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The Phylogenetic Relationships of Eucynodontia (Amniota: Synapsida)

Jun Liu · Paul Olsen

Abstract The phylogeny of Eucynodontia is an important topic in vertebrate paleontology and is the foundation for understanding the origin of mammals. However, consensus on the phylogeny of Eucynodontia remains elusive. To clarify their interrelationships, a cladistic analysis, based on 145 characters and 31 species, and intergrating most prior works, was performed. The monophyly of Eucynodontia is confirmed, although the results slightly differ from those of previous analyses with respect to the composition of both Cynognathia and Probainognathia. This is also the first numerical cladistic analysis to recover a monophyletic Traversodontidae. *Brasilodon* is the plesiomorphic sister taxon of Mammalia, although it is younger than the oldest mammals and is specialized in some characters. A monophyletic Prozostrodontia, including tritheledontids, tritylodontids, and mammals, is well supported by many characters. Pruning highly incomplete taxa generally has little effect on the inferred pattern of relationships among the more complete taxa, although exceptions sometimes occur when basal fragmentary taxa are removed. Taxon sampling of the current data matrix shows that taxon sampling was poor in some previous studies, implying that their results are not reliable. Two major unresolved questions in cynodont phylogenetics are whether tritylodontids are more closely related to mammals or to traversodontids, and whether tritylodontids or tritheledontids are closer to mammals. Analyses of possible synapomorphies support a relatively close relationship between mammals and tritylodontids, to the exclusion of traversodontids, but do not clearly indicate whether or not tritheledontids are closer to mammals than are tritylodontids.

Keywords Phylogeny · Eucynodontia · Tritheledontidae · Tritylodontidae · Traversodontidae · Mammal

Introduction

The origin of mammals is one of the key transitions in vertebrate evolution. [In this paper, Mammalia includes *Adelobasileus* and Mammalia *sensu* Luo et al. (2002), which is defined as a group including the common ancestor of *Sinoconodon*, living monotremes, and living therians, plus all its descendants; and equals to Mammaliformes of Rowe (1988: Fig. 4) but not Rowe (1993: fig. 10.2), because *Sinoconodon* is not included in the latter definition.] This transition is one of the best documented examples in the fossil record of an evolutionary sequence connecting two major structural grades, and thus is an appropriate case for studying macroevolutionary models (e.g., Kemp 2007). To study this transition, the phylogenetic position of mammals must be established first. This is a historically important topic in evolutionary studies and an area of active current research. Mammals were viewed as having a polyphyletic origin from mammal-like reptiles (Simpson 1928, 1929; Olson 1944, 1959). Later, mammals were considered to have evolved from cynodonts (Hopson and Crompton 1969), but controversy persisted regarding the interrelationships within cynodonts and especially within

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Eucynodontia, i.e., those cynodonts more derived than *Thrinaxodon*. However, the monophyletic Eucynodontia proposed by Kemp (1982) has been corroborated by all subsequent students of cynodont phylogeny apart from Battail (1991). Major questions relating to the interrelationships of eucynodonts include: Which taxon is the sister group of mammals? Can distinct monophyletic carnivorous and herbivorous lineages be recognized? What is the phylogenetic position of *Cynognathus*?

Historically, six cynodont groups have been proposed as particularly close relatives of mammals: Thrinaxodontidae (Hopson 1969; Hopson and Crompton 1969; Barghusen and Hopson 1970; Fourie 1974), Probainognathidae (Romer 1970; Crompton and Jenkins 1979), Dromatheriidae (Hopson and Kitching 1972), Tritylodontidae (Kemp 1983; Rowe 1988, 1993; Wible 1991; Wible and Hopson 1993), Tritheledontidae (Hopson and Barghusen 1986; Shubin et al. 1991; Crompton and Luo 1993; Hopson 1994; Luo 1994; Hopson and Kitching 2001), and Brasilodontidae (Bonaparte et al. 2005; Abdala 2007; Martinelli and Rougier 2007). The Thinaxodontidae and Probainognathidae hypotheses have been virtually abandoned in recent studies.

