

(?) Not preserved: *Adelobasileus*, *Megazostrodon*, *Dinnetherium*, *Hadrocodium*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Gobiconodon*, *Amphilestes*, *Jeholodens*, *Priacodon*, *Tinodon*, *Haramiyavia*, *Peramus*, *Henkelotherium*, *Amphitherium*, *Vincelestes*, *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Asiatherium*, *Kokopellia*, *Pucadelphys*, *Pappotherium*, *Prokennalestes*, *Montanalestes*, *Asioryctes*; not applicable: tritylodontids, *Obdurodon*, *Ornithorhynchus*.

113. Replacement of the premolariforms:

(0) Multiple replacement: *Probainognathus*, tritheledontids,

(1) One replacement or none: sequential eruption and one replacement or no replacement: tritylodontids (no replacement), *Sinoconodon* (p2 replaced but p1 is shed without replacement), *Morganucodon*, *Kuehneotherium* (Gill 1974; Parrington 1978), *Haldanodon* (Martin and Nowotny 2001), *Gobiconodon*, *Trioracodon*, “plagiaulacidans” (Hahn and Hahn 1998 showed that at least one paulchoffatiid “plagiaulacidan”, *Kielanodon*, has an alternating pattern of premolar replacement), cimolodontans (Greenwald 1988), *Zhangheotherium*, *Dryolestes* (p2, p4 alternate with p1, p3), *Amphitherium* (based on Butler and Clemens 2001); *Pucadelphys*, *Didelphis* (p3 replacement only), *Asioryctes*, *Erinaceus*;

(?) Not preserved: *Adelobasileus*, *Megazostrodon*, *Dinnetherium*, *Hadrocodium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Haramiyavia*, *Amphilestes*, *Jeholodens*, *Priacodon*, *Tinodon*, *Peramus*, *Henkelotherium*, *Vincelestes*, *Kielantherium*, *Deltatheridium*, *Asiatherium*, *Kokopellia*, *Pappotherium*, *Prokennalestes*, *Montanalestes*; not applicable: tritylodontids, *Obdurodon*, *Ornithorhynchus*.

114. Replacement of at least some functional molariforms:

(0) Present: *Probainognathus*, tritheledontids, *Sinoconodon*, *Megazostrodon* (after Gow 1986a), *Gobiconodon*;

(1) Absent: tritylodontids, *Morganucodon*, *Dinnetherium*, *Kuehneotherium* (Parrington 1978), *Haldanodon*, *Amphilestes*, *Jeholodens*, *Priacodon*, *Trioracodon*, *Ornithorhynchus* (the deciduous teeth are lost early, and are replaced by functional horny pads), “plagiaulacidans”, cimolodontans, *Zhangheotherium*, *Dryolestes*, *Deltatheridium*, *Asiatherium*, *Kokopellia*, *Pucadelphys*, *Didelphis*, *Erinaceus*, *Prokennalestes*, *Asioryctes*;

(?) Unknown: *Adelobasileus*, *Hadrocodium*, *Tinodon*, *Shuotherium*, *Steropodon*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Obdurodon*

(Archer et al. 1993), *Teinolophos*, *Haramiyavia*, *Henkelotherium*, *Amphitherium*, *Vincelestes*, *Peramus*, *Aegialodon*, *Kielantherium*, *Pappotherium*, *Montanalestes*.

115. Procumbent and enlargement of the anteriormost lower incisors:

(0) Absent: *Probainognathus*, tritheledontids, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Priacodon*, *Trioracodon*, *Dryolestes*, *Amphitherium*, *Vincelestes*, *Deltatheridium*, *Kokopellia*, *Pucadelphys*, *Didelphis*, *Erinaceus*, *Asioryctes*;

(1) Both procumbent and enlarged (at least 50% longer than second functional incisors): tritylodontids, *Gobiconodon*, *Jeholodens*, *Haramiyavia*, “plagiaulacidans”, cimolodontans, *Zhangheotherium*;

(?) Not preserved: *Aegialodon*, *Adelobasileus*, *Kuehneotherium*, *Amphilestes*, *Tinodon*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Peramus*, *Asiatherium*, *Henkelotherium*, *Kielantherium*, *Pappotherium*, *Prokennalestes*, *Montanalestes*; not applicable: *Obdurodon*, *Ornithorhynchus*.

116. Bicusperate second upper incisor:

(0) Absent: *Probainognathus*, tritylodontids, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Gobiconodon*, *Jeholodens*, *Priacodon*, *Zhangheotherium*, *Vincelestes*, *Pucadelphys*, *Didelphis*, *Erinaceus*, *Asioryctes*;

(1) Present: *Haramiyavia*, “plagiaulacidans”;

(0/1 polymorphic): tritheledontids; cimolodontans (present {1} in eucosmodontids and other multituberculates, absent {0} in djadochtatherioideans);

(?) Not preserved: *Adelobasileus*, *Kuehneotherium*, *Tinodon*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Amphilestes*, *Trioracodon*, *Dryolestes*, *Henkelotherium*, *Amphitherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Asiatherium*, *Kokopellia*, *Pappotherium*, *Montanalestes*, *Prokennalestes*; not applicable: *Obdurodon*, *Ornithorhynchus*.

117. Enlarged diastema in the lower incisor-canine region (better developed in older individuals, see Parrington 1978; Gow 1986a; Crompton and Luo 1993):

(0) Absent: *Probainognathus*, tritheledontids, *Haldanodon*, *Trioracodon*, *Gobiconodon*, *Amphilestes*, *Haramiyavia* (large diastema between i3 and i4, but there is no diastema behind the canine), *Zhangheotherium*, *Peramus*, *Dryolestes*, *Henkelotherium*, *Amphitherium*, *Vincelestes*, *Kielantherium*, *Deltatheridium*, *Kokopellia*, *Pucadelphys*, *Didelphis*, *Erinaceus*, *Prokennalestes*, *Asioryctes*;

(1) Present and behind the canine: *Sinoconodon*, *Morganucodon* (in older individuals), *Megazostrodon*, *Dinnetherium*, *Hadrocodium*, *Jeholodens*, *Priacodon*;

(2) Present and behind the posterior incisor: tritylodontids, “plagiaulacidans”, cimolodontans;

(?) Not preserved: *Adelobasileus*, *Tinodon*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Aegialodon*, *Asiatherium*, *Pappotherium*, *Montanalestes*; not applicable: *Ornithorhynchus*, *Obdurodon*.

118. Enamel microstructure (following Wood et al. 1999; distribution following Clemens 1997; Sander 1997; Wood and Stern 1997):

(0) Synapsid columnar enamel (prismatic): tritylodontids, *Haramiyavia* (coded from unidentified haramiyids), *Morganucodon*, *Dinnetherium*, *Kuehneotherium*, *Haldanodon*, “plagiaulacidans” (from Fosse et al. 1985), *Ornithorhynchus*;

(1) “Transitional” character state (sheath indistinct, “prismatic” crystallites inclined at less than 45° to “interprismatic” matrix): *Sinoconodon*, *Priacodon* (coded from the “Cloverly triconodontine” as determined by Wood et al. 1999), *Gobiconodon*;

(2) Plesiomorphic prismatic enamel: tritheledontids, *Megazostrodon*, *Gobiconodon*, cimolodontans, *Zhangheotherium* (coded from “spalacotheriids” as determined by Wood et al. 1999), *Dryolestes*, *Deltatheridium* (Wood 2000), *Kokopellia*, *Pucadelphys*, *Didelphis*, *Erinaceus*;

(?) Unknown: *Probainognathus*, *Adelobasileus*, *Hadrocodium*, *Amphilestes*, *Jeholodens*, *Trioracodon*, *Tinodon*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Obdurodon*, *Asiatherium*, *Teinolophos*, *Henkelotherium*, *Amphitherium*, *Peramus*, *Vincelestes*, *Aegialodon*, *Kielantherium*, *Pappotherium*, *Asioryctes*, *Prokennalestes*, *Montanalestes*.

Vertebrae (9 characters)

119. ProAtlas neural arch as a separate ossification in adults (Rowe 1988, character 92):

(0) Present: tritylodontids;

(1) Absent: *Ornithorhynchus*, cimolodontans, *Zhangheotherium*, *Vincelestes*, *Didelphis*, *Pucadelphys*, *Erinaceus*, *Asioryctes* (the atlas neural arch

has a smooth surface, without any evidence for the fusion or attachment of proatlans: it is assumed here that proatlans is absent in *Asioryctes*;

(?) Not preserved: *Probainognathus*, tritheledontids, *Adelobasileus*, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Kuehneotherium*, *Shuotherium*, *Ausktribosphenos*, *Bishops*, *Ambondro*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Gobiconodon*, *Jeholodens*, *Amphilestes*, *Priacodon*, *Trioracodon*, *Haramiyavia*, "plagiaulacidans", *Tinodon*, *Henkelotherium*, *Dryolestes*, *Amphitherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Asiatherium*, *Kokopellia*, *Pappotherium*, *Prokennalestes*, *Montanalestes*.

120. Fusion of atlas neural arch and intercentrum in adults (Rowe 1988, character 93):

(0) Unfused: *Probainognathus*, tritheledontids, tritylodontids, *Sinoconodon*, *Morganucodon*, *Megazostrodon* (unfused, based on Gow 1986a: fig. 14), *Jeholodens*, cimolodontans, *Vincelestes*, *Asioryctes*;

(1) Fused: *Ornithorhynchus*, *Didelphis*, *Pucadelphys*, *Erinaceus*;

(?) Not preserved: *Adelobasileus*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Gobiconodon*, *Amphilestes*, *Priacodon*, *Trioracodon*, *Haramiyavia*, "plagiaulacidans", *Tinodon*, *Zhangheotherium*, *Henkelotherium*, *Dryolestes*, *Amphitherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Asiatherium*, *Kokopellia*, *Pappotherium*, *Prokennalestes*, *Montanalestes*.

121. Atlas rib in adults (Jenkins and Parrington 1976; Rowe 1988: character 96; Kielan-Jaworowska 1977; Kielan-Jaworowska and Gambaryan 1994 observed this independently, and interpreted this feature as absence of transverse foramen in the atlas):

(0) Present: *Probainognathus*, tritheledontids (after Rowe 1988), tritylodontids, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Jeholodens*, cimolodontans;

(1) Absent: *Ornithorhynchus*, *Zhangheotherium*, *Vincelestes*, *Didelphis*, *Pucadelphys*, *Erinaceus*, *Asioryctes* (atlas has a stump for transverse process, although the distal part of the transverse process is broken);

(?) Not preserved: *Adelobasileus*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Kuehneotherium*, *Shuotherium*, *Ausktribosphenos*, *Bishops*, *Ambondro*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Gobiconodon*, *Amphilestes*, *Priacodon*, *Trioracodon*, *Haramiyavia*, "plagiaulacidans", *Tinodon*, *Henkelotherium*, *Dryolestes*, *Amphitherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Asiatherium*, *Kokopellia*, *Pappotherium*, *Prokennalestes*, *Montanalestes*.

122. Prezygapophysis on axis (Jenkins 1971; Rowe 1988, character 97):

(0) Present: tritylodontids;

(1) Absent: *Morganucodon*, *Megazostrodon* (based on Gow 1986a: fig. 14), *Ornithorhynchus*, *Jeholodens*, cimolodontans, *Zhangheotherium*, *Vincelestes*, *Didelphis*, *Pucadelphys*, *Asioryctes*, *Erinaceus*;

(?) Not preserved: *Probainognathus*, tritheledontids, *Adelobasileus*, *Sinoconodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Kuehneotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Shuotherium*, *Gobiconodon*, *Amphilestes*, *Priacodon*, *Trioracodon*, *Haramiyavia*, "plagiaulacidans", *Tinodon*, *Henkelotherium*, *Dryolestes*, *Amphitherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Asiatherium*, *Kokopellia*, *Pappotherium*, *Prokennalestes*, *Montanalestes*.

123. Fusion of dens to axis:

(0) Unfused: tritylodontids, *Morganucodon*, *Megazostrodon* (round anterior margin of the axis, as described by Gow 1986a, is characteristic of an unfused dens), *Jeholodens*;

(1) Fused: *Ornithorhynchus*, cimolodontans, *Zhangheotherium*, *Vincelestes*, *Didelphis*, *Pucadelphys*, *Erinaceus*, *Asioryctes*;

(?) Not preserved: *Probainognathus*, tritheledontids, *Adelobasileus*, *Sinoconodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Gobiconodon*, *Amphilestes*, *Priacodon*, *Trioracodon*, *Haramiyavia*, "plagiaulacidans", *Tinodon*, *Henkelotherium*, *Dryolestes*, *Amphitherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Asiatherium*, *Kokopellia*, *Pappotherium*, *Prokennalestes*, *Montanalestes*.

124. Rib of axis in adults:

(0) Present: *Probainognathus*, tritylodontids, *Morganucodon* (Jenkins and Parrington 1976 showed the attachment facet), *Megazostrodon* (Gow 1986a: fig. 14 illustrates the rib facets on the neural arch), *Ornithorhynchus*, *Jeholodens*, cimolodontans, *Zhangheotherium*;

(1) Absent (rib fused to become transverse process): *Vincelestes*, *Didelphis*, *Pucadelphys*, *Erinaceus*, *Asioryctes*;

(?) Not preserved: tritheledontids, *Adelobasileus*, *Sinoconodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Kuehneotherium*, *Gobiconodon*,

Amphilestes, *Priacodon*, *Trioracodon*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Haramiyavia*, "plagiaulacidans", *Tinodon*, *Henkelotherium*, *Dryolestes*, *Amphitherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Asiatherium*, *Kokopellia*, *Pappotherium*, *Prokennalestes*, *Montanalestes*.

125. Postaxial cervical ribs in adults (Rowe 1988, character 101):

(0) Present: *Probainognathus*, tritylodontids, tritheledontids (Gow in press illustrated the detached anapophysis and diaphophysis on the posterior cervicals, no ribs are attached to these cervicals), *Sinoconodon* (on one specimen, although poorly preserved), *Morganucodon*, *Megazostrodon*, *Jeholodens*, cimolodontans, *Zhangheotherium*;

(1) Absent: *Ornithorhynchus*, *Vincelestes*, *Asiatherium*, *Didelphis*, *Pucadelphys*, *Erinaceus*, *Asioryctes*;

(?) Not preserved: *Adelobasileus*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Gobiconodon*, *Amphilestes*, *Priacodon*, *Trioracodon*, *Haramiyavia*, "plagiaulacidans", *Tinodon*, *Peramus*, *Henkelotherium*, *Dryolestes*, *Amphitherium*, *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Kokopellia*, *Pappotherium*, *Prokennalestes*, *Montanalestes*.

126. Thoracic vertebrae:

(0) 13 thoracic vertebrae: *Gobiconodon* (after the reconstruction by Jenkins and Schaff 1988), cimolodontans, *Zhangheotherium*, *Vincelestes*, *Asiatherium*, *Didelphis*, *Pucadelphys*, *Erinaceus*;

(1) 15 or more: *Ornithorhynchus* (16), *Jeholodens* (15);

(?) Unknown: *Probainognathus*, tritylodontids, tritheledontids, *Adelobasileus*, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Amphilestes*, *Priacodon*, *Trioracodon*, *Haramiyavia*, "plagiaulacidans", *Tinodon*, *Henkelotherium*, *Dryolestes*, *Amphitherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Kokopellia*, *Pappotherium*, *Prokennalestes*, *Asioryctes*.

127. Lumbar ribs (from Jenkins and Schaff 1988):

(0) Unfused to vertebrae: *Probainognathus*, tritylodontids, tritheledontids, *Gobiconodon*, *Jeholodens*;

(1) Synostosed to vertebrae to form transverse processes: *Morganucodon*, *Megazostrodon* (based on the stereophotos of Jenkins and Parrington 1976), *Ornithorhynchus*, cimolodontans, *Zhangheotherium*, *Henkelotherium* (Krebs 1991: Abb. 6), *Vincelestes*, *Didelphis*, *Asiatherium*, *Pucadelphys*, *Erinaceus*;

(?) Not preserved: *Adelobasileus*, *Sinoconodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Amphilestes*, *Priacodon*, *Trioracodon*, *Haramiyavia*, "plagiaulacidans", *Tinodon*, *Dryolestes*, *Amphitherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Kokopellia*, *Pappotherium*, *Asioryctes*, *Prokennalestes*, *Montanalestes*.

Shoulder girdle (16 characters)

128. Interclavicle in adults (Rowe 1988: character 110 merged with character 113, modified by Hu et al. 1997):

(0) Present: tritylodontids, tritheledontids, *Sinoconodon*, *Morganucodon*, *Ornithorhynchus*, *Jeholodens*, cimolodontans, *Zhangheotherium*;

(1) Absent: *Vincelestes*, *Didelphis*, *Pucadelphys*, *Erinaceus*;

(?) Not preserved: *Probainognathus*, *Adelobasileus*, *Haldanodon*, *Hadrocodium*, *Gobiconodon*, *Megazostrodon*, *Dinnetherium*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Amphilestes*, *Priacodon*, *Trioracodon*, *Haramiyavia*, "plagiaulacidans", *Tinodon*, *Henkelotherium*, *Dryolestes*, *Amphitherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Asiatherium*, *Kokopellia*, *Pappotherium*, *Prokennalestes*, *Montanalestes*, *Asioryctes*.

129. Contact relationships in adults between the interclavicle (embryonic membranous element) and the sternal manubrium (embryonic endochondral element) (assuming the homologies of these elements by Klima 1973, 1987) (Hu et al. 1997, 1998):

(0) Two elements distinct from each other, posterior end of interclavicle abuts anterior border of manubrium: tritylodontids (Sun and Li 1985), *Sinoconodon*, *Ornithorhynchus* (Klima 1987), cimolodontans (Meng and Miao 1992; Sereno and McKenna 1995);

(1) Two elements distinct from each other, the interclavicle broadly overlaps the ventral side of the manubrium: *Jeholodens*, *Zhangheotherium* (Hu et al. 1997);

(2) Complete fusion of the embryonic membranous and endochondral elements (Klima 1987): *Vincelestes*, *Didelphis*, *Pucadelphys*, *Erinaceus*;

(?) Not preserved: *Tinodon*, *Adelobasileus*, *Probainognathus*, tritheledontids (posterior end is not preserved), *Morganucodon*, *Megazostrodon*, *Dinne-*

therium, *Haldanodon*, *Hadrocodium*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Gobiconodon*, *Amphilestes*, *Priacodon*, *Triaracodon*, *Haramiyavia*, “plagiaulacidans”, *Henkelotherium*, *Dryolestes*, *Amphitherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Asiatherium*, *Kokopellia*, *Pappotherium*, *Prokennalestes*, *Montanalestes*, *Asioryctes*.

130. Cranial margin of the interclavicle:

(0) Anterior border is emarginated or flat: tritylodontids (*Bienotheroides*, Sun and Li 1985), *Sinoconodon*, *Ornithorhynchus*, cimolodontans (*Bulganbaatar* “clover-shaped interclavicle” Sereno and McKenna 1995; see also Meng and Miao 1992), *Zhangheotherium* (Hu et al. 1997);

(1) With a median process (assuming interclavicle is fused to the sternal manubrium in living therians, Klima 1987): tritheledontids, *Morganucodon* (based on a specimen courtesy of Dr. Susan Evans), *Jeholodens*, *Vincelestes*, *Didelphis*, *Pucadelphys*, *Erinaceus*;

(?) Not preserved: *Priacodon*, *Tinodon*, *Probainognathus*, *Adelobasileus*, *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Gobiconodon*, *Amphilestes*, *Triaracodon*, *Haramiyavia*, “plagiaulacidans”, *Peramus*, *Henkelotherium*, *Dryolestes*, *Amphitherium*, *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Asiatherium*, *Kokopellia*, *Pappotherium*, *Prokennalestes*, *Montanalestes*, *Asioryctes*.

131. Claviculo-sternal apparatus joint (assuming that homologous elements of the interclavicle and the manubrium are fused to each other in therians, Klima 1973, 1987; Sereno and McKenna 1995; Hu et al. 1997):

(0) Immobile: tritylodontids (Sun and Li 1985), *Sinoconodon*, *Ornithorhynchus*;

(1) Mobile: tritheledontids, *Jeholodens*, cimolodontans, *Zhangheotherium*, *Vincelestes*, *Erinaceus*, *Didelphis*, *Pucadelphys*;

(?) Not preserved: *Probainognathus*, *Adelobasileus*, *Morganucodon* (Evans 1981; personal communication from F.A. Jenkins and S.E. Evans), *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Kuehneotherium*, *Shuotherium*, *Ausktribosphenos*, *Bishops*, *Ambondro*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Gobiconodon*, *Amphilestes*, *Priacodon*, *Triaracodon*, *Haramiyavia*, “plagiaulacidans”, *Tinodon*, *Peramus*, *Henkelotherium*, *Dryolestes*, *Amphitherium*, *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Asiatherium*, *Kokopellia*, *Pappotherium*, *Prokennalestes*, *Montanalestes*, *Asioryctes*.

132. Acromioclavicular joint:

(0) Extensive articulation: *Probainognathus*, tritylodontids, tritheledontids, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Ornithorhynchus*;

(1) Limited articulation (either pointed acromion, or pointed distal end of clavicle, or both): *Gobiconodon*, *Jeholodens*, cimolodontans, *Zhangheotherium*, *Henkelotherium*, *Vincelestes*, *Asiatherium*, *Didelphis*, *Pucadelphys*, *Erinaceus*;

(?) Not preserved: *Adelobasileus*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Gobiconodon*, *Amphilestes*, *Priacodon*, *Triaracodon*, *Haramiyavia*, “plagiaulacidans”, *Tinodon*, *Dryolestes*, *Amphitherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Kokopellia*, *Pappotherium*, *Prokennalestes*, *Montanalestes*.