Dromatheriids (*Dromatherium* and *Microconodon*) had been regarded as mammals in the 19th century (Owen 1871; Osborn 1886, 1887), although they were later referred to Cynodontia (Simpson 1926a, b). Their phylogenetic positions were uncertain, but they were regarded as possibly having mammalian affinities by Hopson and Kitching (1972). Dromatheriidae was subsequently redefined to include *Dromatherium*, *Microconodon*, *Pseudotricodon*, *Therioherpeton*, *Tricuspes*, and *Meurthodon* (Hahn et al. 1984, 1994). *Therioherpeton* was excluded from Dromatheriidae by Battail (1991), although retained as sister taxon to the group. Recently, several isolated teeth from India were described as belonging to a new dromatheriid cynodont, *Rewaconodon* (Datta et al. 2004). Fossil dromatheriid remains are scarce and typically restricted to isolated teeth, though some dentary fragments are also known. Poor material limits current understanding of the phylogenetic relationship between dromatheriids and mammals and among non-mammalian eucynodonts (Sues 2001; Datta et al. 2004).

Tritylodontidae is a herbivorous group ranging stratigraphically from the Late Triassic/Early Jurassic to the Late Cretaceous (Kühne 1956; Kamiya et al. 2006). The monophyly of this group is universally accepted. Tritylodontids were once thought to be mammals, but the lack of a dentary-squamosal articulation challenged this interpretation (Watson 1942). Watson (1942) and Kühne (1956) stressed the similarity between the skull of tritylodontids and cynodonts and concluded that tritylodontids were derived from cynodonts, but no more precise statement could be made. Tritylodontids have been classified as

cynodonts since Haughton and Brink (1954), and were subsequently suggested to have been derived from Traversodontidae (Crompton and Ellenberger 1957). This opinion, which implies that Traversodontidae is not monophyletic, has also found favor among more recent authors (Hopson and Kitching 1972, 2001; Sues 1985). Battail (1991: fig. 8) accepted the idea of a close relationship between Traversodontidae and Tritylodontidae, but suggested that traversodontids were monophyletic. Tritylodontids did not represent close relatives of mammals in either case. This implies that many features of the orbital wall and sphenoid region shared by tritylodontids and early mammals as well as several features of the rest of the skull and the postcranium would be tritylodontid-mammal homoplasies (Luo 1994). Kemp (1983) was the first to propose that tritylodontids were more closely related to mammals than is *Probainognathus*, and that there was no close relationship between Traversodontidae and Tritylodontidae. However, he acknowledged that Tritheledontidae might be even more closely related to mammals than Tritylodontidae.

Tritheledontids are small, presumably insectivorous forms occurring from the Late Triassic to the Early Jurassic (Lucas and Hunt 1994). This family initially included only the species *Tritheledon riconoi* (Broom 1912); later *Diarthrognathus broomi* and *Pachygenelus monus* were referred to this family although the former was viewed as a junior synonym of the latter (Hopson and Kitching 1972). Gow (1980) showed *Diarthrognathus broomi* is a valid taxon. Shubin et al. (1991) listed four dental features as diagnostic of Tritheledontidae. On this basis, they included only *Tritheledon*, *Diarthrognathus*, and *Pachygenelus* in Tritheledontidae; *Chalimina*, *Riograndia*, *Irajatherium*, and *Elliotherium* were referred to this family later (Martinelli et al. 2005; Sidor and Hancox 2006), but *Riograndia* sometimes was excluded from this family (Martinelli and Rougier 2007). In the hypothesis of Martinelli and Rougier (2007), Tritheledontidae is a monophyletic group including *Chalimina*, *Irajatherium*, *Elliotherium*, *Tritheledon*, *Diarthrognathus*, and *Pachygenelus*; Ictidosauria includes Tritheledontidae and *Riograndia*. However, Ictidosauria is more inclusive in Abdala (2007)'s usage, it includes not only Tritheledontidae but also Tritylodontidae. Tritheledontids were combined with *Prozostrodon*, *Therioherpeton*, *Brasilitherium*, and *Brasilodon* as the more inclusive taxon Tritheledonta (Kemp 2005).

Bonaparte et al. (2003, 2005) proposed that brasilodontids, including *Brasilodon* and *Brasilitherium* from the Late Triassic of Rio Grande do Sul together constitute the sister taxon to mammals. This opinion was supported by the study of Martinelli and Rougier (2007). Sidor and Hancox (2006) found *Prozostrodon* to be the sister taxon of mammals.

Recently, Abdala (2007) published a phylogenetic analysis of eutheriodonts (including traditional therocepha-

lians, cynodonts and their descendants—the mammals) based on 95 cranial and dental characters. In his results, *Ecteninion* grouped with *Cynognathus* and Gomphodontia (not including Tritylodontidae). Traditionally, four gomphodont groups have been recognized: diademodontids, trirachodontids, traversodontids, and tritylodontids (Seeley 1895; Hopson and Kitching 1972), but recently tritylodontids are excluded from Gomphodontia (Abdala and Ribeiro 2003; Hopson 2005). *Platycraniellus* lay between *Thrinaxodon* and the remaining Eucynodontia. *Pachygenelus* was the sister group of Tritylodontidae, and they formed a monophyletic Ictidosauria. Moreover, *Brasilitherium* was the sister-taxon of mammals but *Brasilodon* was far more basal. Martinelli and Rougier (2007) also published a tree of eucynodonts. They did not include tritylodontids in their analysis, and their result was similar to the trees of Martinelli et al. (2005) and Sidor and Hancox (2006).

These studies document the progress in our knowledge on the phylogenetic relationships of Eucynodontia and the origin of mammals, and offer an opportunity to test sampling strategies in phylogenetic analysis. The multitude of incongruent hypotheses comes from theses studies' diverse taxonomic sampling strategies and their reliance upon different sets of characters. Previous studies varied in their detailed goals, therefore in their taxonomic sampling (Table 1), but employed higher taxa (e.g., genera, families) rather than species as terminal taxa. For example, Tritylodontidae or Tritheledontidae appear as OTUs in most studies (Wible 1991; Luo 1994; Martinez et al. 1996; Hopson and Kitching 2001; Bonaparte et al. 2005). Wiens (1998) found that coding higher taxa as terminals appears to yield less reliable results than the alternative practice of using species as terminals. The rationale is that analysis using higher taxa as terminals sacrifices some information from interspecifically variable characters. Furthermore, any higher taxa used as terminals in a phylogenetic analysis must be monophyletic. Because the monophyly of some cynodont families still needs to be tested, it is inappropriate to use them in this way. For example, some scholars include *Trirachodon* in Diademodontidae (Hopson and Kitching 1972) rather than in Trirachodontidae; therefore, the use of Diademodontidae as a terminal taxon is problematic. Additionally, previous studies often failed to state how the higher taxa used as terminals were coded.

Most previous analyses have sampled few taxa, usually only one genus for each major group. For example, traversodontids were represented only by *Exaeretodon* in Wible (1991), and by *Massetognathus* in Martinez et al. (1996). Furthermore, *Morganucodon* was the sole representative of mammals in some analyses, including those of Martinez et al. (1996), Hopson and Kitching (2001), and Bonaparte et al. (2003). Bonaparte et al. (2003) did not include in their analysis any gomphodont cynodonts or

tritylodontids. Recent works, however, have tended to sample increased numbers of taxa.