133. Curvature of the clavicle (Ji et al. 1999):

(0) Boomerang-shaped: tritylodontids (Sun and Li 1985), *Sinoconodon*, *Morganucodon* (Jenkins and Parrington 1976), *Ornithorhynchus*;

(1) Slightly curved: tritheledontids, *Jeholodens*, cimolodontans, *Zhangheotherium* (Hu et al. 1997), *Henkelotherium* (Krebs 1991: Abb. 7), *Asiatherium*, *Didelphis*, *Pucadelphys*, *Erinaceus*;

(?) Not preserved: *Probainognathus*, *Adelobasileus*, *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Gobiconodon*, *Amphilestes*, *Priacodon*, *Triaracodon*, *Haramiyavia*, “plagiaulacidans”, *Tinodon*, *Vincelestes*, *Dryolestes*, *Amphitherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Kokopellia*, *Pappotherium*, *Prokennalestes*, *Montanalestes*, *Asioryctes*.

134. Scapula—supraspinous fossa (Jenkins and Schaff 1988; Rowe 1988, character 114; new definition of character states by Hu et al. 1997):

(0) Absent (acromion extending from the dorsal border of scapula, and is positioned anterior to the glenoid): *Probainognathus*, tritylodontids, tritheledontids (Gow in press), *Sinoconodon*, *Ornithorhynchus*;

(1) Weakly developed (present only along a part of the scapula, and acromion positioned lateral to the glenoid): *Morganucodon*, *Megazostrodon*, *Haldanodon* (Henkel and Krusat 1980; Krusat 1980), cimolodontans;

(2) Fully developed and present along the entire dorsal border of scapula: *Gobiconodon*, *Jeholodens*, *Zhangheotherium*, *Henkelotherium*, *Vincelestes*, *Asiatherium*, *Didelphis*, *Pucadelphys*, *Erinaceus*;

(?) Not preserved: *Adelobasileus*, *Dinnetherium*, *Hadrocodium*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Amphilestes*, *Priacodon*, *Triaracodon*, *Haramiyavia*, “plagiaulacidans”, *Tinodon*, *Dryolestes*, *Amphitherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Kokopellia*, *Pappotherium*, *Prokennalestes*, *Montanalestes*, *Asioryctes*.

135. Scapula—acromion process (Rowe 1988; Hu et al. 1997, modified here):

(0) Short stump (level with the glenoid, or behind the glenoid): *Probainognathus*, tritylodontids, tritheledontids, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Haldanodon*, *Ornithorhynchus*;

(1) Hook-like and extending below the glenoid: *Gobiconodon*, *Jeholodens*, cimolodontans, *Zhangheotherium*, *Vincelestes*, *Henkelotherium*, *Didelphis*, *Asiatherium*, *Pucadelphys*, *Erinaceus*;

(?) Not preserved: *Adelobasileus*, *Dinnetherium*, *Hadrocodium*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Amphilestes*, *Priacodon*, *Triaracodon*, *Haramiyavia*, “plagiaulacidans”, *Tinodon*, *Dryolestes*, *Amphitherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Kokopellia*, *Pappotherium*, *Prokennalestes*, *Montanalestes*, *Asioryctes*.

136. Scapula—a distinctive fossa for the teres major muscle on the lateral aspect of the scapular plate:

(0) Absent: *Probainognathus*, tritylodontids (Sun and Li 1985), tritheledontids, *Sinoconodon*, *Megazostrodon*, *Haldanodon*, cimolodontans (Sereno and McKenna 1995), *Vincelestes*, *Asiatherium*, *Didelphis*, *Pucadelphys*, *Erinaceus*;

(1) Present: *Ornithorhynchus*, *Jeholodens*, *Zhangheotherium* (Hu et al. 1997), *Henkelotherium* (Krebs 1991: Abb. 7);

(?) Not preserved: tritheledontids, *Adelobasileus*, *Morganucodon*, *Dinnetherium*, *Hadrocodium*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Gobiconodon*, *Amphilestes*, *Priacodon*, *Triaracodon*, *Haramiyavia*, “plagiaulacidans”, *Tinodon*, *Dryolestes*, *Amphitherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Kokopellia*, *Pappotherium*, *Prokennalestes*, *Montanalestes*, *Asioryctes*.

137. Procoracoid (as a separate element in adults) (Klima 1973; Rowe 1988, character 117):

(0) Present: *Probainognathus*, tritylodontids, tritheledontids (Gow in press), *Sinoconodon* (as indicated by the facet on the scapula), *Morganucodon*, *Megazostrodon*, *Ornithorhynchus*;

(1) Fused to the sternal apparatus (Klima 1973) and absent in adult: *Gobiconodon* (on a well preserved proximal portion of scapula, there is no indication for contact of the procoracoid), *Jeholodens*, cimolodontans, *Zhangheotherium*, *Henkelotherium*, *Vincelestes*, *Erinaceus*, *Asiatherium*, *Pucadelphys*, *Didelphis*;

(?) Not preserved: *Priacodon*, *Tinodon*, *Adelobasileus*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Amphilestes*, *Triaracodon*, *Haramiyavia*, “plagiaulacidans”, *Dryolestes*, *Amphitherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Kokopellia*, *Pappotherium*, *Prokennalestes*, *Montanalestes*, *Asioryctes*.

138. Procoracoid foramen:

(0) Present: *Probainognathus*, tritylodontids, tritheledontids (Gow in press), *Sinoconodon*, *Morganucodon*, *Megazostrodon*;

(1) Absent (assuming the procoracoid is fused to the sternal apparatus in living therians, Klima 1973): *Ornithorhynchus*, cimolodontans, *Zhangheotherium*, *Vincelestes*, *Erinaceus*, *Asiatherium*, *Pucadelphys*, *Didelphis*;

(?) Unknown: *Gobiconodon*, *Adelobasileus*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Amphilestes*, *Jeholodens*, *Priacodon*, *Triaracodon*, *Haramiyavia*, “plagiaulacidans”, *Tinodon*, *Henkelotherium*, *Dryolestes*, *Amphitherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Kokopellia*, *Pappotherium*, *Prokennalestes*, *Montanalestes*, *Asioryctes*.

139. Coracoid (Rowe 1988, character 118; revised by Hu et al. 1997):

(0) Large, with posterior process: *Probainognathus*, tritylodontids, tritheledontids, *Sinoconodon*, *Morganucodon*, *Megazostrodon* (inferred from the contacting border on the scapula by Jenkins and Parrington 1976), *Ornithorhynchus*;

(1) Small, without posterior process: *Gobiconodon*, *Jeholodens*, cimolodontans, *Zhangheotherium*, *Henkelotherium*, *Vincelestes*, *Asiatherium*, *Didelphis*, *Pucadelphys*, *Erinaceus*;

(?) Not preserved: *Adelobasileus*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Gobiconodon*, *Amphilestes*, *Priacodon*, *Triaracodon*, *Haramiyavia*, "plagiaulacidans", *Tinodon*, *Dryolestes*, *Amphitherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Kokopellia*, *Pappotherium*, *Prokennalestes*, *Montanalestes*, *Asioryctes*.

140. Size of the anteriormost sternal element ("manubrium") relative to the succeeding sternebrae in the sternal apparatus in adults:

(0) Large: tritylodontids, *Sinoconodon*, *Ornithorhynchus*, *Jeholodens*, cimolodontans (Kielan-Jaworowska 1989 described this in a taeniolabidoid; also see Meng and Miao 1992), *Zhangheotherium* (in *Zhangheotherium* the sternebrae are secondarily fused; the proximal part of the fused sternebrae, as evidenced by the first thoracic rib facet, indicating the anteriormost sternabra is larger than the subsequent segments), *Vincelestes*;

(1) Small: *Didelphis*, *Pucadelphys*, *Erinaceus*;

(?) Not preserved: *Probainognathus*, tritheledontids, *Adelobasileus* *Morganucodon* (Evans 1981; personal communication from S.E. Evans and F.A. Jenkins), *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Gobiconodon*, *Amphilestes*, *Priacodon*, *Triaracodon*, *Haramiyavia*, "plagiaulacidans", *Tinodon*, *Henkelotherium*, *Dryolestes*, *Amphitherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Asiatherium*, *Kokopellia*, *Pappotherium*, *Prokennalestes*, *Montanalestes*, *Asioryctes*.

141. Orientation ("facing" of articular surface) of the glenoid (relative to the plane or the axis of scapula) (Rougier 1993; Hu et al. 1997):

(0) Nearly parallel to the long axis of scapula and facing posterolaterally: *Probainognathus*, tritylodontids, tritheledontids, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Haldanodon*, *Ornithorhynchus*;

(1) Oblique to the long axis of scapula and facing more posteriorly: *Gobiconodon*, *Jeholodens*, cimolodontans, *Zhangheotherium*, *Henkelotherium*, *Vincelestes*;

(2) Articular surface of glenoid is perpendicular to the main plane of the scapular plate: *Asiatherium*, *Didelphis*, *Pucadelphys*, *Erinaceus*;

(?) Not preserved: *Adelobasileus*, *Dinnetherium*, *Hadrocodium*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Amphilestes*, *Priacodon*, *Triaracodon*, *Haramiyavia*, "plagiaulacidans", *Tinodon*, *Dryolestes*, *Amphitherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Pappotherium*, *Kokopellia*, *Prokennalestes*, *Montanalestes*, *Asioryctes*.

142. Shape and curvature of the glenoid (Jenkins 1973; Rowe 1988; Hu et al. 1997):

(0) Saddle-shaped, oval and elongate: *Probainognathus*, tritylodontids, tritheledontids, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Haldanodon*, *Ornithorhynchus*;

(1) Uniformly concave and more rounded in outline: *Jeholodens*, *Gobiconodon*, cimolodontans, *Zhangheotherium*, *Henkelotherium*, *Vincelestes*, *Asiatherium*, *Didelphis*, *Pucadelphys*, *Erinaceus*;

(?) Not preserved: *Adelobasileus*, *Dinnetherium*, *Hadrocodium*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Amphilestes*, *Priacodon*, *Triaracodon*, *Haramiyavia*, "plagiaulacidans", *Tinodon*, *Dryolestes*, *Amphitherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Prokennalestes*, *Montanalestes*, *Asioryctes*, *Deltatheridium*, *Kokopellia*, *Pappotherium*.

143. Medial surface of the scapula (Sereno and McKenna 1995; Hu et al. 1997):

(0) Convex: *Probainognathus*, tritylodontids, tritheledontids, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Ornithorhynchus* (if the curvature of the medial surface near the anterior scapular border is taken into account), cimolodontans;

(1) flat: *Gobiconodon*, *Jeholodens*, *Zhangheotherium*, *Henkelotherium*, *Vincelestes*, *Erinaceus*, *Asiatherium*, *Pucadelphys*, *Didelphis*;

(?) Not preserved: *Adelobasileus*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Amphilestes*, *Priacodon*, *Triaracodon*, *Haramiyavia*, "plagiaulacidans", *Tinodon*, *Dryolestes*, *Amphitherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Kokopellia*, *Pappotherium*, *Prokennalestes*, *Montanalestes*, *Asioryctes*.

Forelimb (12 characters)

144. Humeral head (Rowe 1988, character 120; new definition of character states by Hu et al. 1997):

(0) Subspherical, weakly inflected: *Probainognathus*, tritylodontids, tritheledontids, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Haldanodon*, *Ornithorhynchus*, *Gobiconodon*, *Jeholodens*;

(1) Spherical and strongly inflected: cimolodontans, *Zhangheotherium*, *Henkelotherium*, *Vincelestes*, *Asiatherium*, *Didelphis*, *Pucadelphys*, *Erinaceus*;

(?) Not preserved: *Adelobasileus*, *Dinnetherium*, *Hadrocodium*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Amphilestes*, *Priacodon*, *Triaracodon*, *Haramiyavia*, "plagiaulacidans", *Tinodon*, *Dryolestes*, *Amphitherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Prokennalestes*, *Montanalestes*, *Asioryctes*, *Deltatheridium*, *Kokopellia*, *Pappotherium*.

145. Intertubercular groove that separates deltopectoral crest from lesser tubercle (modified from Rowe 1988, characters 121, 122, 123):

(0) Shallow and broad intertubercular groove: *Probainognathus*, tritylodontids, tritheledontids, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Haldanodon*, *Ornithorhynchus*, *Gobiconodon*, cimolodontans, *Vincelestes*;

(1) Narrow and deep intertubercular groove: *Zhangheotherium*, *Henkelotherium*, *Asiatherium*, *Didelphis*, *Pucadelphys*, *Erinaceus*;

(?) Not preserved: *Adelobasileus*, *Dinnetherium*, *Hadrocodium*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Jeholodens*, *Amphilestes*, *Priacodon*, *Triaracodon*, *Haramiyavia*, "plagiaulacidans", *Tinodon*, *Dryolestes*, *Amphitherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Kokopellia*, *Pappotherium*, *Prokennalestes*, *Montanalestes*, *Asioryctes*.

146. Size of the lesser tubercle of humerus (relative to the greater tubercle) (Gambaryan and Kielan-Jaworowska 1997):

(0) Wider than the greater tubercle: *Probainognathus*, tritylodontids, tritheledontids, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Ornithorhynchus*, *Gobiconodon*, cimolodontans;

(1) Narrower than the greater tubercle: *Zhangheotherium*, *Vincelestes*, *Asiatherium*, *Didelphis*, *Pucadelphys*, *Erinaceus*;

(?) Not preserved: *Adelobasileus*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Jeholodens*, *Amphilestes*, *Priacodon*, *Triaracodon*, *Haramiyavia*, "plagiaulacidans", *Tinodon*, *Dryolestes*, *Amphitherium*, *Peramus*, *Henkelotherium*, *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Kokopellia*, *Pappotherium*, *Prokennalestes*, *Montanalestes*, *Asioryctes*.

147. Torsion between the proximal and distal ends of the humerus (Rougier et al. 1996b; Gambaryan and Kielan-Jaworowska 1997; Kielan-Jaworowska 1998):

(0) Strong ($\geq 30^\circ$): *Probainognathus*, tritylodontids, tritheledontids, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Haldanodon*, *Ornithorhynchus*, *Gobiconodon*, *Jeholodens*, *Vincelestes*;

(1) Moderate ($30-15^\circ$): *Zhangheotherium*, *Henkelotherium*;

(2) Weak ($\leq 15^\circ$): *Asiatherium*, *Didelphis*, *Pucadelphys*, *Erinaceus*;

(1/2 polymorphic): cimolodontans (coded 1, see Kielan-Jaworowska and Qi 1990; Kielan-Jaworowska and Gambaryan 1994; Kielan-Jaworowska 1998; coded 2, see Sereno and McKenna 1995).

(?) Not preserved: *Adelobasileus*, *Dinnetherium*, *Hadrocodium*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Amphilestes*, *Priacodon*, *Triaracodon*, *Haramiyavia*, "plagiaulacidans", *Tinodon*, *Dryolestes*, *Amphitherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Kokopellia*, *Pappotherium*, *Prokennalestes*, *Montanalestes*, *Asioryctes*.

148. Ventral extension of the deltopectoral crest or position of deltoid tuberosity (Hu et al. 1997, 1998):

(0) Not extending beyond the midpoint of the humeral shaft: *Probainognathus*, tritheledontids, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, cimolodontans, *Henkelotherium*, *Vincelestes*, *Asiatherium*, *Didelphis*, *Pucadelphys*, *Erinaceus*;

(1) Extending ventrally (distally) past the midpoint of the shaft: *Haldanodon*, *Ornithorhynchus*, *Gobiconodon*, *Jeholodens*, *Priacodon* (Engelmann and Callison (1998); *Zhangheotherium*, *Dryolestes* (see Martin 2000: fig. 16.8); (0/1 polymorphic) tritylodontids (*Oligokyphus*, 0; *Kayentatherium*, 1);

(?) Not preserved: *Adelobasileus*, *Dinnetherium*, *Hadrocodium*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Amphilestes*, *Triaracodon*, *Haramiyavia*, "plagiaulacidans", *Tinodon*, *Amphitherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Kokopellia*, *Pappotherium*, *Prokennalestes*, *Montanalestes*, *Asioryctes*.

149. Ulnar articulation on the distal humerus (Rowe 1988, character 126, new definitions of character states):

(0) Bulbous ulnar condyle: *Probainognathus*, tritylodontids, tritheledontids, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Haldanodon*, *Ornithorhynchus*, *Haramiyavia* (based on Jenkins et al. 1997), cimolodontans;

(1) Cylindrical trochlea (in posterior view) with vestigial ulnar condyle (in anterior view): *Jeholodens*, *Gobiconodon*, *Priacodon*, *Zhangheotherium*, *Dryolestes*, *Henkelotherium*, *Vincelestes* (personal communication from G.W. Rougier);

(2) Cylindrical trochlea without ulnar condyle (cylindrical trochlea has extended to the anteriorventral side): *Asiatherium*, *Didelphis*, *Pucadelphys*, *Erinaceus*.

(?) Not preserved: *Adelobasileus*, *Dinnetherium*, *Hadrocodium*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Amphilestes*, *Trioracodon*, “plagiaulacidans”, *Tinodon*, *Amphitherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Kokopellia*, *Pappotherium*, *Prokennalestes*, *Montanalestes*, *Asioryctes*.

150. Radial articulation on the distal humerus:

(0) Distinct and rounded condyle in both anterior (ventral) and posterior (dorsal) aspects of the structure that does not form continuous synovial surface with the ulnar articulation in the anteriorventral view of the humerus: *Probainognathus*, tritylodontids, tritheledontids, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Haldanodon*, *Ornithorhynchus*, *Gobiconodon*, *Jeholodens*, *Priacodon*, *Haramiyavia* (based on Jenkins et al. 1997), cimolodontans,

(1) Radial articulation forms a rounded condyle anteriorly but its posterior surface is nearly cylindrical: *Zhangheotherium*, *Dryolestes*, *Henkelotherium*, *Vincelestes*;

(2) Capitulum (radial articulating structure that forms continuous synovial surface with ulnar trochlea; the surface is cylindrical in both anterior and posterior aspects): *Asiatherium*, *Didelphis*, *Pucadelphys*, *Erinaceus*;

(?) Not preserved: *Adelobasileus*, *Dinnetherium*, *Hadrocodium*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Tinodon*, *Amphilestes*, *Trioracodon*, “plagiaulacidans”, *Amphitherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Kokopellia*, *Pappotherium*, *Prokennalestes*, *Montanalestes*, *Asioryctes*.

151. Entepicondyle and ectepicondyle of the humerus (Rowe 1988, character 124):

(0) Robust: *Probainognathus*, tritylodontids, tritheledontids, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Haldanodon*, *Ornithorhynchus*, *Gobiconodon*;

(1) Weak: *Jeholodens*, *Priacodon*, *Zhangheotherium*, *Dryolestes*, *Henkelotherium*, *Vincelestes*, *Asiatherium*, *Didelphis*, *Pucadelphys*, *Erinaceus*;

(0/1 polymorphic): cimolodontans (1 for weak epicondyles in most taxa, 0 for the hypertrophies in *Lambdopsalis*, see Kielan-Jaworowska and Qi 1990; Gambaryan and Kielan-Jaworowska 1997);

(?) Not preserved: *Adelobasileus*, *Dinnetherium*, *Hadrocodium*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Amphilestes*, *Trioracodon*, *Haramiyavia*, “plagiaulacidans”, *Tinodon*, *Amphitherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Kokopellia*, *Pappotherium*, *Prokennalestes*, *Montanalestes*, *Asioryctes*.

152. Rectangular shelf for the supinator ridge extended from the ectepicondyle:

(0) Absent: *Probainognathus*, tritylodontids, tritheletonids, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Haldanodon*, *Gobiconodon*, *Jeholodens*, *Priacodon*, *Ornithorhynchus*, cimolodontans, *Zhangheotherium*, *Dryolestes*, *Henkelotherium*, *Vincelestes*, *Erinaceus*, *Asioryctes*;

(1) Present: *Asiatherium*, *Didelphis*, *Pucadelphys*;

(?) Not preserved: *Adelobasileus*, *Dinnetherium*, *Hadrocodium*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon*, “plagiaulacidans”, *Amphilestes*, *Trioracodon*, *Tinodon*, *Amphitherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Aegialodon*, *Deltatheridium*, *Kokopellia*, *Pappotherium*, *Montanalestes*, *Prokennalestes*.

153. Styloid process of the radius (Rowe 1988, character 129):

(0) Weak: *Probainognathus*, tritylodontids, tritheledontids (Gow in press), *Sinoconodon*, *Morganucodon*, *Haldanodon*, *Ornithorhynchus*, *Gobiconodon*, *Jeholodens*, *Priacodon*, *Zhangheotherium*, *Dryolestes*, *Vincelestes*;

(1) Strong: cimolodontans, *Henkelotherium*, *Asiatherium*, *Didelphis*, *Pucadelphys*, *Erinaceus*, *Asioryctes*;

(?) Not preserved: *Adelobasileus*, *Megazostrodon*, *Dinnetherium*, *Hadrocodium*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Amphilestes*, *Trioracodon*, *Haramiyavia*, “plagiaulacidans”, *Tinodon*, *Amphitherium*, *Peramus*,

Aegialodon, *Kielantherium*, *Deltatheridium*, *Kokopellia*, *Pappotherium*, *Prokennalestes*, *Montanalestes*.

154. Enlargement of the scaphoid with a distomedial projection (Szalay and Trofimov 1996):

(0) Absent: *Probainognathus*, tritylodontids, tritheletonids, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Jeholodens*, *Ornithorhynchus*, cimolodontans, *Zhangheotherium*, *Henkelotherium*, *Vincelestes*, *Erinaceus*, *Asioryctes*;

(1) Present: *Asiatherium*, *Didelphis*, *Pucadelphys*;

(?) Not preserved: *Haramiyavia*, *Adelobasileus*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon*, “plagiaulacidans”, *Gobiconodon*, *Amphilestes*, *Priacodon*, *Trioracodon*, *Tinodon*, *Dryolestes*, *Amphitherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Kokopellia*, *Pappotherium*, *Montanalestes*, *Prokennalestes*.