Wible (1991) used 66 dental and cranial characters in his analysis. Luo (1994) used 82 characters, 11 of which came from the temporomandibular joint, and a further 20 from the petrosal. Martinez et al. (1996) used 68 characters, including 13 from the dentition. Hopson and Kitching (2001) used 101 characters, of which 29 were dental and 19 postcranial. Bonaparte et al. (2005) used 80 characters, including 20 dental ones and 12 postcranial ones. Martinelli et al. (2005) included 63 characters, 13 of which were postcranial. Martinelli and Rougier (2007) included 93 characters, 32 of which were related to the dentition and 17 of which were postcranial. Abdala (2007) used 98 craniodental characters.

Important conflicts among the various hypotheses are the convergent appearance of some characters in traversodontids, tritylodontids, and mammals on the one hand, and among tritheledontids, tritylodontids, and mammals on the other (Luo 1994; Kemp 2005). Partly because of this widespread convergence, character selection has a crucial impact on the conclusions of any analysis of eucynodont phylogeny. However, no author other than Wible (1991) presented explicit criteria for accepting or rejecting characters. No analysis to date has compiled and integrated all previous used anatomical data into a data matrix. Another factor confounding analyses of interrelationships within Eucynodontia is the limited information available for some taxa.

Here we present a compilation of published morphological data and augment it with new taxa and characters. This data set is the largest ever to be simultaneously analyzed for Eucynodontia. Cladistic analyses of these data are performed here in order to (1) determine the phylogenetic position of Tritylodontidae, of Tritheledontidae, and of *Cynognathus*; and (2) examine the effects of missing data and increasing taxonomic sample size.

Institutional Abbreviations BMNH, Natural History Museum, London, UK; BP, Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Johannesburg, South Africa; CUP, Catholic University of Peking, now housed in the Field Museum, Chicago, USA; UFRGS-PV, Setor de Paleovertebrados, Instituto de Geociências, Universidade Federal do Rio Grande do Sul, Porto Alegre RS, Brazil.

Materials and methods

Two appendices contain all the data relevant to this study. Appendix I contains a list of 145 characters, with descriptions of their states. Appendix II is the data matrix.

Table 1 Differences in taxonomic sampling across several studies of eucynodont phylogeny, including the present paper

Wible (1991)	Luo (1994)	Martinez et al. (1996)	Hopson and Kitching (2001)	Bonaparte et al. (2005)	Martinelli and Rougier (2007)	Abdala (2007)	This paper
						......	
			Dvinia			Dvinia	
			Procynosuchus		Procynosuchus	Procynosuchus	Procynosuchus delaharpeae
			Galesaurus			Galesaurus	Galesaurus planiceps
						Progalesaurus	
						Platycraniellus	Platycraniellus elegans
	Thrinaxodontidae	Thrinaxodon	Thrinaxodon	Thrinaxodon	Thrinaxodon	Thrinaxodon	Thrinaxodon liorhinus
Cynognathus		Cynognathus	Cynognathus	Cynognathus	Cynognathus	Cynognathus	Cynognathus crateronotus
Diademodon	Diademodontidae		Diademodon			Diademodon	Diademodon tetragonus
			Trirachodon			Trirachodon	Trirachodon berryi
							Sinognathus gracilis
							Langbergia modisei
	Traversodontidae				Traversodontidae		
			Pascualgnathus	Pascualgnathus			Pascualgnathus polanskii
		Massetognathus	Massetognathus			Massetognathus	Massetognathus pascuali
Exaeretodon			Exaeretodon	Exaeretodon		Exaeretodon	Exaeretodon argentinus
			Scalenodon angustifrons				Scalenodon angustifrons
			"Scalenodon" hirschoni				Scalenodon hirschoni
			Luangwa				Luangwa drysdalli
			Gomphodontosuchus				
			Lumkuia	Lumkuia	Lumkuia	Lumkuia	Lumkuia fuzzi
		Ecteninion	Ecteninion		Ecteninion	Ecteninion	Ecteninion lunensis
		Probelesodon	Probelesodon	Probelesodon			
		Chiniquodon	Chiniquodon	Chiniquodon	Chiniquodon	Chiniquodon	Chiniquodon theotonicus
			Aleodon				
Probainognathus	Probainognathidae	Probainognathus	Probainognathus	Probainognathus	Probainognathus	Probainognathus	Probainognathus jenseni
				Prozostrodon	Prozostrodon		Prozostrodon brasiliensis
				Therioherpeton	Therioherpeton		Therioherpeton cargnini
Tritheledontidae	Tritheledontidae	Tritheledontidae					
				Riograndia	Riograndia	Riograndia	Riograndia guaibaensis
					Irajatherium		
					Chaliminia		
					Tritheledon		
					Elliotheium		
					Diarthrognathus		