155. Size and shape of the hamate (unciform) in the wrist:

(0) Anteroposteriorly compressed (wider than long in dorsal view): *Megazostrodon*, *Jeholodens*, *Ornithorhynchus*, cimolodontans, *Zhangheotherium*;

(1) Mediolaterally compressed (longer than wide): *Erinaceus*, *Asioryctes*, *Didelphis*;

(?) Not preserved: *Probainognathus*, tritylodontids, tritheletonids, *Adelobasileus*, *Sinoconodon*, *Morganucodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon*, “plagiaulacidans”, *Gobiconodon*, *Amphilestes*, *Priacodon*, *Trioracodon*, *Tinodon*, *Dryolestes*, *Henkelotherium*, *Vincelestes*, *Amphitherium*, *Peramus*, *Kielantherium*, *Aegialodon*, *Deltatheridium*, *Asiatherium*, *Pucadelphys*, *Kokopellia*, *Pappotherium*, *Montanalestes*, *Prokennalestes*.

Pelvic girdle (3 characters)

156. Acetabular dorsal emargination (cotyloid notch of Kühne 1956; Rowe 1988, character 134; modified by Hu et al. 1997):

(0) Open (emarginated): *Probainognathus*, tritylodontids, tritheledontids, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Gobiconodon* (inferred from the incomplete iliac circumference to the acetabulum), *Jeholodens*, cimolodontans, *Vincelestes*, *Asiatherium*;

(1) Closed (with a complete rim): *Ornithorhynchus*, *Zhangheotherium*, *Didelphis*, *Pucadelphys*, *Erinaceus*;

(?) Not preserved: *Adelobasileus*, *Sinoconodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Amphilestes*, *Trioracodon*, *Priacodon*, *Haramiyavia*, “plagiaulacidans”, *Tinodon*, *Henkelotherium*, *Dryolestes*, *Amphitherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Kokopellia*, *Pappotherium*, *Prokennalestes*, *Montanalestes*, *Asioryctes*.

157. Sutures of the ilium, ischium, and pubis within the acetabulum in adults (Ji et al. 1999):

(0) Unfused: tritylodontids (Oligokyphus, Kühne 1956), *Morganucodon*, *Megazostrodon*, *Jeholodens*, *Gobiconodon*, *Zhangheotherium*, *Henkelotherium*;

(1) Fused: *Ornithorhynchus*, cimolodontans, *Vincelestes*, *Asiatherium*, *Didelphis*, *Pucadelphys*, *Erinaceus*;

(?) Not preserved: *Probainognathus*, tritheledontids, *Adelobasileus*, *Sinoconodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Amphilestes*, *Trioracodon*, *Priacodon*, *Haramiyavia*, “plagiaulacidans”, *Tinodon*, *Dryolestes*, *Amphitherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Kokopellia*, *Pappotherium*, *Prokennalestes*, *Montanalestes*, *Asioryctes*.

158. Ischiatic dorsal margin and tuberosity:

(0) Dorsal margin concave (emarginated) and ischiatic tuberosity present: tritylodontids, *Morganucodon*, *Megazostrodon*;

(1) Dorsal margin concave and ischiatic tubercle hypertrophied: *Ornithorhynchus*, cimolodontans;

(2) Dorsal margin straight and ischiatic tubercle small: *Gobiconodon*, *Jeholodens*, *Zhangheotherium*, *Henkelotherium*, *Vincelestes*, *Asiatherium*, *Didelphis*, *Pucadelphys*, *Erinaceus*;

(?) Not preserved: *Probainognathus*, tritheledontids, *Adelobasileus*, *Sinoconodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Amphilestes*, *Trioracodon*, *Priacodon*, *Kuehneotherium*, *Tinodon*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Haramiyavia*, “plagiaulacidans”, *Peramus*, *Amphitherium*, *Dryolestes*, *Kielantherium*, *Aegialodon*, *Deltatheridium*, *Kokopellia*, *Pappotherium*, *Asioryctes*, *Prokennalestes*, *Montanalestes*.

Hind limb (11 characters)

159. Head of the femur is inflected and set off from the shaft by a neck (Rowe 1988, characters 141, 142; modified by Hu et al. 1997):

(0) Neck absent (and head oriented dorsally): *Probainognathus*, tritylodontids, tritheledontids, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Haldanodon*, *Ornithorhynchus*, *Jeholodens*, *Gobiconodon*;

(1) Neck present and head inflected medially; head spherical and inflected: cimolodontans, *Zhangheotherium*, *Henkelotherium*, *Vincelestes*, *Asiatherium*, *Didelphis*, *Pucadelphys*, *Erinaceus*;

(?) Not preserved: *Adelobasileus*, *Dinnetherium*, *Haldanodon*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Amphilestes*, *Triaracodon*, *Priacodon*, *Haramiyavia*, "plagiaulacidans", *Tinodon*, *Dryolestes*, *Amphitherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Kokopellia*, *Pappotherium*, *Prokennalestes*, *Montanalestes*, *Asioryctes*.

160. Fovea for the acetabular ligament on femoral head (Gambaryan and Averianov 2001; data from Jenkins 1971; Jenkins and Parrington 1976; Kielan-Jaworowska and Gambaryan 1994):

(0) Absent: *Probainognathus*, tritylodontids (Kühne 1956; Sues 1983), *Sinoconodon*, *Ornithorhynchus*, *Gobiconodon*, *Jeholodens*;

(1) Present: *Morganucodon*, *Megazostrodon*, cimolodontans, *Henkelotherium*, *Vincelestes*, *Didelphis*, *Pucadelphys*, *Erinaceus*;

(?) Unknown: tritheledontids, *Adelobasileus*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Amphilestes*, *Triaracodon*, *Priacodon*, *Haramiyavia*, "plagiaulacidans", *Zhangheotherium*, *Tinodon*, *Dryolestes*, *Amphitherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Asiatherium*, *Kokopellia*, *Pappotherium*, *Asioryctes*, *Prokennalestes*, *Montanalestes*.

161. Greater trochanter (Rowe 1988, character 143):

(0) Directed dorsolaterally: *Probainognathus*, tritylodontids, tritheledontids, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Haldanodon*, *Ornithorhynchus*, *Jeholodens*, *Gobiconodon*;

(1) Directed dorsally: cimolodontans, *Zhangheotherium*, *Henkelotherium*, *Vincelestes*, *Asiatherium*, *Didelphis*, *Pucadelphys*, *Erinaceus*;

(?) Not preserved: *Adelobasileus*, *Dinnetherium*, *Hadrocodium*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Amphilestes*, *Triaracodon*, *Priacodon*, *Haramiyavia*, "plagiaulacidans", *Tinodon*, *Dryolestes*, *Amphitherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Kokopellia*, *Pappotherium*, *Prokennalestes*, *Montanalestes*, *Asioryctes*.

162. Orientation of the lesser trochanter (Rowe 1988, character 144):

(0) On medial side of shaft: *Probainognathus*, tritylodontids, tritheledontids, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Haldanodon*, *Ornithorhynchus*, *Jeholodens*, *Gobiconodon*, *Vincelestes*;

(1) On the ventromedial or ventral side of the shaft: cimolodontans (ventral), *Zhangheotherium*, *Henkelotherium*, *Erinaceus*, *Asiatherium*, *Pucadelphys*, *Didelphis*,

(?) Not preserved: *Adelobasileus*, *Dinnetherium*, *Hadrocodium*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Amphilestes*, *Triaracodon*, *Priacodon*, *Haramiyavia*, "plagiaulacidans", *Tinodon*, *Dryolestes*, *Amphitherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Kokopellia*, *Pappotherium*, *Prokennalestes*, *Montanalestes*, *Asioryctes*.

163. Size of the lesser trochanter:

(0) Large: *Probainognathus*, tritylodontids, tritheledontids, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Haldanodon*, *Ornithorhynchus*, *Gobiconodon*, *Jeholodens*, cimolodontans, *Zhangheotherium*, *Henkelotherium*, *Vincelestes*;

(1) Small: *Asiatherium*, *Pucadelphys*, *Didelphis*, *Erinaceus*;

(?) Not preserved: *Adelobasileus*, *Dinnetherium*, *Hadrocodium*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Amphilestes*, *Triaracodon*, *Priacodon*, *Haramiyavia*, "plagiaulacidans", *Tinodon*, *Dryolestes*, *Amphitherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Kokopellia*, *Pappotherium*, *Prokennalestes*, *Montanalestes*, *Asioryctes*.

164. Patellar facet ("groove") of the femur (Rowe 1988, character 145; distribution modified):

(0) Absent: *Probainognathus*, tritylodontids, *Sinoconodon*;

(1) Shallow and weakly developed: *Morganucodon* (Jenkins and Parrington 1976), *Jeholodens*, *Gobiconodon*, *Asiatherium*, *Didelphis*, *Pucadelphys* (marsupials coded after the interpretation by Szalay and Trofimov 1996);

(2) Well developed: *Ornithorhynchus*, cimolodontans, *Zhangheotherium*, *Henkelotherium*, *Vincelestes*, *Erinaceus*;

(?) Not preserved: tritheledontids, *Adelobasileus*, *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Amphilestes*, *Triaracodon*, *Priacodon*, *Haramiyavia*, "plagiaulacidans", *Tinodon*, *Dryolestes*, *Amphitherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Kokopellia*, *Pappotherium*, *Prokennalestes*, *Montanalestes*, *Asioryctes*.

165. Proximolateral tubercle or tuberosity of the tibia (Jenkins and Parrington 1976; Kielan-Jaworowska and Gambaryan 1994):

(0) Large and hook-like: tritylodontids, *Morganucodon*, *Megazostrodon*, *Haldanodon*, *Gobiconodon*, *Jeholodens*, *Ornithorhynchus*, cimolodontans;

(1) Indistinctive: *Zhangheotherium*, *Henkelotherium*, *Vincelestes*, *Asiatherium*, *Didelphis*, *Pucadelphys*, *Erinaceus*;

(?) Not preserved: *Probainognathus*, tritheledontids, *Adelobasileus*, *Sinoconodon*, *Dinnetherium*, *Hadrocodium*, *Amphilestes*, *Priacodon*, *Triaracodon*, *Kuehneotherium*, *Tinodon*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Haramiyavia*, "plagiaulacidans", *Peramus*, *Amphitherium*, *Dryolestes*, *Kielantherium*, *Aegialodon*, *Deltatheridium*, *Kokopellia*, *Pappotherium*, *Asioryctes*, *Prokennalestes*, *Montanalestes*.

166. Distal tibial malleolus:

(0) Weak: *Probainognathus*, tritylodontids, *Megazostrodon*, *Jeholodens*, *Gobiconodon*, *Zhangheotherium*,

(1) Distinct: *Ornithorhynchus*, cimolodontans, *Henkelotherium*, *Vincelestes*, *Asiatherium*, *Pucadelphys*, *Didelphis*, *Erinaceus*, *Asioryctes*;

(?) Not preserved: tritheledontids, *Adelobasileus*, *Sinoconodon*, *Morganucodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Amphilestes*, *Triaracodon*, *Priacodon*, *Haramiyavia*, "plagiaulacidans", *Tinodon*, *Dryolestes*, *Amphitherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Kokopellia*, *Pappotherium*, *Prokennalestes*, *Montanalestes*.

167. Fibula contacting distal end of the femur (Szalay and Trofimov 1996):

(0) Present: *Probainognathus*, tritylodontids, tritheledontids, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Ornithorhynchus*, cimolodontans, *Henkelotherium*, *Vincelestes*, *Erinaceus*, *Asioryctes*;

(1) Absent: *Gobiconodon*, *Jeholodens*, *Zhangheotherium*, *Asiatherium*, *Didelphis*, *Pucadelphys*;

(?) Not preserved: *Adelobasileus*, *Dinnetherium*, *Hadrocodium*, *Haldanodon*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Amphilestes*, *Triaracodon*, *Priacodon*, *Haramiyavia*, "plagiaulacidans", *Tinodon*, *Dryolestes*, *Amphitherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Aegialodon*, *Deltatheridium*, *Kokopellia*, *Pappotherium*, *Montanalestes*, *Prokennalestes*.

168. Distal fibular styloid process:

(0) Weak or absent: *Probainognathus*, tritylodontids, *Megazostrodon*, *Ornithorhynchus*, *Gobiconodon*, *Jeholodens*, cimolodontans, *Zhangheotherium*, *Pucadelphys*, *Asiatherium*, *Didelphis*;

(1) Distinct: *Henkelotherium*, *Vincelestes*, *Asioryctes*, *Erinaceus*;

(?) Not preserved: tritheledontids, *Adelobasileus*, *Sinoconodon*, *Morganucodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Amphilestes*, *Triaracodon*, *Priacodon*, *Haramiyavia*, "plagiaulacidans", *Tinodon*, *Dryolestes*, *Amphitherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Kokopellia*, *Pappotherium*, *Prokennalestes*, *Montanalestes*.

169. Fibula contacting the calcaneus (= "tricontact upper ankle joint" of Szalay 1993b):

(0) Extensive contact: *Probainognathus*, tritylodontids, *Morganucodon*, *Megazostrodon*, *Ornithorhynchus*, *Jeholodens*, *Gobiconodon*, cimolodontans, *Zhangheotherium*, *Henkelotherium*, *Vincelestes*;

(1) Reduced: *Deltatheridium* (Horovitz 2000), *Asiatherium*, *Pucadelphys*, *Didelphis*;

(2) Mortise and tenon contact of fibula to the ankle (Szalay 1984, 1994): *Erinaceus*, *Asioryctes*;

(?) Not preserved: tritheledontids, *Adelobasileus*, *Bishops*, *Sinoconodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Amphilestes*, *Triaracodon*, *Priacodon*, *Haramiyavia*, "plagiaulacidans", *Tinodon*, *Dryolestes*, *Amphitherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Kokopellia*, *Pappotherium*, *Prokennalestes*, *Montanalestes*.

Ankle joint (10 characters)

170. Superposition (overlap) of the astragalus over the calcaneus (lower ankle joint) (Jenkins 1971; Rowe 1988; Kielan-Jaworowska 1997):

(0) Little or absent: *Probainognathus*, tritylodontids, *Morganucodon*, *Megazostrodon*, *Ornithorhynchus*, *Jeholodens*;

(1) Weakly developed: cimolodontans, *Zhangheotherium*;

(2) Present: *Vincelestes*, *Deltatheridium*, *Didelphis*, *Pucadelphys*, *Erinaceus*, *Asioryctes*;

(?) Not preserved: tritheledontids, *Adelobasileus*, *Sinoconodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Kuehneotherium*, *Gobiconodon*, *Amphilestes*, *Trioracodon*, *Priacodon*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Haramiyavia*, “plagiaulacidans”, *Tinodon*, *Dryolestes*, *Amphitherium*, *Peramus*, *Henkelotherium*, *Aegialodon*, *Kielantherium*, *Asiatherium*, *Kokopellia*, *Pappotherium*, *Prokennalestes*, *Montanalestes*.

171. Orientation of the sustentacular facet of the calcaneus with regard to horizontal plane astragalus over (lower ankle joint) (Szalay 1994; Horovitz 2000):

(0) Nearly vertical: tritylodontids, *Morganucodon*, *Megazostrodon*, *Ornithorhynchus*, *Jeholodens*, cimolodontans;

(1) Oblique ($\leq 70^\circ$) to nearly horizontal: *Zhangheotherium*, *Vincelestes*, *Deltatheridium*, *Didelphis*, *Pucadelphys*, *Erinaceus*, *Asioryctes*;

(?) Not preserved: *Probainognathus*, tritheledontids, *Adelobasileus*, *Sinoconodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Kuehneotherium*, *Gobiconodon*, *Amphilestes*, *Trioracodon*, *Priacodon*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Haramiyavia*, “plagiaulacidans”, *Tinodon*, *Dryolestes*, *Amphitherium*, *Peramus*, *Henkelotherium*, *Aegialodon*, *Kielantherium*, *Asiatherium*, *Kokopellia*, *Pappotherium*, *Prokennalestes*, *Montanalestes*.

172. Astragalar neck (Ji et al. 1999):

(0) Absent: tritylodontids, *Morganucodon*, *Megazostrodon*, *Ornithorhynchus*, *Jeholodens*, cimolodontans, *Zhangheotherium*, *Vincelestes*;

(1) Weakly developed: *Didelphis*, *Pucadelphys*;

(2) Present: *Erinaceus*, *Asioryctes*;

(?) Not preserved: *Probainognathus*, tritheledontids, *Adelobasileus*, *Sinoconodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Gobiconodon*, *Amphilestes*, *Trioracodon*, *Priacodon*, *Haramiyavia*, “plagiaulacidans”, *Tinodon*, *Dryolestes*, *Amphitherium*, *Henkelotherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Asiatherium*, *Kokopellia*, *Pappotherium*, *Prokennalestes*, *Montanalestes*.

173. Astragalar trochlea:

(0) Absent: tritylodontids, *Morganucodon*, *Megazostrodon*, *Jeholodens*, cimolodontans, *Zhangheotherium* (new specimen);

(1) Present: *Vincelestes*, *Erinaceus*, *Asioryctes*, *Pucadelphys*, *Didelphis*;

(?) Not preserved: *Probainognathus*, tritheledontids, *Adelobasileus*, *Sinoconodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Bishops*, *Ausktribosphenos*, *Steropodon*, *Teinolophos*, *Obdurodon*; not applicable: *Ornithorhynchus* (The platypus has a condyle on the dorsomedial aspect of the astragalus for the trough on the distal end of the tibia. It serves to allow the tibio-astragal joint to rotate with respect to the transverse axis of the foot for extension and flexion, see Szalay 1993b. However, the astragalus lacks a true trough as in the astragalar trochlea of extant therians. For these reasons we coded *Ornithorhynchus* as “?”), *Gobiconodon*, *Amphilestes*, *Trioracodon*, *Priacodon*, *Haramiyavia*, “plagiaulacidans”, *Henkelotherium*, *Tinodon*, *Dryolestes*, *Amphitherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Asiatherium*, *Kokopellia*, *Pappotherium*, *Prokennalestes*, *Montanalestes*.

174. Calcaneal tubercle (Rowe 1988, character 151):

(0) Short, without terminal swelling: *Probainognathus*, tritylodontids, *Morganucodon*, *Megazostrodon*, *Ornithorhynchus*, *Jeholodens*;

(1) Elongate, vertically deep, and mediolaterally compressed; with terminal swelling: cimolodontans, *Zhangheotherium*, *Vincelestes*, *Henkelotherium*, *Deltatheridium* (Horovitz 2000), *Pucadelphys*, *Didelphis*, *Erinaceus*, *Asioryctes*,

(?) Not preserved: tritheledontids, *Adelobasileus*, *Sinoconodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Gobiconodon*, *Amphilestes*, *Trioracodon*, *Priacodon*, *Haramiyavia*, “plagiaulacidans”, *Tinodon*, *Dryolestes*, *Amphitherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Asiatherium*, *Kokopellia*, *Pappotherium*, *Prokennalestes*, *Montanalestes*.

175. Peroneal process and groove of the calcaneus (modified from Kielan-Jaworowska and Gambaryan 1994):

(0) Forming laterally directed shelf, and without a distinct process: *Probainognathus*, tritylodontids, *Morganucodon*, *Megazostrodon*, *Gobiconodon*, *Jeholodens*;

(1) Weakly developed with shallow groove on lateral side of process: *Zhangheotherium*, *Vincelestes*, *Didelphis*, *Pucadelphys*, *Erinaceus*, *Asioryctes*;

(2) With a distinct peroneal process: *Ornithorhynchus* (after the homology proposed by Szalay 1993b), cimolodontans (with a distinct peroneal process: demarcated by a deep peroneal groove at the base);

(?) Not preserved: tritheledontids, *Adelobasileus*, *Sinoconodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Amphilestes*, *Trioracodon*, *Priacodon*, *Haramiyavia*, “plagiaulacidans”, *Tinodon*, *Henkelotherium*, *Dryolestes*, *Amphitherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Asiatherium*, *Kokopellia*, *Pappotherium*, *Prokennalestes*, *Montanalestes*, *Deltatheridium*.

176. Contact of the cuboid on the calcaneus (following the orientation identified by Lewis 1983; Szalay 1993b) (new character, modified from Kielan-Jaworowska 1997):

(0) On the anterior (distal) end of the calcaneus (the cuboid is aligned with the long axis of the calcaneus): tritylodontids (*Oligokyphus* as illustrated by Szalay 1993b), *Morganucodon* (inferred from the orientation of the cuboid facet on the calcaneus), *Zhangheotherium*, *Vincelestes* (Rougier 1993), *Didelphis*, *Pucadelphys*, *Erinaceus*, *Asioryctes*;

(1) On the anteromedial aspect of the calcaneus: (the cuboid is skewed to the medial side of the long axis of the calcaneus): *Ornithorhynchus* (Grassé 1955; Szalay 1993b; personal observations of American Museum of Natural History – AMNH 65831), *Jeholodens*, cimolodontans (Krause and Jenkins 1983; Kielan-Jaworowska and Gambaryan 1994);

(?) Not preserved: *Probainognathus*, tritheledontids, *Adelobasileus*, *Sinoconodon*, *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Gobiconodon*, *Amphilestes*, *Trioracodon*, *Priacodon*, *Haramiyavia*, “plagiaulacidans”, *Tinodon*, *Dryolestes*, *Amphitherium*, *Henkelotherium*, *Kielantherium*, *Deltatheridium*, *Asiatherium*, *Kokopellia*, *Pappotherium*, *Prokennalestes*, *Montanalestes*, *Asioryctes*.

177. Orientation and placement of the sustentacular facet on the calcaneus (modified from Szalay 1993b):

(0) The sustentacular facet is vertically oriented on the medial edge of calcaneus: tritylodontids, *Morganucodon*, *Megazostrodon*, *Ornithorhynchus* (ankle orientation and identification of facet in the platypus following Szalay 1993b), *Jeholodens*;

(1) The sustentacular facet is on the dorsal aspect of calcaneus and positioned medial to anteromedial to the astragalar facet on the calcaneus: cimolodontans (medial, for identification of facets see Krause and Jenkins 1983), *Vincelestes*, *Deltatheridium* (anteromedial), *Pucadelphys*, *Didelphis*;

(2) The sustentacular facet is on the dorsal aspect of calcaneus and positioned anterior to the astragalar facet on the calcaneus: *Erinaceus*, *Asioryctes*;

(?) Not preserved: *Probainognathus*, tritheledontids, *Adelobasileus*, *Sinoconodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Kuehneotherium*, *Gobiconodon*, *Amphilestes*, *Trioracodon*, *Priacodon*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Haramiyavia*, “plagiaulacidans”, *Tinodon*, *Zhangheotherium*, *Henkelotherium*, *Dryolestes*, *Amphitherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Asiatherium*, *Kokopellia*, *Pappotherium*, *Prokennalestes*, *Montanalestes*.