Pachygenelus monus
Brasilodon quadrangularis
Tritylodon longaevus
Oligokyphus major
Bienotherium yunnanense
Kayentatherium wellesi
Adelobasileus cromptoni
Sinoconodon rigneyi
Morganucodon oehleri

Pachygenelus
Brasilitherium
Brasilodon
Oligokyphus
Kayentatherium
Sinoconodon
Morganucodon

Pachygenelus
Brasilitherium
Brasilodon
Sinoconodon
Morganucodon

Pachygenelus
Brasilitherium
Brasilodon
Tritylodontidae
Adelobasileus
Haldanodon
Morganucodon
Megazostrodon
Dinnetherium
Kuehneotherium

Pachygenelus
Tritylodontidae
Morganucodon

Tritylodontidae
Adelobasileus
Sinoconodon
Haldanodon
Morganucodon
Megazostrodon
Dinnetherium
Kuehneotherium
Multituberculata
Haramiyidae
Triconodontidae
Monotremata
Vincelestes
Marsupialia
Placentalia

Taxonomic sampling

The following supra-generic groups have been recognized within Cynodontia: Procynosuchidae, Galesauridae, Cynognathidae, Diademodontidae, Trirachodontidae, Traversodontidae, Chiniquodontidae, Probainognathidae, Tritylodontidae, Tritheledontidae, Brasilodontidae, and Mammalia (Hopson and Kitching 1972; Battail 1991). However, some of these groupings are not monophyletic. Some of the mentioned groups are monotypical and therefore monophyletic, for example, Cynognathidae and Probainognathidae. Tritylodontidae and Mammalia can be considered as well-established monophyletic groups at the present time (Hopson and Barghusen 1986; Rowe 1993; Luo 1994; Luo et al. 2002). The different groups also vary greatly in the number of species that they contain. Most proposed supragenoric groups include only a few genera and species, and indeed some are monogeneric. However, Traversodontidae and Tritylodontidae have more than ten genera and 20 species, and Mammalia of course includes a far greater number.

Recent papers have suggested that adding more species to a cladistic analysis can greatly reduce phylogenetic error, increasing the accuracy of phylogenetic estimates generated by computer simulations (Pollock et al. 2002; Zwickl and Hillis 2002; Debry 2005). However, it is impractical to include all or most relevant species in analyses attempting to resolve relationships among higher taxa (Donoghue 1994; Rice et al. 1997), leading to the problem of selecting particular species as exemplar for higher taxa. Wiens' (1998) simulation showed that sampling a single randomly chosen species per higher taxon yields low accuracy under many conditions. Nevertheless, mammals were represented in some studies by only a single taxon, *Morganucodon* (Hopson and Kitching 2001), and other studies have used either *Exaeretodon* or *Massetognathus* as the sole representative of Traversodontidae (Wible 1991; Martinez et al. 1996). A close relationship between tritylodontids and traversodontids has been suggested on the basis of comparisons between members of the tritylodontids and either *Exaeretodon*, a derived traversodont (Sues 1985), or *Scalenodon hirschoni* (Hopson and Kitching 2001). Accordingly, both *Exaeretodon* and *Scalenodon* are important taxa that should be included. Nonetheless, if only one species is selected to represent a particular group, it should be the most basal member of that group that is available. If only derived taxa are included, the morphological gaps among clades will be exaggerated, and problems with long-branch attraction could possibly result, as in the example involving iguanid lizards given by Wiens and Hollingsworth (2000).