178. Relationships of the proximal end of metatarsal V to the cuboid:

(0) Metatarsal V is offset from the cuboid: *Megazostrodon*, *Jeholodens*;

(1) Metatarsal V is far offset from the cuboid, so that it contacts the calcaneus: *Ornithorhynchus* (metatarsal V is bound by ligament to the peroneal tubercle of calcaneus, Szalay 1993b, and confirmed by our personal observations of AMNH 65831), cimolodontans (after Kielan-Jaworowska and Gambaryan 1994);

(2) Metatarsal V is aligned with the cuboid: *Vincelestes*, *Didelphis*, *Pucadelphys*, *Erinaceus*, *Asioryctes*;

(?) Not preserved: *Probainognathus*, tritylodontids, tritheledontids, *Adelobasileus*, *Sinoconodon*, *Morganucodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Gobiconodon*, *Amphilestes*, *Trioracodon*, *Priacodon*, *Haramiyavia*, “plagiaulacidans”, *Tinodon*, *Zhangheotherium*, *Henkelotherium*, *Dryolestes*, *Amphitherium*, *Peramus*, *Kielantherium*, *Deltatheridium*, *Asiatherium*, *Kokopellia*, *Pappotherium*, *Prokennalestes*, *Montanalestes*, *Asioryctes*.

179. Angle of metatarsal III to the calcaneus (which indicates how much the sole of the foot is "bent" from the long axis of the ankle):

(0) Metatarsal III is aligned with (or parallel to) an imaginary line through the long axis of the calcaneus: *Megazostrodon*, *Vincelestes*, *Didelphis*, *Pucadelphys*, *Erinaceus*, *Asioryctes*;

(1) Metatarsal III is oriented oblique to an imaginary line through the long axis of the calcaneus: *Ornithorhynchus*, *Jeholodens*, cimolodontans;

(?) Not preserved: *Probainognathus*, tritylodontids, tritheledontids, *Adelobasileus*, *Sinoconodon*, *Morganucodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Gobiconodon*, *Amphilestes*, *Trioracodon*, *Priacodon*, *Haramiyavia*, "plagiaulacidans", *Zhangheotherium*, *Henkelotherium*, *Tinodon*, *Dryolestes*, *Amphitherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Prokennalestes*, *Deltatheridium*, *Asiatherium*, *Kokopellia*, *Pappotherium*, *Montanalestes*, *Asioryctes*.

Other postcranial characters (2 characters)

180. Sesamoid bones in flexor tendons (Rowe 1988, character 158):

(0) Absent: *Probainognathus*, tritylodontids, *Megazostrodon*, *Jeholodens*;

(1) Present and unpaired: *Ornithorhynchus*;

(2) Present and paired: cimolodontans, *Zhangheotherium*, *Asiatherium*, *Didelphis*, *Erinaceus*;

(?) Not preserved: tritheledontids, *Adelobasileus*, *Sinoconodon*, *Morganucodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Gobiconodon*, *Amphilestes*, *Trioracodon*, *Priacodon*, *Haramiyavia*, "plagiaulacidans", *Tinodon*, *Henkelotherium*, *Dryolestes*, *Amphitherium*, *Peramus*, *Vincelestes*, *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Pucadelphys*, *Kokopellia*, *Pappotherium*, *Prokennalestes*, *Montanalestes*, *Asioryctes*.

181. External pedal (tarsal) spur present in male (modified from Hu et al. 1997, 1998):

(0) Absent: tritylodontids, *Megazostrodon*, *Jeholodens*, *Vincelestes*, *Asiatherium*, *Didelphis*, *Pucadelphys*, *Erinaceus*, *Asioryctes*;

(1) Present: *Gobiconodon*, *Ornithorhynchus*¹, cimolodontans (Wible and Rougier 2000), *Zhangheotherium*, *Henkelotherium* (personal communication from J.R. Wible).

(?) Not preserved: *Probainognathus*, tritheledontids, *Adelobasileus*, *Sinoconodon*, *Morganucodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Bishops*, *Ausktribosphenos*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Amphilestes*, *Trioracodon*, *Priacodon*, *Haramiyavia*, "plagiaulacidans", *Tinodon*, *Dryolestes*, *Amphitherium*, *Peramus*, *Kielantherium*, *Deltatheridium*, *Kokopellia*, *Pappotherium*, *Prokennalestes*, *Montanalestes*, *Asioryctes*.

Basicranium (46 characters)

182. External size of the cranial moiety of squamosal (Rowe 1988; Wible 1991; Luo 1994):

(0) Narrow: *Probainognathus*, tritylodontids, tritheledontids, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Haldanodon*, *Ornithorhynchus*, *Obdurodon*, *Gobiconodon*, *Jeholodens*, cimolodontans;

(1) Broad: *Adelobasileus*, *Hadrocodium*, *Henkelotherium* (Krebs 1991: Abb. 1), *Vincelestes*, *Deltatheridium*, *Asiatherium*, *Pucadelphys*, *Didelphis*, *Asioryctes*, *Erinaceus*;

(?) Not preserved: *Dinnetherium*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Amphilestes*, *Priacodon*, *Trioracodon*, *Haramiyavia*, "plagiaulacidans", *Tinodon*, *Zhangheotherium*, *Dryolestes*, *Amphitherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Kokopellia*, *Pappotherium*, *Prokennalestes*, *Montanalestes*.

¹ The ankle (external pedal) spur is a sexually dimorphic character in living platypus and echidna, present mainly in adult males, and as a rule absent in females or juveniles. Luo and Kielan-Jaworowska (MS in preparation) documented the presence of pedal spur in some multituberculate specimens but not in other individuals of the same species, as mentioned previously also by Wible and Rougier (2000). A similar pattern also occurs in *Zhangheotherium* (the holotype has a spur, but a second specimen of the same taxon lacks it). The best available biological interpretation is that the spur was a (sexually) dimorphic feature in fossils as in extant monotreme families. Alternative, this character can be coded as (0/1) polymorphic: 0, absent for females and juveniles; 1, present for males.

183. Participation of the cranial moiety of the squamosal to the braincase:

(0) Does not participate in the endocranial wall of the braincase (Wible 1991; Luo 1994): *Probainognathus*, tritylodontids, tritheledontids, *Adelobasileus*, *Sinoconodon*, *Morganucodon*, *Haldanodon*, *Hadrocodium*, *Jeholodens*, *Gobiconodon*, *Obdurodon*, *Ornithorhynchus*, "plagiaulacidans", cimolodontans (based on Hurum, 1998);

(1) Participates in the endocranial wall of the braincase: *Vincelestes*, *Deltatheridium*, *Asiatherium*, *Pucadelphys*, *Didelphis*, *Erinaceus*, *Asioryctes*;

(?) Not preserved: *Megazostrodon*, *Dinnetherium*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Amphilestes*, *Priacodon*, *Trioracodon*, *Haramiyavia*, *Tinodon*, *Zhangheotherium*, *Dryolestes*, *Amphitherium*, *Henkelotherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Kokopellia*, *Pappotherium*, *Prokennalestes*, *Montanalestes*.

184. Entoglenoid constriction (neck) between the the craniomandibular joint (or glenoid) and the cranial moiety of the squamosal (only applicable to taxa with the dentary-squamosal joint; this character is best seen in the ventral view) (modified from Luo 1994; Hu et al. 1998):

(0) Absent: *Probainognathus*, tritylodontids, tritheledontids, *Sinoconodon*, *Hadrocodium*, *Obdurodon*, *Ornithorhynchus*, *Vincelestes*;

(1) Present: *Morganucodon*, *Megazostrodon*, *Haldanodon*, *Gobiconodon*, *Jeholodens*, "plagiaulacidans", cimolodontans, *Zhangheotherium*, *Henkelotherium*, *Deltatheridium*, *Asiatherium*, *Pucadelphys*, *Didelphis*, *Erinaceus*, *Asioryctes* (note that among other eutherians this feature is polymorphic; the constriction is absent in zalambdalestids and leptictids, but present in other eutherians);

(?) Not preserved: *Adelobasileus*, *Kuehneotherium*, *Dinnetherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Amphilestes*, *Priacodon*, *Trioracodon*, *Haramiyavia*, *Tinodon*, *Dryolestes*, *Amphitherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Kokopellia*, *Pappotherium*, *Prokennalestes*, *Montanalestes*.

185. Postglenoid depression on squamosal (= "external auditory meatus"):

(0) Present as the post-cranio-mandibular joint sulcus ("external auditory meatus"): *Probainognathus*, tritylodontids;

(1) Absent: tritheledontids, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Ornithorhynchus*, *Jeholodens*, "plagiaulacidans", cimolodontans;

(2) Present: *Jeholodens*, *Haldanodon*, *Hadrocodium*, *Obdurodon*, *Gobiconodon*, *Zhangheotherium*, *Henkelotherium*, *Vincelestes*, *Deltatheridium*, *Asiatherium*, *Pucadelphys*, *Didelphis*, *Asioryctes*, *Erinaceus*;

(?) Not preserved: *Adelobasileus*, *Dinnetherium*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Amphilestes*, *Priacodon*, *Trioracodon*, *Haramiyavia*, *Tinodon*, *Dryolestes*, *Amphitherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Kokopellia*, *Pappotherium*, *Prokennalestes*, *Montanalestes*.

186. Position of the craniomandibular joint (Rowe 1988; Wible 1991):

(0) Posterior or lateral to the level to the fenestra vestibuli: *Probainognathus*, tritylodontids, tritheledontids, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Haldanodon*, *Ornithorhynchus*, *Gobiconodon*, *Jeholodens*;

(1) Anterior to the level of fenestra vestibuli: *Hadrocodium*, *Obdurodon* (see Musser and Archer 1998 for the distinction between *Obdurodon* and *Ornithorhynchus* in this feature), "plagiaulacidans", *Zhangheotherium*, *Vincelestes*, *Deltatheridium*, *Asiatherium*, *Pucadelphys*, *Didelphis*, *Asioryctes*, *Erinaceus*;

(0/1 polymorphic) cimolodontans: ptilodontoids and taeniolabidoids (0); *Chulsanbaatar* and *Nemegtbaatar* (1);

(?) Not preserved: *Adelobasileus*, *Dinnetherium*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Amphilestes*, *Priacodon*, *Trioracodon*, *Haramiyavia*, *Tinodon*, *Dryolestes*, *Amphitherium*, *Peramus*, *Henkelotherium*, *Aegialodon*, *Kielantherium*, *Kokopellia*, *Pappotherium*, *Prokennalestes*, *Montanalestes*.

187. Orientation of the glenoid on the squamosal for the craniomandibular joint (CMJ):

(0) On the inner side of the zygoma and facing ventromedially: *Sinoconodon*, *Hadrocodium*; tritheledontids (a dentary-squamosal contact on the inner side of the zygoma but lack a distinctive glenoid fossa);

(1) On platform of the zygoma and facing ventrally, *Haldanodon*, *Obdurodon*, *Ornithorhynchus*, *Gobiconodon*, *Jeholodens*, "plagiaulacidans", cimolodontans, *Zhangheotherium*, *Henkelotherium*, *Vincelestes*, *Deltatheridium*, *Asiatherium*, *Pucadelphys*, *Didelphis*, *Erinaceus*, *Asioryctes*;

(0/1 polymorphic): *Morganucodon*;

(?) Not applicable: *Probainognathus* (with a squamosal-surangular contact), tritylodontids; not preserved: *Adelobasileus*, *Megazostrodon*, *Dinnetherium*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Amphilestes*, *Priacodon*, *Trioracodon*, *Hara-*

myavia, *Tinodon*, *Dryolestes*, *Amphitherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Kokopellia*, *Pappotherium*, *Prokennalestes*, *Montanalestes*.

188. Postglenoid process:

(0) Absent: *Sinoconodon*, *Obdurodon*, *Ornithorhynchus*, “plagiaulacidans”, cimolodontans;

(1) Present as a distinctive process: *Hadrocodium*, *Haldanodon*, *Gobiconodon*, *Jeholodens*, *Zhangheotherium*, *Henkelotherium*, *Vincelestes*, *Deltatheridium*, *Asiatherium*, *Pucadelphys*, *Didelphis*, *Erinaceus*, *Asioryctes*;

(0/1 polymorphic): *Morganucodon*;

(?) Not applicable: *Probainognathus*, tritylodontids, tritheledontids (tritheledontids have a dentary-squamosal contact on the inner side of the zygoma but lack a distinctive glenoid fossa); not preserved: *Adelobasileus*, *Megazostrodon*, *Dinnetherium*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Amphilestes*, *Priacodon*, *Trioracodon*, *Haramiyavia*, *Tinodon*, *Dryolestes*, *Amphitherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Kokopellia*, *Pappotherium*, *Prokennalestes*, *Montanalestes*.

189. Postglenoid foramen within the squamosal bone:

(0) Absent: *Probainognathus*, tritylodontids, tritheledontids, *Adelobasileus*, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Haldanodon*, *Hadrocodium*, *Obdurodon*, *Ornithorhynchus*, “plagiaulacidans”, cimolodontans, *Gobiconodon*, *Jeholodens*, *Zhangheotherium*, *Vincelestes*, *Henkelotherium*;

(1) Present: *Asiatherium*, *Pucadelphys*, *Didelphis*, *Erinaceus*, *Asioryctes*;

(?) Not preserved: *Adelobasileus*, *Dinnetherium*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Amphilestes*, *Priacodon*, *Trioracodon*, *Tinodon*, *Haramiyavia*, *Dryolestes*, *Amphitherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Kokopellia*, *Pappotherium*, *Prokennalestes*, *Montanalestes*.

190. Basisphenoid wing on the ventral aspect of the skull:

(0) Present, overlapping a part of or the whole cochlear housing: *Probainognathus*, tritylodontids, tritheledontids, *Adelobasileus*;

(1) Basisphenoid wing is absent, the bone does not overlap the petrosal cochlear housing: *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Obdurodon*, *Ornithorhynchus*, *Gobiconodon*, *Trioracodon*, “plagiaulacidans”, cimolodontans, *Zhangheotherium*, *Vincelestes*, *Deltatheridium*, *Asiatherium*, *Pucadelphys*, *Didelphis*, *Erinaceus*, *Asioryctes*, *Prokennalestes* (inferred from pars cochlearis);

(?) Not preserved or not visible: *Kuehneotherium*, *Shuotherium*, *Ausktribosphenos*, *Ambondro*, *Bishops*, *Steropodon*, *Teinolophos*, *Amphilestes*, *Jeholodens*, *Priacodon*, *Haramiyavia*, *Tinodon*, *Dryolestes*, *Amphitherium*, *Peramus*, *Henkelotherium*, *Aegialodon*, *Kielantherium*, *Kokopellia*, *Pappotherium*, *Montanalestes*.

191. Relationship of the pars cochlearis to the lateral lappet of basioccipital (Crompton 1995; Luo 2001):

(0) Pars cochlearis is entirely covered by basioccipital: *Probainognathus*, tritylodontids (Luo 2001), tritheledontids (Crompton 1995);

(1) Pars cochlearis partially covered by basioccipital: *Adelobasileus* (reinterpreted from Lucas and Luo 1993), *Sinoconodon* (Luo, Crompton, and Sun 2001);

(2) Pars cochlearis fully exposed as promontorium: *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Ornithorhynchus*, *Obdurodon*, *Gobiconodon*, *Priacodon*, *Trioracodon*, “plagiaulacidans”, cimolodontans, *Zhangheotherium*, *Vincelestes*, *Deltatheridium*, *Asiatherium*, *Pucadelphys*, *Didelphis*, *Prokennalestes* (Wible et al. 2001), *Asioryctes*, *Erinaceus*;

(?) Not preserved: *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Amphilestes*, *Jeholodens*, *Haramiyavia*, *Tinodon*, *Henkelotherium*, *Dryolestes*, *Amphitherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Kokopellia*, *Pappotherium*, *Montanalestes*.

192. The medial flat facet of the promontorium of the pars cochlearis:

(0) Medial flat facet is present on pars cochlearis: *Sinoconodon*, *Megazostrodon*, *Haldanodon*;

(1) Medial aspect of the promontorium is inflated and convex: *Morganucodon*, *Dinnetherium*, *Hadrocodium*, *Obdurodon*, *Ornithorhynchus*, *Priacodon*, *Trioracodon*, “plagiaulacidans”, cimolodontans, *Zhangheotherium*, *Henkelotherium*, *Vincelestes*, *Deltatheridium*, *Asiatherium*, *Pucadelphys*, *Didelphis*, *Erinaceus*, *Asioryctes*, *Prokennalestes*;

(?) Not preserved: *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Jeholodens*, *Gobiconodon*, *Haramiyavia*, *Amphilestes*, *Tinodon*, *Dryolestes*, *Amphitherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Kokopellia*, *Pappotherium*, *Montanalestes*; not applicable: the pars cochlearis is concealed medially by

the basioccipital: *Probainognathus*, tritylodontids, tritheledontids, *Adelobasileus*.

193. External outline and morphology of the promontorium (Rougier, Wible, and Hopson 1996):

(0) Triangular, with steep and slightly concave lateral wall: *Adelobasileus*, *Sinoconodon*, *Haldanodon*;

(1) Elongate and cylindrical petrosal cochlear housing: *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Ornithorhynchus*, *Obdurodon*, *Gobiconodon*, *Priacodon*, *Trioracodon*, *Jeholodens* (not exposed but based on CT scans), “plagiaulacidans”, cimolodontans (slightly curved), *Zhangheotherium*;

(2) Bulbous and oval-shaped promontorium: *Hadrocodium*, *Vincelestes*, *Deltatheridium*, *Asiatherium*, *Pucadelphys*, *Didelphis*, *Prokennalestes* (Wible et al. 2001), *Asioryctes*, *Erinaceus*;

(?) Not preserved: *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Amphilestes*, *Tinodon*, *Haramiyavia*, *Henkelotherium*, *Dryolestes*, *Amphitherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Kokopellia*, *Pappotherium*, *Montanalestes*; not applicable (pars cochlearis does not have an external exposure): *Probainognathus*, tritylodontids, tritheledontids.

194. Cochlea (Rowe 1988; Wible 1991; Luo 1994; Rougier, Wible, and Hopson 1996; Hurum 1998b):

(0) Short and uncoiled: *Probainognathus*, tritylodontids (Luo 2001), tritheledontids (Crompton 1995), *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Gobiconodon* (partially preserved on the Chinese materials), *Jeholodens* (as inferred from CT scan and the internal aspect of the pars cochlearis), *Priacodon*, *Trioracodon*, “plagiaulacidans”, cimolodontans, *Zhangheotherium*;

(1) Elongate and partly coiled: *Ornithorhynchus*, *Vincelestes*;

(2) Elongate and coiled to about 360°: *Didelphis*, *Asiatherium*, *Pucadelphys*, *Deltatheridium*, *Erinaceus*, *Prokennalestes* (Wible et al. 2001), *Asioryctes*;

(?) Not preserved: *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Haramiyavia*, *Amphilestes*, *Tinodon*, *Peramus*, *Henkelotherium*, *Dryolestes*, *Amphitherium*, *Aegialodon*, *Kielantherium*, *Kokopellia*, *Pappotherium*, *Montanalestes*. Unknown in the intact type specimens: *Adelobasileus*, *Hadrocodium*.

195. Morphology of the internal acoustic meatus:

(0) The region for the VII and VIII cranial nerves is poorly ossified and no clearly developed internal auditory meatus is present: *Probainognathus*;

(1) The floor is well ossified and the meatus is a deep tube: tritylodontids, *Sinoconodon*, *Vincelestes*;

(2) Present as a shallow depression: *Megazostrodon*, *Morganucodon*, *Haldanodon*, *Jeholodens*, *Priacodon*, *Trioracodon*, “plagiaulacidans” (the meatus is a shallow depression, but its bottom is preserved, see Hahn 1988; Lillegraven and Hahn 1993);

(3) Present and the floor is developed as the cribriform foramina for auditory nerve: *Ornithorhynchus*, *Didelphis*, *Pucadelphys*, *Erinaceus*, *Prokennalestes* (Wible et al. 2001);

(1/2 polymorphic) cimolodontans;

(?) Not preserved: tritheledontids, *Adelobasileus*, *Dinnetherium*, *Hadrocodium*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Haramiyavia*, *Gobiconodon*, *Amphilestes*, *Tinodon*, *Zhangheotherium*, *Amphitherium*, *Peramus*, *Dryolestes*, *Henkelotherium*, *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Asiatherium*, *Kokopellia*, *Pappotherium*, *Asioryctes*, *Montanalestes*.

196. Primary bony lamina within the cochlear canal (Meng and Fox 1995b; Fox and Meng 1997):

(0) Absent: *Probainognathus*, tritylodontids (Luo 2001), tritheledontids, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Haldanodon*, *Ornithorhynchus*, *Gobiconodon*, cimolodontans;

(1) Present (Meng and Fox 1995a): *Didelphis*, *Erinaceus*, *Prokennalestes* (Wible et al. 2001);

(?) Preserved but not exposed: *Adelobasileus*, *Dinnetherium*, *Obdurodon*, *Jeholodens*, *Amphilestes*, *Priacodon*, *Trioracodon*, *Tinodon*, *Zhangheotherium*, *Vincelestes*, *Deltatheridium*, *Asioryctes*. Not preserved: *Hadrocodium*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Haramiyavia*, “plagiaulacidans”, *Peramus*, *Henkelotherium*, *Dryolestes*, *Amphitherium*, *Aegialodon*, *Kielantherium*, *Asiatherium*, *Kokopellia*, *Pucadelphys*, *Pappotherium*, *Montanalestes*.

197. Secondary bony lamina for the basilar membrane within the cochlear canal (Meng and Fox 1995a; Rougier, Wible, and Hopson 1996; Wible et al. 2001):

(0) Absent: *Probainognathus*, tritylodontids, tritheledontids, *Sinoconodon*, *Morganucodon*, *Haldanodon*, *Ornithorhynchus*, cimolodontans;

(1) Present: *Vincelestes* (Rougier, Wible, and Hopson 1996), *Didelphis* (Meng and Fox 1995a), *Erinaceus*, *Prokennalestes* (Wible et al. 2001);

(?) Unknown (in the intact specimens): *Adelobasileus*, *Megazostrodon*, *Hadrocodium*, *Dinnetherium*, *Obdurodon*, *Jeholodens*, *Amphilestes*, *Trioracodon*, *Priacodon*, *Zhangheotherium*, *Deltatheridium*, *Asioryctes*; not preserved: *Tinodon*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Haramiyavia*, "plagiaulacidans", *Dryolestes*, *Amphitherium*, *Peramus*, *Henkelotherium*, *Aegialodon*, *Kielantherium*, *Asiatherium*, *Kokopellia*, *Pucadelphys*, *Pappotherium*, *Montanalestes*.

198. Crista interfenestralis (Rougier, Wible, and Hopson 1996):

(0) Horizontal and extending to base of paroccipital process: *Probainognathus*, tritylodontids, tritheledontids, *Adelobasileus*, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Obdurodon*, *Ornithorhynchus*, *Gobiconodon*, *Priacodon*, *Trioracodon*; "plagiaulacidans";

(1) Vertical, delimiting the back of the promontorium: cimolodontans, *Zhangheotherium*, *Vincelestes*, *Deltatheridium*, *Didelphis*, *Asiatherium*, *Pucadelphys*, *Erinaceus*, *Prokennalestes*, *Asioryctes*;

(?) Not preserved: *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Jeholodens* (not exposed), *Amphilestes*, *Tinodon*, *Haramiyavia*, *Henkelotherium*, *Dryolestes*, *Amphitherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Kokopellia*, *Pappotherium*, *Montanalestes*.

199. Post-tympanic recess (Rougier, Wible, and Hopson 1996):

(0) Absent: *Probainognathus*, tritylodontids, tritheledontids, *Adelobasileus*, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Obdurodon*, *Ornithorhynchus*, *Gobiconodon*, *Priacodon*, *Trioracodon*, "plagiaulacidans", cimolodontans;

(1) Present: *Zhangheotherium*, *Vincelestes*, *Deltatheridium*, *Asiatherium*, *Pucadelphys*, *Didelphis*, *Erinaceus*, *Asioryctes*, *Prokennalestes*;

(?) Not preserved: *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Jeholodens*, *Amphilestes*, *Tinodon*, *Haramiyavia*, *Zhangheotherium*, *Dryolestes*, *Amphitherium*, *Peramus*, *Henkelotherium*, *Aegialodon*, *Kielantherium*, *Kokopellia*, *Pappotherium*, *Montanalestes*.

200. Caudal tympanic process of the petrosal (Rougier, Wible, and Hopson 1996):

(0) Absent: *Probainognathus*, tritylodontids, tritheledontids, *Adelobasileus*, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Obdurodon*, *Ornithorhynchus*, *Gobiconodon*, *Priacodon*, *Trioracodon*, "plagiaulacidans";

(1) Present: *Zhangheotherium*, *Vincelestes*, *Asiatherium*, *Didelphis*, *Pucadelphys*, *Deltatheridium*;

(2) Caudal tympanic process notched (after Wible 1990; Rougier et al. 1998; Wible et al. 2001): *Erinaceus*, *Asioryctes*, *Prokennalestes*;

(0/1) Polymorphic: cimolodontans (present in some, but not all Cretaceous cimolodontan multituberculates);

(?) Not preserved: *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Haramiyavia*, *Amphilestes*, *Jeholodens*, *Tinodon*, *Dryolestes*, *Amphitherium*, *Peramus*, *Henkelotherium*, *Aegialodon*, *Kielantherium*, *Kokopellia*, *Pappotherium*, *Montanalestes*.

201. The prootic canal (modified from Crompton and Sun 1985; Kielan-Jaworowska et al. 1986; Lucas and Luo 1993; Luo 1994; Wible and Hopson 1995; Rougier, Wible, and Hopson 1996):

(0) Prootic canal absent: tritylodontids, tritheledontids, *Asioryctes*, *Erinaceus*;

(1) Prootic canal present, and its tympanic aperture is a distinct foramen (and separated from the pterygoparoccipital foramen = foramen for the ramus superior of stapedial artery, if the latter is present): *Probainognathus*, *Adelobasileus*, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Haldanodon* (personal communication from J.R. Wible), *Hadrocodium*, *Jeholodens*, *Priacodon*, *Trioracodon*, *Zhangheotherium*, *Vincelestes*, *Deltatheridium*, *Pucadelphys*, *Didelphis* (lacking the ramus superior for the stapedial artery, but has a distinctive prootic canal, see Wible and Hopson 1995), "plagiaulacidans";

(2) Prootic canal is present, and its tympanic aperture is confluent with the pterygoparoccipital foramen: *Ornithorhynchus*, *Obdurodon*, *Prokennalestes* (Wible et al. 2001, prootic canal is absent in other eutherians);

(1/2 polymorphic) cimolodontans (present and confluent in some Paleocene ptilodontoid and taeniolabidid petrosals from North America, present and separate in Asian multituberculata taxa);

(?) Not preserved: *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Gobiconodon*, *Amphilestes*, *Tinodon*, *Haramiyavia*, *Dryolestes*, *Amphitherium*, *Peramus*, *Henkelotherium*, *Aegialodon*, *Kielantherium*, *Asiatherium*, *Kokopellia*, *Pappotherium*, *Montanalestes*.

202. Lateral trough floor anterior to the tympanic aperture of the prootic canal and/or the primary facial foramen (modified from Lucas and Luo 1993; Luo 1994):

(0) Open lateral trough but no bony floor: *Probainognathus*, tritylodontids, tritheledontids (tritylodontids and tritheledontids both lack the prootic canal; in these two groups the primary facial foramen is used as a landmark for assessment of the lateral trough floor);

(1) Present: *Adelobasileus*, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Obdurodon*, *Ornithorhynchus*, *Priacodon*, *Trioracodon*, *Gobiconodon*, "plagiaulacidans", cimolodontans, *Zhangheotherium*, *Vincelestes*;

(2) Lateral trough absent: *Deltatheridium*, *Asiatherium*, *Pucadelphys*, *Didelphis*, *Erinaceus*, *Asioryctes*, *Prokennalestes*;

(?) Not preserved: *Kuehneotherium*, *Shuotherium*, Preserved but not exposed: *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Jeholodens*, *Amphilestes*, *Tinodon*, *Haramiyavia*, *Dryolestes*, *Amphitherium*, *Peramus*, *Henkelotherium*, *Aegialodon*, *Kielantherium*, *Kokopellia*, *Pappotherium*, *Montanalestes*.

203. Enclosure of the geniculate ganglion by bony floor of the petrosal (modified from Crompton and Sun 1985; Wible and Hopson 1993; Luo 1994; Rougier, Wible, and Hopson 1996):

(0) Absent: *Probainognathus*, tritylodontids (with possible exception of *Oligokyphus*), tritheledontids, *Adelobasileus*;

(1) Present: *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Obdurodon*, *Ornithorhynchus*, *Priacodon*, *Trioracodon*, "plagiaulacidans", cimolodontans, *Vincelestes*, *Deltatheridium*, *Pucadelphys*, *Didelphis*, *Erinaceus*, *Asioryctes*, *Prokennalestes*;

(?) Unknown: *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Gobiconodon*, *Jeholodens*, *Amphilestes*, *Tinodon*, *Haramiyavia*, *Zhangheotherium*, *Dryolestes*, *Amphitherium*, *Peramus*, *Henkelotherium*, *Aegialodon*, *Kielantherium*, *Asiatherium*, *Kokopellia*, *Pappotherium*, *Montanalestes*.

204. The anteroventral opening of the cavum epiptericum:

(0) Present: *Probainognathus*, tritylodontids, tritheledontids, *Adelobasileus*;

(1) Present with reduced size (due to the anterior expansion of the lateral trough floor): *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Hadrocodium*, *Obdurodon*, *Ornithorhynchus*;

(2) Present and partially enclosed by the petrosal: *Haldanodon*, *Gobiconodon*, *Priacodon*, *Trioracodon*, "plagiaulacidans", cimolodontans, *Vincelestes*;

(3) Enclosed by both the alisphenoid and the petrosal: *Deltatheridium*, *Asiatherium*, *Pucadelphys*, *Didelphis*, *Erinaceus*, *Asioryctes*, *Prokennalestes*;

(?) Not preserved: *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Jeholodens*, *Amphilestes*, *Tinodon*, *Haramiyavia*, *Zhangheotherium*, *Dryolestes*, *Amphitherium*, *Peramus*, *Henkelotherium*, *Aegialodon*, *Kielantherium*, *Kokopellia*, *Pappotherium*, *Montanalestes*.

205. The anterior lamina of the petrosal and ascending process of the alisphenoid and their relationships to the exit of mandibular branch (V₃) of the trigeminal nerve;

(0) V₃ trigeminal foramen placed at the suture of the alisphenoid ascending process and the anterior lamina of petrosal: *Probainognathus*, tritheledontids, *Haldanodon*;

(1) V₃ trigeminal foramen placed within the enlarged anterior lamina of the petrosal: tritylodontids, *Megazostrodon*, *Dinnetherium*, *Priacodon* (anterior lamina is large, but V₃ foramen is not preserved); *Trioracodon*, *Obdurodon*, *Ornithorhynchus*, *Vincelestes*;

(2) Double trigeminal foramina within the anterior lamina (foramina masticatorium versus inferiorium) in addition to the trigeminal foramen at anterior lamina border with alisphenoid: *Adelobasileus*, *Sinoconodon*, *Morganucodon*, "plagiaulacidans";

(3) V₃ trigeminal foramen within the ascending process of the alisphenoid: *Asiatherium*, *Pucadelphys*, *Didelphis*, *Erinaceus*, *Asioryctes*;

(2/3 polymorphic): state {2} for most cimolodontans, state {3} for *Lambdopsalis* (Miao 1988);

(?) Not preserved: *Haramiyavia*, *Hadrocodium* (not exposed), *Gobiconodon*, *Amphilestes*, *Jeholodens*, *Kuehneotherium*, *Tinodon*, *Shuotherium*,

Ambondro, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Zhangheotherium*, *Dryolestes*, *Henkelotherium*, *Amphitherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Kokopellia*, *Pappotherium*, *Prokennalestes*, *Montanalestes*.

206. The “quadrate ramus” of the alisphenoid:

(0) Forming a rod overlapping with the anterior part of the lateral flange: *Probainognathus*, tritylodontids, tritheledontids, *Adelobasileus*, *Sinoconodon*, *Morganucodon*, *Megazostrodon* (Gow 1986a), *Haldanodon*;

(1) Quadrate ramus absent: *Hadrocodium*, *Obdurodon*, *Ornithorhynchus*, *Gobiconodon*, *Trioracodon*, “plagiaulacidans”, cimolodontans (from Hurum 1998a), *Vincelestes*, *Deltatheridium*, *Asiatherium*, *Pucadelphys*, *Didelphis*, *Erinaceus*, *Asioryctes*;

(?) Not preserved: *Dinnetherium*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Jeholodens*, *Amphilestes*, *Priacodon*, *Tinodon*, *Haramiyavia*, *Zhangheotherium*, *Henkelotherium*, *Dryolestes*, *Amphitherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Kokopellia*, *Pappotherium*, *Prokennalestes*, *Montanalestes*.

207. Orientation of the anterior part of the lateral flange (modified from Luo 1994; Rougier, Wible, and Hopson 1996):

(0) Horizontal shelf: tritylodontids, tritheledontids, *Sinoconodon*;

(1) Ventrally directed: *Probainognathus*, *Adelobasileus*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Obdurodon*, *Ornithorhynchus*, *Gobiconodon*, *Priacodon*, *Trioracodon*, *Vincelestes*;

(2) Medially directed and contacting the promontorium: “plagiaulacidans”, cimolodontans;

(3) Vestigial or absent: *Deltatheridium*, *Asiatherium*, *Pucadelphys*, *Didelphis*, *Erinaceus*, *Asioryctes*, *Prokennalestes*;

(?) Not exposed: *Haldanodon*; not preserved: *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Jeholodens*, *Amphilestes*, *Haramiyavia*, *Tinodon*, *Zhangheotherium* (present but damaged on the type specimen), *Dryolestes*, *Amphitherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Kokopellia*, *Pappotherium*, *Montanalestes*.

208. Vertical component of the lateral flange (“L-shaped” and forming a vertical wall to pterygoparoccipital foramen) (modified from Luo 1994):

(0) Present: tritylodontids, *Sinoconodon*;

(1) Absent: *Probainognathus*, tritheledontids, *Adelobasileus*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Hadrocodium*, *Obdurodon*, *Ornithorhynchus*, *Gobiconodon*, *Priacodon*, *Trioracodon*, “plagiaulacidans”, cimolodontans, *Vincelestes*;

(?) Not preserved: *Haldanodon*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Jeholodens*, *Amphilestes*, *Tinodon*, *Haramiyavia*, *Zhangheotherium* (damaged on the type specimen), *Dryolestes*, *Amphitherium*, *Henkelotherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Kokopellia*, *Pappotherium*, *Montanalestes*; not applicable: *Deltatheridium*, *Asiatherium*, *Pucadelphys*, *Didelphis*, *Erinaceus*, *Asioryctes*, *Prokennalestes*.

209. Vascular foramen in the posterior part of the lateral flange (and anterior to the pterygoparoccipital or the “ramus superior foramen”):

(0) Present: tritylodontids, *Adelobasileus*, *Sinoconodon*, *Morganucodon*, *Hadrocodium*;

(1) Absent: *Probainognathus*, tritheledontids, *Obdurodon*, *Ornithorhynchus*, *Priacodon*, *Trioracodon*, “plagiaulacidans”, cimolodontans, *Zhangheotherium*, *Vincelestes*, *Deltatheridium*, *Pucadelphys*, *Didelphis*, *Erinaceus*, *Asioryctes*, *Prokennalestes*;

(?) Unknown: *Megazostrodon*, *Dinnetherium*, *Haldanodon* (unknown due to damage in the relevant area on the specimen illustrated by Lillegraven and Krusat 1991), *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Gobiconodon*, *Amphilestes*, *Tinodon*, *Jeholodens*, *Haramiyavia*, *Tinodon*, *Dryolestes*, *Amphitherium*, *Henkelotherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Asiatherium*, *Kokopellia*, *Pappotherium*, *Montanalestes*.

210. Relationship of the petrosal lateral flange to the crista parotica (or the anterior paroccipital process that bears the crista) (modified from Rougier, Wible, and Hopson 1996: character 30):

(0) Widely separated: *Probainognathus*, tritylodontids, tritheledontids, *Sinoconodon*;

(1) Narrowly separated: *Adelobasileus* (there is a squamosal bridge between the lateral flange and the paroccipital region), *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Priacodon*, *Trioracodon*;

(2) Continuous bone formed by petrosal: *Hadrocodium*, *Obdurodon*, *Ornithorhynchus*, cimolodontans, *Zhangheotherium*, *Vincelestes*;

(?) Uncertain: *Haldanodon* (damaged on the specimens illustrated by Lillegraven and Krusat 1991); not preserved: *Kuehneotherium*, *Shuotherium*,

Ambondro, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Gobiconodon*, *Amphilestes*, *Jeholodens*, *Tinodon*, *Haramiyavia*, “plagiaulacidans”, *Dryolestes*, *Amphitherium*, *Peramus*, *Henkelotherium*, *Aegialodon*, *Kielantherium*, *Kokopellia*, *Pappotherium*, *Montanalestes*; not applicable (the lateral flange of petrosal is reduced or absent): *Deltatheridium*, *Asiatherium*, *Pucadelphys*, *Didelphis*, *Erinaceus*, *Asioryctes*, *Prokennalestes*.

211. Morphology of the pterygoparoccipital foramen (for the ramus superior of the stapedial artery):

(0) Laterally open notch (laterally open pterygoparoccipital foramen): tritylodontids, tritheledontids, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Priacodon*, *Trioracodon*;

(1) Foramen enclosed by the petrosal or squamosal or both: *Probainognathus*, *Adelobasileus* (by squamosal only), *Hadrocodium*, *Obdurodon*, *Ornithorhynchus*, cimolodontans, *Zhangheotherium*, *Vincelestes* (“ascending canal” of Rougier et al. 1992), *Erinaceus*, *Asioryctes*, *Prokennalestes* (Wible et al. 2001);

(?) Not preserved: *Haldanodon*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Gobiconodon*, *Amphilestes*, *Jeholodens*, *Tinodon*, *Haramiyavia*, “plagiaulacidans”, *Tinodon*, *Dryolestes*, *Amphitherium*, *Henkelotherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Kokopellia*, *Pappotherium*, *Montanalestes*; not applicable: *Deltatheridium*, *Didelphis*, *Pucadelphys*, *Asiatherium*.

212. Position of the pterygoparoccipital foramen relative to the fenestra vestibuli (adapted from Wible et al. 1995):

(0) The pterygoparoccipital foramen is posterior or lateral to the level of the fenestra vestibuli: *Probainognathus*, tritylodontids, tritheledontids, *Adelobasileus*, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Obdurodon*, *Ornithorhynchus*, *Priacodon*, *Trioracodon*, *Zhangheotherium*;

(1) The foramen is anterior to the level of the fenestra vestibuli: *Vincelestes*, *Erinaceus*, *Asioryctes*, *Prokennalestes*;

(0/1 polymorphic): cimolodontans;

(?) Not applicable: *Deltatheridium*, *Pucadelphys*, *Didelphis*; not preserved: *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Gobiconodon*, *Amphilestes*, *Jeholodens*, *Tinodon*, *Haramiyavia*, “plagiaulacidans”, *Dryolestes*, *Amphitherium*, *Peramus*, *Henkelotherium*, *Aegialodon*, *Kielantherium*, *Asiatherium*, *Kokopellia*, *Pappotherium*, *Montanalestes*.

213. “Bifurcation of paroccipital process”—presence versus absence (this is modified from the character used in several previous studies):

(0) Bifurcation absent: *Probainognathus*, tritheledontids, *Adelobasileus*, *Hadrocodium*, “plagiaulacidans”, cimolodontans, *Zhangheotherium*, *Vincelestes*, *Deltatheridium*, *Asiatherium*, *Pucadelphys*, *Didelphis*, *Erinaceus*, *Asioryctes*, *Prokennalestes*;

(1) Bifurcation present: tritylodontids, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Ornithorhynchus*, *Obdurodon*, *Trioracodon*;

(?) Not preserved: *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Gobiconodon*, *Amphilestes*, *Jeholodens*, *Priacodon*, *Tinodon*, *Haramiyavia*, *Dryolestes*, *Amphitherium*, *Peramus*, *Henkelotherium*, *Aegialodon*, *Kielantherium*, *Kokopellia*, *Pappotherium*, *Montanalestes*.

214. Posterior paroccipital process of the petrosal:

(0) No ventral projection below the level of its surrounding structures: *Probainognathus*, tritylodontids, tritheledontids, *Adelobasileus*, *Sinoconodon*, *Haldanodon* (posteromedial condyle of main body of crista parotica, as described by Lillegraven and Krusat 1991), *Hadrocodium*, *Deltatheridium*, *Asiatherium*, *Pucadelphys*, *Didelphis*, *Erinaceus*, *Asioryctes*, *Prokennalestes*;

(1) Projecting below the surrounding structures: *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Obdurodon*, *Ornithorhynchus*, *Trioracodon*, “plagiaulacidans”, cimolodontans, *Zhangheotherium*, *Vincelestes*;

(?) Uncertain: *Amphilestes*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Gobiconodon*, *Jeholodens*, *Priacodon*, *Haramiyavia*, *Tinodon*, *Dryolestes*, *Amphitherium*, *Peramus*, *Henkelotherium*, *Aegialodon*, *Kielantherium*, *Kokopellia*, *Pappotherium*, *Montanalestes*.

215. Morphological differentiation of the anterior paroccipital region:

(0) Anterior paroccipital region is indistinct from surrounding structures: *Probainognathus*, tritheledontids, *Adelobasileus*;

(1) Anterior paroccipital region is bulbous and distinctive from the surrounding structures: tritylodontids, *Sinoconodon*;

(2) Anterior paroccipital region has a distinct crista parotica: *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Obdu-*

rodon, *Ornithorhynchus*, *Priacodon*, *Trioracodon*, "plagiaulacidans", cimolodontans, *Zhangheotherium*, *Vincelestes*, *Deltatheridium*, *Pucadelphys*, *Didelphis*, *Erinaceus*, *Asioryctes*, *Prokennalestes*;

(?) Not preserved: *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Gobiconodon*, *Amphilestes*, *Jeholodens*, *Tinodon*, *Haramiyavia*, *Dryolestes*, *Amphitherium*, *Henkelotherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Asiatherium*, *Kokopellia*, *Pappotherium*, *Montanalestes*.

216. Epitympanic recess lateral to the crista parotica:

(0) Absent: *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Ornithorhynchus*, *Obdurodon*, *Gobiconodon*, *Priacodon*, *Trioracodon*;

(1) Present (as a large depression on the crista parotica): *Hadrocodium*, "plagiaulacidans", *Zhangheotherium*, *Vincelestes*, *Deltatheridium*, *Asiatherium*, *Pucadelphys*, *Didelphis*, *Erinaceus*, *Asioryctes*, *Prokennalestes*;

(0/1 polymorphic) cimolodontans (Rougier, Wible, and Hopson 1996);
(?) Not applicable for those taxa in which the crista parotica is not differentiated: *Probainognathus*, tritylodontids, tritheledontids, *Adelobasileus*, *Sinoconodon*; not preserved: *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Jeholodens*, *Amphilestes*, *Tinodon*, *Haramiyavia*, *Dryolestes*, *Amphitherium*, *Henkelotherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Kokopellia*, *Pappotherium*, *Montanalestes*.