Specific strategies have sometimes been proposed for taxonomic sampling in phylogenetic analyses. Prendini (2001) advocated choosing at least two species per non-monotypic higher taxon, with preference given to type taxa, basal taxa, and sets of taxa that capture as much morphological disparity as possible within the clades they represent. Luo et al. (2002) suggested criteria such as morphological informativeness, within-group morphological diversity, within-group geological age (early members of respective lineages), and consideration of anatomical transformation (morphologically distinctive taxa, particularly those with a potential bearing on structural transformations).

Taxa were selected for the present analysis with attention to all these criteria, and we also tried to incorporate taxa used in previous analyses. We selected 31 cynodont species, two of which were used as outgroups (Table 1). Individual species were used as terminal taxa in order to avoid a priori assumptions of monophyly within large, supragenoric clades. Some taxa represented in previous analyses were excluded from the current study. Within mammals, only *Adelobasileus*, *Sinoconodon*, and *Morganucodon* were selected because our study is not intended to consider the interrelationships of early mammals. Among primitive cynodonts, *Dvinia* was excluded, whereas *Procynosuchus* and *Galesaurus* are used as outgroups. *Probelesodon* was removed because it is regarded as a junior synonym of *Chiniquodon* (Abdala and Giannini 2002). *Aleodon* was original described as a gomphodont cynodont, but Hopson and Kitching (1972) reassigned this taxon to Chiniquodontidae based on undescribed specimens that they may have subsequently used (Hopson and Kitching 2001) to code its morphological characters. Based on BMNH 9390 and 10048. Abdala and Giannini (2002) excluded *Aleodon* from Chiniquodontidae and concluded that the evidence was insufficient to determine its true taxonomic position. The known material is poorly preserved, so this genus is not included in the present analysis. We regard Chiniquodontidae as a monogeneric taxon, containing two species of *Chiniquodon*, one of which we included in our analysis. *Gomphodontosuchus* was excluded, because the only known specimen is a juvenile (Hopson 1985) and the analysis already incorporated six other traversodontids.

Only *Brasilodon quadrangularis* was considered in our analysis, because *Brasilitherium riograndensis* is regarded as a synonym of this species. Bonaparte et al. (2005) used some characters to differentiate *Brasilitherium* from *Brasilodon* (Table 2). However, putative specimens of *Brasilodon* and *Brasilitherium* are not distinguishable by these characters. The absence of cusp d in some described specimens of *Brasilodon* may be a result of wear, and this cusp is clearly present on a lower postcanine of specimen UFRGS-PV 0765T. Any visible suture between the prootic and opisthotic would have to lie on the lateral side of the fenestra ovalis. This area is incomplete in UFRGS-PV

Table 2 Characters to differentiate *Brasilitherium* and *Brasilodon* by Bonaparte et al. (2005). Number in parentheses is the original character number of Bonaparte et al. (2005)

Character and corresponding number in their original character list	*Brasilitherium*	*Brasilodon*
Cusp d in lower postcanines	Present	Absent
Prootic and ophistotic (56)	Fused	Separated
Petrosal promontorium (57)	Incipiently developed	Absent
Separation of perilymphatic foramen from jugular foramen (60)	Completely separated	Partially separated
Length of secondary palate related to tooth row (36)	About equal	Longer