217. Relationship of the squamosal on the paroccipital process:

(0) Squamosal covers the entire paroccipital region: *Probainognathus*, tritheledontids, *Adelobasileus*, *Sinoconodon*;

(1) No squamosal cover on anterior paroccipital region: tritylodontids, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Obdurodon*, *Ornithorhynchus*, *Trioracodon*, "plagiaulacidans", cimolodontans;

(2) Squamosal covering a part of the paroccipital region, but not on the crista parotica (the squamosal wall and the crista parotica are separated by the epitympanic recess): *Zhangheotherium*, *Vincelestes*, *Deltatheridium*, *Asiatherium*, *Pucadelphys*, *Didelphis*, *Erinaceus*, *Asioryctes*;

(?) Not preserved: *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Gobiconodon*, *Amphilestes*, *Jeholodens*, *Priacodon*, *Tinodon*, *Haramiyavia*, *Dryolestes*, *Amphitherium*, *Henkelotherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Kokopellia*, *Pappotherium*, *Prokennalestes*, *Montanalestes*.

218. Medial process of the squamosal reaching toward the foramen ovale (Muizon 1994):

(0) Absent: *Probainognathus*, tritylodontids, tritheledontids, *Adelobasileus*, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Hadrocodium*, *Haldanodon*, *Obdurodon*, *Ornithorhynchus*, *Gobiconodon*, *Jeholodens*, "plagiaulacidans", cimolodontans, *Zhangheotherium*, *Henkelotherium*, *Vincelestes*, *Erinaceus*, *Asioryctes*;

(1) Present: *Asiatherium*, *Didelphis*, *Pucadelphys*;

(?) Not preserved: *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Amphilestes*, *Priacodon*, *Trioracodon*, *Haramiyavia*, *Tinodon*, *Dryolestes*, *Amphitherium*, *Peramus*, *Kielantherium*, *Aegialodon*, *Deltatheridium*, *Kokopellia*, *Pappotherium*, *Montanalestes*, *Prokennalestes*.

219. Stapedial artery sulcus on the petrosal (Wible 1990; Rougier et al. 1998):

(0) Absent: *Probainognathus*, tritylodontids, tritheledontids, *Adelobasileus*, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Obdurodon*, *Ornithorhynchus*, *Priacodon*, *Trioracodon*, *Zhangheotherium*, *Deltatheridium*, *Pucadelphys*, *Didelphis*;

(1) Present: *Vincelestes* (Rougier et al. 1992), *Prokennalestes* (Wible et al. 2001), *Asioryctes*, *Erinaceus*;

(0/1 polymorphic) cimolodontans (conditions are variable);

(?) Not preserved: *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Gobiconodon*, *Amphilestes*, *Jeholodens*, *Tinodon*, *Haramiyavia*, "plagiaulacidans", *Henkelotherium*, *Dryolestes*, *Amphitherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Asiatherium*, *Kokopellia*, *Pappotherium*, *Montanalestes*.

220. Transpromontorial sulcus for internal carotid artery on the pars cochlearis (Wible 1987; Rougier et al. 1998):

(0) Absent: *Adelobasileus*, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Obdurodon*, *Ornithorhynchus*, *Priacodon*, *Trioracodon*, "plagiaulacidans", cimolodontans, *Zhangheotherium*, *Deltatheridium* (coded following Rougier et al. 1998), *Pucadelphys*, *Didelphis*, *Asioryctes* (Wible 1983);

(1) Present: *Vincelestes*, *Erinaceus*, *Prokennalestes* (Wible et al. 2001);

(?) Not preserved: *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Gobiconodon*, *Amphilestes*, *Jeholodens*, *Tinodon*, *Haramiyavia*, *Peramus*, *Henkelotherium*, *Dryolestes*, *Amphitherium*, *Aegialodon*, *Kielantherium*, *Asiatherium*, *Kokopellia*, *Pappotherium*, *Montanalestes*; not applicable: *Probainognathus*, tritylodontids, tritheledontids (promontorium is absent because the pars cochlearis is not exposed externally).

221. Site for the attachment of the tensor tympani muscle on the petrosal (modified from Rougier, Wible, and Hopson 1996):

(0) Absent: *Probainognathus*, tritylodontids, tritheledontids, *Adelobasileus*, *Sinoconodon*;

(1) Present on a shallow anterior embayment of the lateral trough: *Morganucodon*, *Dinnetherium*, *Hadrocodium*;

(2) Present as a longitudinal groove on the lateral trough: *Haldanodon*, *Obdurodon*, *Ornithorhynchus*, *Gobiconodon*, *Priacodon*, *Trioracodon*, *Vincelestes*;

(3) Present on an oval shaped fossa (although the position of the fossa may be variable): "plagiaulacidans", cimolodontans, *Deltatheridium*, *Pucadelphys*, *Didelphis*, *Erinaceus*, *Asioryctes*, *Prokennalestes*;

(?) Not preserved or not exposed: *Kuehneotherium*, *Megazostrodon*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Amphilestes*, *Jeholodens*, *Tinodon*, *Haramiyavia*, *Zhangheotherium*, *Dryolestes*, *Amphitherium*, *Henkelotherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Asiatherium*, *Kokopellia*, *Pappotherium*, *Montanalestes*.

222. Bullar process of the alisphenoid:

(0) Absent: *Probainognathus*, tritylodontids, tritheledontids, *Adelobasileus*, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Hadrocodium*, *Haldanodon*, *Obdurodon*, *Ornithorhynchus*, *Gobiconodon*, "plagiaulacidans", cimolodontans, *Zhangheotherium*, *Vincelestes*, *Erinaceus*, *Asioryctes*, *Pucadelphys* (coded after Muizon 1994; Marshall and Muizon 1995);

(1) Present: *Asiatherium*, *Didelphis*, *Deltatheridium*;

(?) Not preserved: *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Amphilestes*, *Jeholodens*, *Priacodon*, *Trioracodon*, *Haramiyavia*, *Tinodon*, *Dryolestes*, *Henkelotherium*, *Amphitherium*, *Peramus*, *Kielantherium*, *Aegialodon*, *Kokopellia*, *Pappotherium*, *Montanalestes*, *Prokennalestes*.

223. Hypotympanic recess in the junction of the alisphenoid, squamosal, and petrosal:

(0) Absent: *Probainognathus*, tritylodontids, tritheledontids, *Adelobasileus*, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Hadrocodium*, *Haldanodon*, *Obdurodon*, *Ornithorhynchus*, "plagiaulacidans", cimolodontans, *Gobiconodon*, *Zhangheotherium*, *Vincelestes*, *Erinaceus*, *Asioryctes*;

(1) Present: *Asiatherium*, *Didelphis*, *Pucadelphys* (coded from a depression posteromedial to the foramen ovale, Marshall and Muizon 1995: fig. 18);

(?) Not preserved: *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Amphilestes*, *Jeholodens*, *Priacodon*, *Trioracodon*, *Haramiyavia*, *Tinodon*, *Dryolestes*, *Henkelotherium*, *Amphitherium*, *Peramus*, *Kielantherium*, *Aegialodon*, *Kokopellia*, *Deltatheridium*, *Pappotherium*, *Montanalestes*; *Prokennalestes*.

224. Separation of the fenestra cochleae from the jugular foramen:

(0) Fenestra cochleae and jugular foramen within the same depression (although better separated in tritheledontids): *Probainognathus*, tritylodontids, tritheledontids, *Obdurodon*, *Ornithorhynchus*;

(1) Separate (do not share the same depression): *Adelobasileus*, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Priacodon*, *Trioracodon*, "plagiaulacidans", cimolodontans, *Zhangheotherium*, *Vincelestes*, *Deltatheridium*, *Asiatherium*, *Pucadelphys*, *Didelphis*, *Erinaceus*, *Asioryctes*, *Prokennalestes*;

(?) Not preserved: *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Gobiconodon*, *Amphilestes*, *Jeholodens*, *Tinodon*, *Haramiyavia*, *Henkelotherium*, *Dryolestes*, *Amphitherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Kokopellia*, *Pappotherium*, *Montanalestes*.

225. Channel of the perilymphatic duct (Zeller 1989; Wible and Hopson 1993; Rougier, Wible, and Hopson 1996, division of characters modified to suit this study):

(0) Open channel and sulcus: *Probainognathus*, tritylodontids, tritheledontids, *Adelobasileus*, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Hadrocodium*, *Obdurodon*, *Ornithorhynchus*, *Priacodon*, *Trioracodon*, "plagiaulacidans";

(1) channel partially or fully enclosed: *Haldanodon*, *Vincelestes*, *Deltatheridium*, *Asiatherium*, *Pucadelphys*, *Didelphis*, *Erinaceus*, *Prokennalestes*, *Asioryctes*;

(0/1) cimolodontans (cimolodontan multituberculates may have open or partially enclosed perilymphatic channel, but this group never develops fully enclosed channel, polymorphic conditions following Rougier, Wible, and Hopson 1996);

(?) Not preserved: *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Gobiconodon*, *Amphilestes*, *Jeholodens*, *Tinodon*, *Haramiyavia*, *Zhangheotherium*, *Dryolestes*, *Amphitherium*, *Henkelotherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Kokopellia*, *Pappotherium*, *Montanalestes*.

226. Stapedial muscle fossa (modified from Rowe 1988; Wible 1991; Luo 1994; Rougier, Wible, and Hopson 1996):

(0) Absent: *Probainognathus*, tritheledontids, *Adelobasileus*, *Ornithorhynchus*, *Obdurodon*;

(1) Present and in alignment with the crista interfenestralis: tritylodontids, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*;

(2) Present and lateral to the crista interfenestralis: *Priacodon*, *Trioracodon*, “plagiaulacidans”, cimolodontans, *Zhangheotherium*, *Vincelestes*, *Deltatheridium*, *Pucadelphys*, *Didelphis*, *Erinaceus*, *Asioryctes*, *Prokennalestes*;

(?) Uncertain: *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Gobiconodon*, *Amphilestes*, *Jeholodens*, *Tinodon*, *Haramiyavia*, *Peramus*, *Amphitherium*, *Dryolestes*, *Henkelotherium*, *Aegialodon*, *Kielantherium*, *Asiatherium*, *Kokopellia*, *Pappotherium*, *Montanalestes*.

227. The hypoglossal foramen (Lucas and Luo 1993; as modified by Rougier, Wible, and Hopson 1996):

(0) Indistinct, either confluent with the jugular foramen or sharing a depression with the jugular foramen: *Probainognathus*, tritylodontids (confluent), tritheledontids (sharing the same depression), *Obdurodon*, *Ornithorhynchus*;

(1) Separated from the jugular foramen: *Adelobasileus*, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Haldanodon*, *Hadrocodium*, *Priacodon*, “plagiaulacidans”, cimolodontans, *Vincelestes*, *Deltatheridium*, *Asiatherium*, *Pucadelphys*, *Didelphis*, *Erinaceus*, *Asioryctes*;

(?) Not preserved: *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Gobiconodon*, *Trioracodon*, *Amphilestes*, *Jeholodens*, *Tinodon*, *Haramiyavia*, *Zhangheotherium*, *Dryolestes*, *Amphitherium*, *Henkelotherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Kokopellia*, *Pappotherium*, *Montanalestes*, *Prokennalestes*.

Incus (quadrate) characters (9 characters)

228. Geometry (shape) of the incudo-malleolar contact:

(0) Trochlear (convex and cylindrical) surface of the incus: *Probainognathus*, tritylodontids, tritheledontids, *Morganucodon*, *Megazostrodon*, *Dinnetherium* (based on an isolated quadrate), *Haldanodon* (inferred from the articulating facet of articular, Lillegraven and Krsat 1991);

(1) Trough or saddle-shaped contact on the incus: *Sinoconodon*, *Didelphis*, *Erinaceus*;

(2) Flat surface (following Zeller 1993; Meng and Wyss 1995): cimolodontans, *Ornithorhynchus*;

(?) Unknown: *Adelobasileus*, *Hadrocodium*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Gobiconodon*, *Amphilestes*, *Jeholodens*, *Priacodon*, *Trioracodon*, *Haramiyavia*, “plagiaulacidans”, *Tinodon*, *Zhangheotherium*, *Dryolestes*, *Amphitherium*, *Henkelotherium*, *Peramus*, *Vincelestes*, *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Asiatherium*, *Pucadelphys*, *Kokopellia*, *Pappotherium*, *Montanalestes*, *Prokennalestes*, *Asioryctes*.

229. Alignment of the incus and malleus by the “center of mass” (Zeller 1989, 1993; Meng and Wyss 1995; Hurum et al. 1996; as modified by Rougier, Wible, and Novacek 1996):

(0) Anteroposterior (Luo and Crompton 1994): *Probainognathus*, tritylodontids, tritheledontids, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Haldanodon* (inferred from the articulating facet of articular, Lillegraven and Krsat 1991);

(1) Posterolateral to anterior medial: *Didelphis*, *Erinaceus*;

(2) Dorsoventral (Zeller 1993; Meng and Wyss 1995; Hurum et al. 1996): *Ornithorhynchus*, cimolodontans;

(?) Unknown: *Adelobasileus*, *Dinnetherium*, *Hadrocodium*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Gobiconodon*, *Amphilestes*, *Jeholodens*, *Priacodon*, *Trioracodon*, *Tinodon*, *Haramiyavia*, “plagiaulacidans”, *Zhangheotherium*, *Dryolestes*, *Amphitherium*, *Henkelotherium*, *Vincelestes*, *Peramus*,

Aegialodon, *Kielantherium*, *Deltatheridium*, *Asiatherium*, *Pucadelphys*, *Kokopellia*, *Pappotherium*, *Montanalestes*, *Prokennalestes*, *Asioryctes*.

230. Presence of a quadrate-incus neck (separation of the dorsal plate and the trochlea; this represents the differentiation between the “body” and crus brevis of the incus) (distributions modified from Luo 1994; Luo and Crompton 1994):

(0) Absent: *Probainognathus*, tritylodontids, *Sinoconodon*;

(1) Present: tritheledontids, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Didelphis*, *Erinaceus*;

(?) Unknown: *Adelobasileus*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Kuehneotherium*, *Shuotherium*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Gobiconodon*, *Jeholodens*, *Amphilestes*, *Priacodon*, *Trioracodon*, *Tinodon*, *Haramiyavia*, “plagiaulacidans”, *Zhangheotherium*, *Peramus*, *Henkelotherium*, *Dryolestes*, *Amphitherium*, *Vincelestes*, *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Asiatherium*, *Kokopellia*, *Pucadelphys*, *Pappotherium*, *Montanalestes*, *Prokennalestes*, *Asioryctes*; not applicable: cimolodontans (Hurum et al. 1995; 1996), *Ornithorhynchus*.

231. The stapedial process (crus longum) of the incus-quadrate:

(0) Absent: *Probainognathus*, tritheledontids, *Sinoconodon*;

(1) Present: tritylodontids, *Morganucodon*, *Dinnetherium*, *Ornithorhynchus*, *Jeholodens*, cimolodontans, *Didelphis*, *Erinaceus*;

(?) Unknown: *Adelobasileus*, *Megazostrodon*, *Haldanodon*, *Hadrocodium*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Gobiconodon*, *Amphilestes*, *Priacodon*, *Trioracodon*, *Haramiyavia*, “plagiaulacidans”, *Zhangheotherium*, *Tinodon*, *Dryolestes*, *Amphitherium*, *Henkelotherium*, *Peramus*, *Vincelestes*, *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Asiatherium*, *Kokopellia*, *Pappotherium*, *Pucadelphys*, *Montanalestes*, *Prokennalestes*, *Asioryctes*.

232. Dorsal plate (= crus brevis) of the quadrate-incus:

(0) Broad plate: *Probainognathus*, tritylodontids, tritheledontids, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*;

(1) Pointed triangle: *Didelphis*, *Erinaceus*;

(2) Reduced: *Ornithorhynchus*, *Jeholodens*, cimolodontans;

(?) Unknown: *Adelobasileus*, *Haldanodon*, *Hadrocodium*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Gobiconodon*, *Amphilestes*, *Priacodon*, *Trioracodon*, *Tinodon*, *Haramiyavia*, “plagiaulacidans”, *Zhangheotherium*, *Dryolestes*, *Amphitherium*, *Henkelotherium*, *Peramus*, *Vincelestes*, *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Asiatherium*, *Pucadelphys*, *Kokopellia*, *Pappotherium*, *Montanalestes*, *Prokennalestes*, *Asioryctes*.

233. Incus: angle of the crus brevis to crus longum (modified from Hurum et al. 1996):

(0) Alignment of stapedial process (crus longum) and the dorsal plate (crus brevis) (or an obtuse angle between the two structures): *Probainognathus* (distinctive process is lacking, stapes-incus contact is on the medial side of the quadrate trochlea); tritylodontids, tritheledontids, *Sinoconodon*, *Morganucodon*;

(1) Perpendicular: *Ornithorhynchus* (assuming the top of the flat “T” is homologous to crus brevis, see Zeller 1993), *Didelphis*, *Erinaceus*;

(2) Acute angle of the crus brevis and crus longum (A-shaped incus of Hurum et al. 1996; Rougier, Wible, and Novacek 1996): *Jeholodens*, cimolodontans;

(?) Unknown: *Adelobasileus*, *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Gobiconodon*, *Amphilestes*, *Priacodon*, *Trioracodon*, *Tinodon*, *Haramiyavia*, “plagiaulacidans”, *Zhangheotherium*, *Dryolestes*, *Amphitherium*, *Henkelotherium*, *Peramus*, *Vincelestes*, *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Asiatherium*, *Pucadelphys*, *Kokopellia*, *Pappotherium*, *Montanalestes*, *Prokennalestes*, *Asioryctes*.

234. Primary suspension of the incus-quadrate on the basicranium:

(0) By squamosal and quadratojugal: *Probainognathus*, tritylodontids;

(1) By squamosal only: tritheledontids (absence of the quadratojugal in this taxon determined by Luo and Crompton 1994), *Sinoconodon*;

(2) By petrosal (either by the preserved direct contact of incus, or by the inference from the presence of a well defined crista parotica): *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Haldanodon* (no squamosal pit for quadrate, Lillegraven and Krsat 1991), *Hadrocodium*, *Obdurodon*, *Ornithorhynchus*, *Priacodon*, *Trioracodon*, “plagiaulacidans”, cimolodontans, *Zhangheotherium* (incus not preserved, its suspension structure inferred to the epitympanic features), *Vincelestes* (incus not preserved, its suspension structure inferred from the epitympanic features), *Deltatheridium*, *Asiatherium*, *Pucadelphys*, *Didelphis*, *Asioryctes*, *Erinaceus*, *Prokennalestes*;

(?) Not preserved: *Adelobasileus*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Gobiconodon*,

Amphilestes, *Jeholodens*, *Tinodon*, *Haramiyavia*, *Dryolestes*, *Amphitherium*, *Henkelotherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Kokopellia*, *Pappotherium*, *Montanalestes*.

235. Quadratojugal notch in the squamosal:

(0) Present as an independent element in adult: *Probainognathus*, tritylodontids;

(1) Absent: tritheledontids, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Ornithorhynchus*, *Gobiconodon*, *Jeholodens*, cimolodontans, *Asiatherium*, *Pucadelphys*, *Didelphis*, *Erinaceus*, *Asioryctes*;

(?) Not preserved (relevant part of the cranium is not preserved to assess the presence versus absence of this feature): *Adelobasileus*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Amphilestes*, *Priacodon*, *Trioracodon*, *Tinodon*, *Haramiyavia*, "plagiaulacidans", *Zhangheotherium*, *Dryolestes*, *Amphitherium*, *Henkelotherium*, *Vincelestes*, *Peramus*, *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Kokopellia*, *Pappotherium*, *Prokennalestes*, *Montanalestes*.

236. Morphology of the stapes (descriptive terms modified from Novacek and Wyss 1986b; Meng 1992; Hurum et al. 1995; Rougier, Wible, and Novacek 1996):

(0) Columniform-macroporolate: *Probainognathus*, tritylodontids, tritheledontids, *Sinoconodon* (Luo and Crompton, unpublished data), *Morganucodon*, *Haldanodon* (tentative interpretation; *Haldanodon* has preserved the footplate and proximal parts of the crura, so it can not be ruled out that it could be character state 2);

(1) Columelliform-imperforate (or microperforate): *Ornithorhynchus*, cimolodontans (djadchtatherians and *Lambdopsalis*);

(2) Bicurrate-perforate: *Didelphis*, *Erinaceus* (Doran 1878);

(?) Not preserved: *Adelobasileus*, *Dinnetherium*, *Megazostrodon*, *Hadrocodium*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Gobiconodon*, *Jeholodens*, *Amphilestes*, *Priacodon*, *Trioracodon*, *Tinodon*, *Haramiyavia*, "plagiaulacidans", *Zhangheotherium*, *Dryolestes*, *Henkelotherium*, *Vincelestes*, *Amphitherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Asiatherium*, *Kokopellia*, *Pucadelphys*, *Prokennalestes*, *Asioryctes*, *Pappotherium*, *Montanalestes*.

Palatal, orbital, and zygomatic characters (14 characters)

237. Bony secondary palate:

(0) Ending anterior to the posterior end of the tooth row: *Probainognathus*, tritylodontids, "plagiaulacidans", cimolodontans;

(1) Level with the posterior end of the tooth row: tritheledontids, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Vincelestes*;

(2) Extending posterior to the tooth row: *Haldanodon*, *Hadrocodium*, *Obdurodon*, *Ornithorhynchus*, *Gobiconodon*, *Priacodon*, *Deltatheridium*, *Asiatherium*, *Pucadelphys*, *Didelphis*, *Erinaceus*, *Asioryctes*;

(?) not preserved: *Adelobasileus*, *Dinnetherium*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Trioracodon*, *Amphilestes*, *Jeholodens*, *Tinodon*, *Haramiyavia*, *Zhangheotherium*, *Dryolestes*, *Amphitherium*, *Peramus*, *Henkelotherium*, *Aegialodon*, *Kielantherium*, *Kokopellia*, *Pappotherium*, *Montanalestes*, *Prokennalestes*.

238. Relationship of the maxilla to the subtemporal margin or the orbit:

(0) Participating in the rounded subtemporal margin of the orbit: *Probainognathus*, tritylodontids, tritheledontids;

(1) Forming a well defined edge along the subtemporal margin: *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Ornithorhynchus*, *Gobiconodon*, *Jeholodens*, *Priacodon*, *Trioracodon*, "plagiaulacidans", cimolodontans, *Zhangheotherium*, *Vincelestes*, *Henkelotherium*, *Deltatheridium*, *Asiatherium*, *Pucadelphys*, *Didelphis*, *Erinaceus*, *Asioryctes*;

(?) Not preserved: *Adelobasileus*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Amphilestes*, *Tinodon*, *Haramiyavia*, *Dryolestes*, *Amphitherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Kokopellia*, *Pappotherium*, *Montanalestes*, *Prokennalestes*.

239. Pterygopalatine ridges:

(0) Present: *Probainognathus*, tritylodontids, tritheledontids, *Adelobasileus*, *Sinoconodon*, *Morganucodon*, "plagiaulacidans", cimolodontans;

(1) Absent: *Haldanodon*, *Hadrocodium*, *Obdurodon*, *Ornithorhynchus*, *Vincelestes*, *Deltatheridium*, *Asiatherium*, *Pucadelphys*, *Didelphis*, *Asioryctes*, *Erinaceus*;

(?) Not preserved: *Megazostrodon*, *Dinnetherium*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*,

Gobiconodon, *Jeholodens*, *Amphilestes*, *Priacodon*, *Trioracodon*, *Tinodon*, *Haramiyavia*, *Zhangheotherium*, *Dryolestes*, *Amphitherium*, *Henkelotherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Kokopellia*, *Pappotherium*, *Montanalestes*, *Prokennalestes*.

240. Transverse process of the pterygoid:

(0) Present and massive: *Probainognathus*, tritheledontids;

(1) Present but reduced (as the hamulus): *Sinoconodon*, *Morganucodon*, *Megazostrodon* (Gow 1986a: fig. 5), *Vincelestes*, *Deltatheridium*, *Asiatherium*, *Pucadelphys*, *Didelphis*, *Erinaceus*, *Asioryctes*;

(2) Greatly reduced or absent: *Haldanodon*, *Obdurodon*, *Ornithorhynchus*, *Hadrocodium*; "plagiaulacidans";

(0/1 polymorphic) tritylodontids (enlarged for some tritylodontids, see Sues 1985; but not in others, see Kemp 1983);

(1/2 polymorphic): cimolodontans (present in *Kryptobaatar*; absent in others, Wible and Rougier 2000);

(?) Not preserved: *Adelobasileus*, *Dinnetherium*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Gobiconodon*, *Jeholodens*, *Amphilestes*, *Priacodon*, *Trioracodon*, *Tinodon*, *Haramiyavia*, *Zhangheotherium*, *Dryolestes*, *Amphitherium*, *Henkelotherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Kokopellia*, *Pappotherium*, *Montanalestes*, *Prokennalestes*.

241. Basisphenoid constricture (= palatal width anterior to the basisphenoid):

(0) Strongly developed (very narrow anterior to the basisphenoid): *Probainognathus*, tritylodontids, tritheledontids;

(1) Intermediate (wide anterior to the basisphenoid): *Adelobasileus*, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Vincelestes*, *Deltatheridium*, *Asiatherium*, *Pucadelphys*, *Didelphis*, *Erinaceus*, *Asioryctes*;

(2) No constricture (palatal width is as broad at the basisphenoid as in the internal choanae): *Haldanodon*, *Hadrocodium*, *Obdurodon*, *Ornithorhynchus*, "plagiaulacidans", cimolodontans;

(?) Not preserved: *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Gobiconodon*, *Jeholodens*, *Amphilestes*, *Priacodon*, *Trioracodon*, *Tinodon*, *Haramiyavia*, *Zhangheotherium*, *Dryolestes*, *Amphitherium*, *Henkelotherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Kokopellia*, *Pappotherium*, *Montanalestes*, *Prokennalestes*.

242. Vault of the naso-oral pharyngeal passage near the pterygoid-basisphenoid junction:

(0) Roof of the pharynx is V-shaped in transverse section, narrowing toward the basisphenoid: *Probainognathus*, tritylodontids, tritheledontids, *Sinoconodon*, *Morganucodon*, *Deltatheridium*, *Asiatherium*, *Pucadelphys*, *Didelphis*, *Erinaceus*, *Asioryctes*;

(1) Roof of the pharynx is U-shaped in transverse section: *Adelobasileus*, *Haldanodon*, *Hadrocodium*, *Obdurodon*, *Ornithorhynchus*, "plagiaulacidans", cimolodontans, *Vincelestes*;

(?) Not preserved: *Megazostrodon*, *Dinnetherium*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Gobiconodon*, *Amphilestes*, *Jeholodens*, *Priacodon*, *Trioracodon*, *Tinodon*, *Haramiyavia*, *Zhangheotherium*, *Dryolestes*, *Amphitherium*, *Henkelotherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Kokopellia*, *Pappotherium*, *Montanalestes*, *Prokennalestes*.

243. Complete ossification of the orbital floor:

(0) Absent: *Probainognathus*, tritheledontids;

(1) Present: tritylodontids, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Haldanodon*, *Hadrocodium*, *Ornithorhynchus*, *Obdurodon*, cimolodontans, *Vincelestes*, *Deltatheridium*, *Asiatherium*, *Pucadelphys*, *Didelphis*, *Erinaceus*, *Asioryctes*;

(?) Not preserved: *Dinnetherium*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Gobiconodon*, *Amphilestes*, *Jeholodens*, *Priacodon*, *Trioracodon*, *Tinodon*, *Haramiyavia*, "plagiaulacidans", *Zhangheotherium*, *Henkelotherium*, *Tinodon*, *Haramiyavia*, *Zhangheotherium*, *Dryolestes*, *Amphitherium*, *Henkelotherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Kokopellia*, *Prokennalestes*, *Pappotherium*, *Montanalestes*.

244. Pattern of orbital mosaic as exposed externally (modified from Hopson and Crompton 1969; Kielan-Jaworowska and Kermack 1971; Wible and Hopson 1993; Luo 1994; Rougier, Wible, and Novacek 1996; Hurum 1998a; Wible and Rougier 2000):

(0) Alisphenoid contacts the frontal and parietal, thereby separating the petrosal anterior lamina from the orbitosphenoid in external view of the orbit: *Probainognathus*, tritylodontids, tritheledontids, *Adelobasileus*, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Haldanodon*, *Hadrocodium*, *Vincelestes*, *Asiatherium*, *Pucadelphys*, *Didelphis*, *Erinaceus*, *Asioryctes*;

(1) The petrosal anterior lamina contacts the orbitosphenoid thereby separating the alisphenoid from the front and the parietal: *Ornithorhynchus*, *Obdurodon*;

(0/1 polymorphic) cimolodontans;

(?) Not preserved: *Dinnetherium*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Gobiconodon*, *Jeholodens*, *Amphilestes*, *Priacodon*, *Triaracodon*, *Tinodon*, *Haramiyavia*, “plagiaulacidans”, *Zhangheotherium*, *Dryolestes*, *Amphitherium*, *Henkelotherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Kokopellia*, *Pappotherium*, *Montanalestes*, *Prokennalestes*.

245. Overhanging roof of the orbit:

(0) Overhanging roof of the orbit formed by prefrontal: *Probainognathus* (Romer 1970);

(1) Overhanging roof of the orbit is absent: tritylodontids, tritheledontids, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Haldanodon*, *Hadrocodium*, *Jeholodens*, *Obdurodon*, *Ornithorhynchus*, *Vincelestes*, *Deltatheridium*, *Asiatherium*, *Pucadelphys*, *Didelphis*, *Erinaceus*, *Asioryctes*;

(2) Overhanging roof of the orbit formed by the frontal: “plagiaulacidans”, cimolodontans;

(?) Not preserved: *Adelobasileus*, *Dinnetherium*, *Amphilestes*, *Priacodon*, *Triaracodon*, *Kuehneotherium*, *Tinodon*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Haramiyavia*, *Zhangheotherium*, *Dryolestes*, *Henkelotherium*, *Amphitherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Pappotherium*, *Kokopellia*, *Prokennalestes*, *Montanalestes*.

246. Outline of the facial part of the lacrimal:

(0) Large, triangular, and pointed anteriorly: *Probainognathus*, tritylodontids, tritheledontids, *Sinoconodon*, *Morganucodon*, *Haldanodon*, *Hadrocodium*, cimolodontans, *Jeholodens*, *Gobiconodon*;

(1) Small and rectangular or crescentic: “plagiaulacidans” (based on reconstruction by Hahn 1978), *Henkelotherium*, *Vincelestes*, *Deltatheridium*, *Pucadelphys*, *Didelphis*, *Erinaceus*, *Asioryctes*;

(2) Excluded from the facial (and pre-orbital) part of the skull: *Obdurodon*, *Ornithorhynchus*;

(?) Not preserved: *Adelobasileus*, *Megazostrodon*, *Dinnetherium*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Amphilestes*, *Priacodon*, *Triaracodon*, *Haramiyavia*, *Tinodon*, *Zhangheotherium*, *Dryolestes*, *Peramus*, *Amphitherium*, *Aegialodon*, *Kielantherium*, *Asiatherium*, *Kokopellia*, *Pappotherium*, *Prokennalestes*, *Montanalestes*.

247. Pila antotica:

(0) Present: *Probainognathus*, tritylodontids, tritheledontids, *Adelobasileus*, *Sinoconodon* (Luo and Crompton, unpublished data), *Morganucodon* (Crompton and Luo, unpublished data), *Haldanodon* (based on photos in Lillegraven and Krusat 1991: fig. 15), cimolodontans (Hurum 1998a; Wible and Rougier 2000);

(1) Absent (in adult): *Hadrocodium*, *Ornithorhynchus*, *Vincelestes*, *Pucadelphys*, *Didelphis*, *Erinaceus*, *Prokennalestes*, *Asioryctes*;

(?) Unknown: *Megazostrodon*, *Dinnetherium*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Gobiconodon*, *Amphilestes*, *Jeholodens*, *Priacodon*, *Triaracodon*, *Tinodon*, *Haramiyavia*, “plagiaulacidans”, *Zhangheotherium*, *Dryolestes*, *Amphitherium*, *Peramus*, *Henkelotherium*, *Aegialodon*, *Kielantherium*, *Asiatherium*, *Kokopellia*, *Pappotherium*, *Montanalestes*.

248. Frontal-parietal suture on the alisphenoid (modified from Rowe 1988; Wible 1991; Luo 1994):

(0) Dorsal plate of alisphenoid contacting the frontal by the anterior corner: *Probainognathus*, tritylodontids, tritheledontids, *Adelobasileus*, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Haldanodon* (based on Lillegraven and Krusat 1991: fig. 15), *Hadrocodium*, *Vincelestes*;

(1) Dorsal plate of alisphenoid has more extensive contact to the frontal (~50% of its dorsal border): *Pucadelphys*, *Didelphis*, *Erinaceus*, *Asioryctes*;

(?) Not applicable: *Ornithorhynchus*, *Obdurodon*, cimolodontans; not preserved: *Dinnetherium*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Gobiconodon*, *Amphilestes*, *Jeholodens*, *Priacodon*, *Triaracodon*, *Tinodon*, *Haramiyavia*, “plagiaulacidans”, *Zhangheotherium*, *Dryolestes*, *Amphitherium*, *Henkelotherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Asiatherium*, *Prokennalestes*, *Kokopellia*, *Pappotherium*, *Montanalestes*, *Prokennalestes*.

249. Jugal on the zygoma (Hopson and Barghusen 1986):

(0) Anterior part of jugal extends on the facial part of the maxillary and forming a part of the anterior orbit: *Probainognathus*, tritylodontids, tritheledontids, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Haldanodon*, *Hadrocodium*, *Henkelotherium*, *Vincelestes*, *Deltatheridium*, *Asiatherium*, *Pucadelphys*, *Didelphis*, *Erinaceus*, *Asioryctes*;

(1) Anterior part of jugal does not reach the facial part of the maxillary and is excluded from the anterior part of the orbit: *Ornithorhynchus*, *Obdurodon*, *Jeholodens*, *Gobiconodon*, “plagiaulacidans”, cimolodontans;

(?) Not preserved: *Adelobasileus*, *Dinnetherium*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Amphilestes*, *Triaracodon*, *Priacodon*, *Tinodon*, *Haramiyavia*, *Zhangheotherium*, *Dryolestes*, *Amphitherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Kokopellia*, *Pappotherium*, *Montanalestes*, *Prokennalestes*.

250. Maximum vertical depth of the zygomatic arch relative to the length of the skull (this character is designed to indicate the robust versus gracile nature of the zygomatic arch) (distribution modified from Luo 1994):

(0) Between 10–20%: *Probainognathus*, tritylodontids; tritheledontids, *Haldanodon*, *Gobiconodon*, *Vincelestes*;

(1) Between 5–7%: *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Hadrocodium*, *Obdurodon*, *Ornithorhynchus*, *Jeholodens*, “plagiaulacidans”, cimolodontans, *Zhangheotherium*, *Henkelotherium*, *Deltatheridium*, *Asiatherium*, *Pucadelphys*, *Didelphis*, *Erinaceus*, *Asioryctes*;

(?) Not preserved: *Adelobasileus*, *Dinnetherium*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Amphilestes*, *Triaracodon*, *Priacodon*, *Tinodon*, *Haramiyavia*, *Dryolestes*, *Amphitherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Kokopellia*, *Pappotherium*, *Montanalestes*, *Prokennalestes*.

Occipital and other skull characters (13 characters)

251. The posterior opening of the post-temporal canal:

(0) At the junction of the petrosal, squamosal and the tabular: *Probainognathus*, tritylodontids, tritheledontids (following Crompton 1958);

(1) Between the petrosal and the squamosal: *Adelobasileus*, *Sinoconodon*, *Morganucodon*, *Hadrocodium*, *Obdurodon*, *Ornithorhynchus*, *Gobiconodon*, *Priacodon*, *Triaracodon*, “plagiaulacidans”, cimolodontans (following Kielan-Jaworowska et al. 1986; Hurum 1998a), *Vincelestes*, *Deltatheridium*, *Pucadelphys*, *Didelphis*, *Erinaceus*, *Asioryctes*;

(?) Not preserved: *Megazostrodon*, *Dinnetherium*, *Haldanodon* (uncertain, post-temporal canal opening has not been identified), *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Jeholodens*, *Amphilestes*, *Tinodon*, *Haramiyavia*, *Zhangheotherium*, *Dryolestes*, *Amphitherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Asiatherium*, *Kokopellia*, *Pappotherium*, *Montanalestes*, *Prokennalestes*.

252. The anterior ascending vascular channel (for the arteria diploetica magna) in the temporal region:

(0) Open groove: *Probainognathus*, tritylodontids, tritheledontids, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Ornithorhynchus*;

(1) Partially enclosed in a canal: *Adelobasileus*, *Haldanodon*, *Priacodon*, *Triaracodon*, *Hadrocodium*;

(2) Completely enclosed in a canal or endocranial: *Gobiconodon*, “plagiaulacidans”, cimolodontans, *Vincelestes*, *Pucadelphys*, *Didelphis*, *Erinaceus* (as the endocranial part of superior ramus of the stapedial artery), *Asioryctes*;

(?) Not preserved: *Dinnetherium*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Jeholodens*, *Amphilestes*, *Tinodon*, *Haramiyavia*, *Zhangheotherium*, *Dryolestes*, *Amphitherium*, *Henkelotherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Asiatherium*, *Kokopellia*, *Pappotherium*, *Montanalestes*, *Prokennalestes*.

253. The lambdoidal crest:

(0) Crest overhanging the concave or straight supraocciput: *Probainognathus*, tritylodontids, tritheledontids, *Adelobasileus*, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Haldanodon*, *Gobiconodon*, *Jeholodens*, *Vincelestes*, *Pucadelphys*, *Didelphis*, *Erinaceus*, *Asioryctes*;

(1) Weak crest with convex dorsal part of the occipital plate: *Hadrocodium*, *Obdurodon*, *Ornithorhynchus*;

(0/1 polymorphic) cimolodontans (e.g., *Chulsanbaatar* and *Nemegtbaatar* 1; e.g., *Ptilodus* 0);

(?) Not preserved: *Dinnetherium*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Amphilestes*, *Priacodon*, *Triaracodon*, *Tinodon*, *Haramiyavia*, “plagiaulacidans”, *Zhangheotherium*, *Dryolestes*, *Amphitherium*, *Henkelotherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Asiatherium*, *Kokopellia*, *Pappotherium*, *Montanalestes*, *Prokennalestes*.

254. The sagittal crest:

(0) Prominently developed: *Probainognathus*, tritylodontids, tritheledontids, *Sinoconodon*, *Gobiconodon*, *Vincelestes*, *Didelphis*;

(1) Weakly developed: *Adelobasileus*, *Morganucodon*, *Megazostrodon*, *Haldanodon*, *Jeholodens*, *Asiatherium*, *Pucadelphys*, *Erinaceus*, *Asioryctes*;
 (2) Absent: *Hadrocodium*, *Obdurodon*, *Ornithorhynchus*;
 (1/2 polymorphic) cimolodontans;

(?) Unknown: *Dinnetherium*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Amphilestes*, *Trioracodon*, *Priacodon*, *Tinodon*, *Haramiyavia*, "plagiaulacidans", *Zhangheotherium*, *Henkelotherium*, *Dryolestes*, *Amphitherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Kokopellia*, *Pappotherium*, *Montanalestes*, *Prokennalestes*.

255. The tabular bone:

(0) Present: *Probainognathus*, tritylodontids, tritheledontids, *Sinoconodon* (Luo and Crompton, unpublished data);

(1) Absent: *Adelobasileus*, *Morganucodon*, *Haldanodon*, *Hadrocodium*, *Obdurodon*, *Ornithorhynchus*, *Jeholodens*, *Gobiconodon*, "plagiaulacidans", cimolodontans, *Vincelestes*, *Didelphis*, *Asiatherium*, *Pucadelphys*, *Erinaceus*, *Asioryctes*;

(?) Unknown: *Megazostrodon*, *Dinnetherium*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Priacodon*, *Trioracodon*, *Amphilestes*, *Tinodon*, *Haramiyavia*, *Zhangheotherium*, *Henkelotherium*, *Dryolestes*, *Amphitherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Kokopellia*, *Pappotherium*, *Montanalestes*, *Prokennalestes*.

256. Shape of the occipital condyles:

(0) Bulbous: *Probainognathus*, tritylodontids, *Sinoconodon*;

(1) Ovoid: tritheledontids, *Morganucodon*, *Megazostrodon*, *Haldanodon*, *Vincelestes*;

(2) Subcylindrical: *Adelobasileus*, *Hadrocodium*, *Obdurodon*, *Ornithorhynchus*, *Priacodon*, "plagiaulacidans", *Asiatherium*, *Pucadelphys*, *Didelphis*, *Erinaceus*, *Asioryctes*;

(1/2 polymorphic) cimolodontans;

(?) Not applicable: *Probainognathus*; unknown: *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Gobiconodon*, *Jeholodens*, *Amphilestes*, *Trioracodon*, *Tinodon*, *Haramiyavia*, *Zhangheotherium*, *Henkelotherium*, *Dryolestes*, *Amphitherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Kokopellia*, *Pappotherium*, *Montanalestes*, *Prokennalestes*.

257. The occiput slope:

(0) Occiput slopes posterodorsally (or is vertically oriented) from the occipital condyles: *Probainognathus*, tritylodontids, tritheledontids, *Adelobasileus*, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Gobiconodon*, "plagiaulacidans", cimolodontans, *Vincelestes*, *Asiatherium*, *Pucadelphys*, *Didelphis*;

(1) Occiput slopes anterodorsally from the occipital condyles (such that the lambdoidal crest is leveled anterior to the occipital condyle and the condyle is fully visible in dorsal view of the skull): *Haldanodon*, *Hadrocodium*, *Obdurodon*, *Ornithorhynchus*, *Erinaceus*, *Asioryctes*;

(?) Not preserved: *Dinnetherium*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Amphilestes*, *Jeholodens*, *Priacodon*, *Trioracodon*, *Tinodon*, *Haramiyavia*, *Zhangheotherium*, *Dryolestes*, *Amphitherium*, *Henkelotherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Kokopellia*, *Pappotherium*, *Montanalestes*, *Prokennalestes*.

258. Foramina on the dorsal surface of the nasal bone:

(0) Absent: *Probainognathus*, tritylodontids, *Sinoconodon*, *Hadrocodium*, *Jeholodens*, *Obdurodon*, *Ornithorhynchus*, *Deltatheridium*, *Asiatherium*, *Pucadelphys*, *Didelphis*, *Erinaceus*, *Asioryctes*;

(1) Present: *Morganucodon*, *Haldanodon*, cimolodontans, *Vincelestes*;

(?) Not preserved: tritheledontids, *Adelobasileus*, *Megazostrodon*, *Dinnetherium*, *Kuehneotherium*, *Gobiconodon*, *Amphilestes*, *Priacodon*, *Trioracodon*, *Tinodon*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Haramiyavia*, "plagiaulacidans", *Zhangheotherium*, *Henkelotherium*, *Amphitherium*, *Peramus*, *Kielantherium*, *Aegialodon*, *Pappotherium*, *Kokopellia*, *Prokennalestes*, *Montanalestes*.

259. Septomaxilla (Wible et al. 1990):

(0) Present and with a ventromedial shelf: *Probainognathus*, tritylodontids, tritheledontids, *Sinoconodon*;

(1) Present and without the septomaxillary shelf: *Morganucodon*, *Haldanodon*, *Hadrocodium*, *Jeholodens*, *Gobiconodon*, *Ornithorhynchus* (fused to the premaxillary secondarily, Wible et al. 1990), *Obdurodon* (Archer et al. 1993), *Vincelestes*;

(2) Absent: cimolodontans, *Deltatheridium*, *Pucadelphys*, *Didelphis*, *Erinaceus*, *Asioryctes*;

(?) Unknown: *Adelobasileus*, *Megazostrodon*, *Dinnetherium*, *Kuehneotherium*, *Shuotherium*, *Amphilestes*, *Tinodon*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Amphilestes*, *Priacodon*, *Trioracodon*, *Haramiyavia*, "plagiaulacidans", *Tinodon*, *Zhangheotherium*, *Dryolestes*, *Amphitherium*, *Henkelotherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Asiatherium*, *Kokopellia*, *Pappotherium*, *Montanalestes*, *Prokennalestes*.

260. Premaxillary internarial process:

(0) Present: *Probainognathus*, tritylodontids (Sues 1986), tritheledontids (personal communication from C.E. Gow), *Sinoconodon* (Crompton and Luo 1993), *Morganucodon*, *Haldanodon* (Lillegraven and Krusat 1991);

(1) Absent: cimolodontans, *Ornithorhynchus*, *Obdurodon*, *Vincelestes*, *Pucadelphys*, *Didelphis*, *Erinaceus*, *Asioryctes*;

(?) Uncertain: *Adelobasileus*, *Megazostrodon*, *Dinnetherium*, *Hadrocodium*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Gobiconodon*, *Jeholodens*, *Amphilestes*, *Priacodon*, *Trioracodon*, *Tinodon*, *Haramiyavia*, "plagiaulacidans", *Zhangheotherium*, *Dryolestes*, *Amphitherium*, *Henkelotherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Asiatherium*, *Kokopellia*, *Pappotherium*, *Montanalestes*, *Prokennalestes*.

261. Facial part of the premaxillary borders on the nasal:

(0) Absent: *Probainognathus*, *Sinoconodon*, *Morganucodon*, *Haldanodon*, *Hadrocodium*, *Gobiconodon*, *Jeholodens*, *Ornithorhynchus* (following Wible et al. 1990 in regarding the "embryonic" septomaxillary as fused to "embryonic premaxillary" in adult), *Vincelestes*;

(1) Present: tritheledontids, cimolodontans, *Deltatheridium*, *Pucadelphys*, *Didelphis*, *Erinaceus*, *Asioryctes*;

(0/1) polymorphic tritylodontids (*Kayentatherium* 0: Sues 1986; *Bocatherium* 1: Hopson 1994);

(?) Uncertain: *Adelobasileus*, *Megazostrodon*, *Dinnetherium*, *Trioracodon*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Amphilestes*, *Priacodon*, *Trioracodon*, *Tinodon*, *Haramiyavia*, "plagiaulacidans", *Zhangheotherium*, *Henkelotherium*, *Dryolestes*, *Amphitherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Asiatherium*, *Kokopellia*, *Pappotherium*, *Montanalestes*, *Prokennalestes*.

262. Ossified ethmoidal cribriform plate of the nasal cavity:

(0) Absent: *Probainognathus*, tritylodontids, *Sinoconodon*, *Morganucodon*, *Haldanodon* (Lillegraven and Krusat 1991 reported the presence of only a fragment ethmoid), *Hadrocodium*, *Ornithorhynchus*, cimolodontans (Hurum 1998a);

(1) Present: *Didelphis*, *Erinaceus*;

(?) Unknown: tritheledontids, *Adelobasileus*, *Megazostrodon*, *Dinnetherium*, *Kuehneotherium*, *Gobiconodon*, *Amphilestes*, *Jeholodens*, *Priacodon*, *Trioracodon*, *Tinodon*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Haramiyavia*, "plagiaulacidans", *Tinodon*, *Zhangheotherium*, *Dryolestes*, *Amphitherium*, *Henkelotherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Asiatherium*, *Kokopellia*, *Pucadelphys*, *Pappotherium*, *Montanalestes*, *Prokennalestes*, *Asioryctes*.

Note: Zeller (1998) documented a cartilaginous cribriform plate in early ontogenetic stages of *Ornithorhynchus* but secondarily lost in adults. Zeller (1988, 1989) considers the absence of the ossified cribriform plate in adult *Ornithorhynchus* to be a secondary condition of monotremes due to the aquatic adaptation of the platypus. *Tachyglossus* has a well developed cribriform plate. It has been shown that this structure is absent in various cimolodontan multituberculates. The unpublished serial sectioning data by Luo, Sun, and Cui show no sign of cribriform plate in *Yunnanodon*, *Sinoconodon*, and *Morganucodon*.

263. Posterior excavation of the nasal cavity into the bony sphenoid complex (modified from Hurum 1994; Luo 1997; Wible and Rougier 2000):

(0) Absent: *Probainognathus*, tritheledontids, *Ornithorhynchus*, *Haldanodon*;

(1) Present: tritylodontids (Luo 1997), *Sinoconodon*, *Morganucodon*;

(2) Present and partitioned from the nasal cavity: "plagiaulacidans" (inferred from Hahn's 1981 illustration), cimolodontans, *Didelphis*, *Pucadelphys*, *Erinaceus*;

(?) Unknown: *Adelobasileus*, *Megazostrodon*, *Dinnetherium*, *Hadrocodium*, *Kuehneotherium*, *Gobiconodon*, *Jeholodens*, *Priacodon*, *Trioracodon*, *Amphilestes*, *Tinodon*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Haramiyavia*, *Zhangheotherium*, *Henkelotherium*, *Dryolestes*, *Amphitherium*, *Peramus*, *Vincelestes*, *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Asiatherium*, *Kokopellia*, *Pappotherium*, *Montanalestes*, *Prokennalestes*, *Asioryctes*.

Note: This character is defined as a blind space in the ethmoid-sphenoid complex that opens into the nasal cavity anteriorly; it can be considered to be the posterior extension of the nasal cavity, or a precursor to the sphenoid sinus; the posterior extension of nasal cavity can be transformed into the sphenoidal sinus if the space is partially partitioned from the nasal cavity proper.

Cranial vault and brain endocast characters (10 characters)

264. External bulging of braincase in the parietal region:

- (0) Absent: *Probainognathus*, tritylodontids, tritheledontids, *Adelobasileus*, *Sinoconodon*, *Morganucodon*, *Haldanodon*, *Gobiconodon*;
 (1) Expanded (the parietal part of the cranial vault is wider than the frontal part, but expansion does not extend to lambdoidal region): *Jeholodens*, *Trioracodon* (coded from *Triconodon*), *Vincelestes*, *Didelphis*, *Pucadelphys*, *Asioryctes*;
 (2) Greatly expanded (expansion of cranial vault extends to lambdoidal region): *Hadrocodium*, *Obdurodon*, *Ornithorhynchus*, *Asiatherium*, *Erinaceus*;
 (1/2 polymorphic): cimolodontans;
 (?) Not preserved: *Dinnetherium*, *Kuehneotherium*, *Amphilestes*, *Priacodon*, *Tinodon*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Haramiyavia*, “plagiaulacidans”, *Tinodon*, *Zhangheotherium*, *Henkelotherium*, *Dryolestes*, *Amphitherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Kokopellia*, *Pappotherium*, *Montanalestes*, *Prokennalestes*.

265. The interparietal (Rowe 1988; Lillegraven and Krusat 1991):

- (0) Present as a separate element in adult: *Probainognathus*, *Haldanodon* (Lillegraven and Krusat 1991);
 (1) Absent: tritylodontids, tritheledontids, *Adelobasileus*, *Sinoconodon*, *Megazostrodon*, *Morganucodon*, *Dinnetherium*, *Hadrocodium*, *Obdurodon*, *Ornithorhynchus*, *Jeholodens*, *Gobiconodon*, “plagiaulacidans”, cimolodontans, *Vincelestes*, *Deltatheridium*, *Asiatherium*, *Pucadelphys*, *Didelphis*, *Erinaceus*, *Asioryctes*;
 (?) Not preserved: *Kuehneotherium*, *Amphilestes*, *Priacodon*, *Tinodon*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Haramiyavia*, *Trioracodon*, *Zhangheotherium*, *Dryolestes*, *Henkelotherium*, *Amphitherium*, *Peramus*, *Aegialodon*, *Kielantherium*, *Kokopellia*, *Pappotherium*, *Prokennalestes*, *Montanalestes*.

266. Bony tentorium septum:

- (0) Present: tritylodontids, *Sinoconodon*, *Morganucodon* (preserved on the medial part of the parietal roof, laterally it was identified as “transverse sulcus”, Kermack et al. 1981), *Haldanodon*, *Didelphis*, *Asioryctes*, *Erinaceus*;
 (1) Absent: cimolodontans, *Trioracodon* (coded from *Triconodon*), *Ornithorhynchus*;
 (?) Unknown: tritheledontids, *Adelobasileus*, *Megazostrodon*, *Dinnetherium*, *Hadrocodium*, *Kuehneotherium*, *Amphilestes*, *Priacodon*, *Tinodon*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Jeholodens*, *Gobiconodon*, *Haramiyavia*, “plagiaulacidans”, *Tinodon*, *Zhangheotherium*, *Henkelotherium*, *Dryolestes*, *Amphitherium*, *Peramus*, *Vincelestes*, *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Asiatherium*, *Kokopellia*, *Pucadelphys*, *Pappotherium*, *Montanalestes*, *Prokennalestes*.

267. Anterior expansion of the vermis (central lobe of cerebellum):

- (0) Absent: tritylodontids, *Sinoconodon* (based on Luo and Crompton, unpublished data), *Morganucodon*, *Ornithorhynchus*, *Didelphis*, *Asioryctes*, *Erinaceus*;
 (1) Present, to cover and conceal mesencephalon (midbrain) on endocast (= the cryptomesencephalic condition of Kielan-Jaworowska 1986, 1997): *Trioracodon* (coded from *Triconodon*), cimolodontans;
 (?) Unknown: *Probainognathus*, tritheledontids, *Adelobasileus*, *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Kuehneotherium*, *Amphilestes*, *Priacodon*, *Tinodon*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Gobiconodon*, *Jeholodens*, *Priacodon*, *Haramiyavia*, “plagiaulacidans”, *Henkelotherium*, *Dryolestes*, *Amphitherium*, *Peramus*, *Vincelestes*, *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Asiatherium*, *Kokopellia*, *Pucadelphys*, *Pappotherium*, *Montanalestes*, *Prokennalestes*.

268. Overall size of the vermis:

- (0) Small: *Sinoconodon*, *Morganucodon*;
 (1) Enlarged: *Ornithorhynchus*, *Trioracodon* (coded from *Triconodon*), cimolodontans, *Didelphis*, *Asioryctes*, *Erinaceus*.
 (?) Unknown: *Probainognathus*, tritylodontids, tritheledontids, *Adelobasileus*, *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Kuehneotherium*, *Amphilestes*, *Tinodon*, *Shuotherium*, *Ambondro*,

Ausktribosphenos, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Jeholodens*, *Gobiconodon*, *Priacodon*, *Haramiyavia*, “plagiaulacidans”, *Zhangheotherium*, *Henkelotherium*, *Dryolestes*, *Amphitherium*, *Peramus*, *Vincelestes*, *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Asiatherium*, *Kokopellia*, *Pucadelphys*, *Pappotherium*, *Montanalestes*, *Prokennalestes*.

269. Lateral cerebellar hemisphere (excluding the paraflocculus):

- (0) Absent: *Probainognathus*, tritylodontids (based on Kühne 1956), *Sinoconodon*, *Morganucodon*, *Trioracodon* (coded from *Triconodon*), cimolodontans;
 (1) Present: *Hadrocodium*, *Ornithorhynchus*, *Didelphis*, *Asioryctes*, *Erinaceus*;
 (?) Unknown: tritheledontids, *Adelobasileus*, *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Gobiconodon*, *Amphilestes*, *Jeholodens*, *Priacodon*, *Tinodon*, *Haramiyavia*, “plagiaulacidans”, *Zhangheotherium*, *Dryolestes*, *Amphitherium*, *Henkelotherium*, *Peramus*, *Vincelestes*, *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Asiatherium*, *Kokopellia*, *Pucadelphys*, *Pappotherium*, *Montanalestes*, *Prokennalestes*.

270. Lateral extension of the paraflocculus:

- (0) Less than 30% of total cerebellar width: *Hadrocodium*, *Probainognathus*, tritylodontids, *Sinoconodon*, *Morganucodon*, *Ornithorhynchus*, *Didelphis*, *Asioryctes*, *Erinaceus*;
 (1) More than 30% of the cerebellar width: *Hadrocodium*, *Trioracodon* (coded from *Triconodon*), cimolodontans;
 (?) Unknown: tritheledontids, *Adelobasileus*, *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Gobiconodon*, *Amphilestes*, *Jeholodens*, *Priacodon*, *Tinodon*, *Haramiyavia*, “plagiaulacidans”, *Tinodon*, *Zhangheotherium*, *Dryolestes*, *Henkelotherium*, *Amphitherium*, *Peramus*, *Vincelestes*, *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Asiatherium*, *Kokopellia*, *Pucadelphys*, *Pappotherium*, *Montanalestes*, *Prokennalestes*.

271. External division on the endocast between the olfactory lobe and cerebral hemisphere (presence versus absence of the circular sulcus that defines the external aspect of the olfactory lobe):

- (0) Absent: *Probainognathus*, tritylodontids, *Sinoconodon*, *Morganucodon*;
 (1) Present: *Haldanodon* (described by Lillegraven and Krusat 1991 on the underside of the frontal bone), *Hadrocodium*, *Ornithorhynchus*, *Trioracodon* (coded from *Triconodon*), cimolodontans, *Didelphis*, *Asioryctes*, *Erinaceus*;
 (?) Unknown: tritheledontids, *Adelobasileus*, *Megazostrodon*, *Dinnetherium*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Gobiconodon*, *Amphilestes*, *Jeholodens*, *Priacodon*, *Tinodon*, *Haramiyavia*, “plagiaulacidans”, *Zhangheotherium*, *Dryolestes*, *Henkelotherium*, *Amphitherium*, *Peramus*, *Vincelestes*, *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Asiatherium*, *Kokopellia*, *Pucadelphys*, *Pappotherium*, *Montanalestes*, *Prokennalestes*.

272. Anterior expansion of the cerebral hemisphere:

- (0) Absent: *Probainognathus*, tritylodontids, *Sinoconodon*, *Morganucodon*, *Haldanodon* (inferred from the olfactory demarcation on the frontal);
 (1) Developed: *Hadrocodium*, *Trioracodon* (coded from *Triconodon*), cimolodontans, *Ornithorhynchus*, *Didelphis*, *Asioryctes*, *Erinaceus*;
 (?) Unknown: tritheledontids, *Adelobasileus*, *Megazostrodon*, *Dinnetherium*, *Kuehneotherium*, *Shuotherium*, *Ausktribosphenos*, *Ambondro*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Gobiconodon*, *Amphilestes*, *Jeholodens*, *Priacodon*, *Tinodon*, *Haramiyavia*, “plagiaulacidans”, *Zhangheotherium*, *Dryolestes*, *Henkelotherium*, *Amphitherium*, *Peramus*, *Vincelestes*, *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Asiatherium*, *Kokopellia*, *Pucadelphys*, *Pappotherium*, *Montanalestes*, *Prokennalestes*.

273. Expansion of the posterior cerebral hemisphere (for each hemisphere, not the combined width of the posterior hemispheres):

- (0) Absent: *Probainognathus*, tritylodontids, *Sinoconodon*, *Morganucodon*, *Trioracodon* (coded from *Triconodon*), cimolodontans;
 (1) Present: *Hadrocodium*, *Ornithorhynchus*, *Didelphis*, *Asioryctes*, *Erinaceus*;
 (?) Unknown: tritheledontids, *Adelobasileus*, *Haldanodon*, *Megazostrodon*, *Dinnetherium*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Jeholodens*, *Amphilestes*, *Gobiconodon*, *Priacodon*, *Tinodon*, *Haramiyavia*, “plagiaulacidans”, *Zhangheotherium*, *Dryolestes*, *Amphitherium*, *Henkelotherium*, *Peramus*, *Vincelestes*, *Aegialodon*, *Kielantherium*, *Deltatheridium*, *Asiatherium*, *Kokopellia*, *Pucadelphys*, *Pappotherium*, *Montanalestes*, *Prokennalestes*.

Jaw characters (2)

274. Direction of jaw movement during occlusion (Crompton and Luo 1993; Luo 1994; Gambaryan and Kielan-Jaworowska 1995):

(0) Dorsomedial movement (as inferred from teeth): *Probainognathus*, tritheledontids (Shubin et al. 1991), *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Dinnetherium*, *Haldanodon*, *Hadrocodium*, *Kuehneotherium*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Gobiconodon*, *Amphilestes*, *Jeholodens*, *Priacodon*, *Trioracodon*, *Tinodon*;

(1) Dorsomedial movement with a significant medial component: *Zhangheotherium*, *Peramus*, *Dryolestes*, *Henkelotherium*, *Amphitherium*, *Vincelestes*, *Kielantherium*, *Deltatheridium*, *Asiatherium*, *Kokopellia*, *Pucadelphys*, *Didelphis*, *Erinaceus*, *Asioryctes*, *Montanalestes*, *Prokennalestes*;

(2) Dorsoposterior movement: tritylodontids (Crompton 1972b), *Haramiyavia* (Butler 2000, but see Jenkins et al. 1997), "plagiailacidans", cimolodontans;

(0/2 polymorphic): *Ornithorhynchus* (Hopson and Crompton 1969 inferred from the wear patterns on the cusps of the juvenile teeth and the shape of the

craniomandibular joint that the mandible of the platypus could have both dorsoposteriorly directed and dorsomedially directed movement);

(?) Not preserved: *Adelobasileus*, *Aegialodon*, *Pappotherium*.

275. Mode of occlusion as inferred from the mandibular symphysis (Crompton and Luo 1993; Luo 1994):

(0) Bilateral (with more or less rigid symphysis): tritylodontids (following Crompton 1974; Sues 1985), tritheledontids, *Haramiyavia*, "plagiailacidans", cimolodontans (following Wall and Krause 1992), *Sinoconodon* (rigid symphysis);

(1) Unilateral (with mobile symphysis): *Probainognathus* (see Crompton and Hylander 1986), *Morganucodon*, *Dinnetherium*, *Megazostrodon*, *Haldanodon*, *Hadrocodium*, *Kuehneotherium*, *Gobiconodon*, *Amphilestes*, *Priacodon*, *Jeholodens*, *Trioracodon*, *Tinodon*, *Shuotherium*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon* (inferred from the occlusal pattern of teeth), *Teinolophos*, *Obdurodon* (mobile symphysis), *Ornithorhynchus* (after Simpson 1929b; Hopson and Crompton 1969; Archer et al. 1993), *Zhangheotherium*, *Dryolestes*, *Henkelotherium*, *Amphitherium*, *Peramus*, *Vincelestes*, *Kielantherium*, *Deltatheridium*, *Asiatherium*, *Kokopellia*, *Pucadelphys*, *Didelphis*, *Erinaceus*, *Asioryctes*, *Montanalestes*, *Prokennalestes*;

(?) Not preserved: *Adelobasileus*, *Aegialodon*, *Pappotherium*.

Appendix 2

Pair-wise non-parametric tests

Templeton tests (Templeton 1983; as implemented in PAUP 4.0b5 by Swofford 2000) on alternative placements of some major Mesozoic mammal clades. Each pair of alternative hypotheses are compared by: A, their respective strict consensus trees, and B, their respective fundamental (equally parsimonious) trees that are compatible with the strict consensus. Steps, total number of transformational steps for each tree topology. *p*, significance level at which the paired hypotheses are different (generated from the tree score function of PAUP 4.0b5, Swofford 2000).

I. Nonparametric tests on alternative placements of allotherians (including multituberculates)

Ranking	A. Comparison of consensus trees		B. Comparison of fundamental trees	
	Steps	<i>p</i>	Steps	<i>p</i>
(1) Multituberculate-trechnotherian sister-taxa (Fig. 1)	939		935	
(2) Allotherian clade as stem taxon outside crown Mammalia (Fig. 2)	944	0.6222	942	0.4823
(3) Multituberculate and haramiyidans as unrelated stem taxa outside crown Mammalia	945	0.4771	941	0.4771

(2) In this suboptimal topology, all allotherians are constrained to form a clade (e.g., as proposed by the empirical study of Butler 2000) (see Fig. 2).

(3) In this topology *Haramiyavia* is placed separately from multituberculates. These topologies have small differences in steps. Both topologies (2) and (3) are not significantly different from the multituberculate-trechnotherian placement (Fig. 1), given our dataset (Appendix 1).

II. Nonparametric tests on alternative placements of eutriconodonts

Ranking	A. Comparison of consensus trees		B. Comparison of fundamental trees	
	Steps	<i>p</i>	Steps	<i>p</i>
(1) Monophyletic eutriconodonts within crown Mammalia (Fig. 1)	939		935	
(2) Paraphyletic "eutricodonts" outside crown Mammalia (Fig. 2) (and allotherians are a clade)	944	0.6222	942	0.4823
(3) Paraphyletic "eutricodonts" outside crown Mammalia (and "allotherians" are also paraphyletic)	945	0.4771	941	0.4771

(2) In this topology, paraphyletic "eutricodont" stem taxa are concurrent with an allotherian clade (see Fig. 2).

(3) In this topology, paraphyletic "eutricodont" stem taxa are concurrent with separate placements of *Haramiyavia* from multituberculates. These topologies have small differences in steps and in *p* value. Both topologies (2) and (3) are not significantly different from the placement of eutriconodonts within crown Mammalia (Fig. 1) by nonparametric tests, given our dataset (Appendix 1).

III. Nonparametric tests on placements of early southern tribosphenic mammals

Ranking	A. Comparison of consensus trees		B. Comparison of fundamental trees	
	Steps	<i>p</i>	Steps	<i>p</i>
(1) Placement with toothed monotremes (australosphenidan clade) (see Fig. 1)	939		935	
(2) <i>Ambondro</i> , <i>Ausktribosphenos</i> , <i>Bishops</i> as placentals	979	0.005*	949	0.1441
(3) <i>Ambondro</i> as basal tribosphenic (Flynn et al. 1999) and <i>Ausktribosphenos</i> , <i>Bishops</i> as placentals (Rich et al. 1999)	1325	<0.0001*	966	0.0049*

* Alternative topologies from constrained searches are significantly different from the topology and preferred and most parsimonious trees (Fig. 1).