0804T and not well preserved in UFRGS-PV 0929T. No complete petrosal is preserved in referred specimens of *Brasilodon*. Even the area corresponding to the promontorium of *Brasilitherium* (UFRGS-PV 0929T) is incomplete in UFRGS-PV 0628T; the preserved adjacent part of the skull is reminiscent of *Brasilitherium* and implies the presence rather than absence of the promontorium. In both taxa, the posterior extension of the secondary palate continues approximately to the level of the posterior end of the tooth row (see Bonaparte et al. 2005: fig. 5, character 36). The jugular foramen is generally bordered by the petrosal, the exoccipital, and possibly the basioccipital. Although Bonaparte et al. (2005) identified this foramen within the petrosal in UFRGS-PV0628T (see their fig. 7), this area is in fact identical in this specimen and in UFRGS-PV 0929T and UFRGS-PV 0804T. The petrosal of UFRGS-PV 0628T also encloses a separate fenestra rotunda. The hypoglossal foramen is coded as indistinct in *Brasilitherium*, but both primitive (indistinct) and derived states (separated from the jugular foramen) are coded in *Brasilodon* (Bonaparte et al. 2005: character 65). Accordingly, this character provided no evidence to differentiate *Brasilitherium* and *Brasilodon*.

Selection and coding of the characters

The morphological characters used in this study were taken from several sources. An initial character list was generated by combining anatomical characters used in the following studies: (1) Rowe (1988), with corrections noted by Wible (1991); (2) Lucas and Luo (1993), most characters were adopted by Luo (1994), and some characters modified by Luo et al (2001); (3) Luo and Crompton (1994) (on the quadrate); (4) Martinez et al. (1996); (5) Hopson and Kitching (2001); (6) Bonaparte and his colleagues (Bonaparte et al. 2003, 2005; Martinelli et al. 2005); and (7) Abdala (2007). The definitions of all characters were examined and some were revised for the present study. Following initial compilation, the character set was examined carefully to identify and remove redundant or covariant characters. Elimination of redundant characters ensured that all characters in the analysis were logically independent. For

clearly covariant characters, the definition of the characters was revised to ensure the biological independence of the character. However, the biological independence or non-independence of characters is uncertain in the vast majority of cases, so that covariant characters cannot be completely eliminated. Single characters that were created by combining multiple characters from different sources are identified as such in the character list, and all contributing sources are cited accordingly (Appendix I).

Because of differences in taxonomic sampling, some characters used by previous authors are clearly uninformative in the context of this analysis. Characters in this category were excluded. Only some characters of *Adelobasileus*, *Sinoconodon*, and *Morganucodon* were included, because the monophyly of mammals is well supported by several other characters. The synapomorphies of ingroups were partially included too.

This process of character selection was intended to ensure that the analysis was based on data that were as accurate as possible, and secondarily to maximize the information content of our data matrix. Inapplicable characters were coded as dashes (missing data) rather than as numerical character states. Although this method has its disadvantages, it is preferred here because it has been shown to produce trees that best reflect the information content of the observations (Strong and Lipscomb 1999).

The final character list included a total of 145 characters. Of all characters, 81 are from the skull, 10 from the lower jaw, 28 from the dentition, and 26 from the postcranial skeleton. Character states were then scored either from first-hand observations of specimens in museum collections, or from original published descriptions and photographs. When two previous analyses gave conflicting information on a character, an assessment of the correct character state was made based on first-hand observations. We did not treat any one published analysis as being more reliable a priori than the others. In addition to morphological characters gleaned from published analyses, we introduced three new cranial characters (characters 12, 18, and 124; Appendix I). The relative large amount of missing and inapplicable data in the matrix largely results from the fact

that only fragmentary material is available for many species.

Multistate characters generally should be treated as unordered in cladistic analysis except when they represent a transformation series based on prior knowledge (Hauser and Presch 1991; Slowinski 1993). Hopson and Kitching (2001) also showed that ordered multistate characters resulted in a different topology from unordered characters. We apply different strategies: some multistate characters are treated as both unordered and ordered in our analyses. Postcranial characters were excluded from many previous analyses. To direcly compare with these studies and to evaluate the effect of postcranial characters on the phylogenetic relationships of Eucynodontia, the postcranial characters were excluded in some of our analyses.

Hypotheses of tooth homology

The cheek teeth of most cynodonts are usually classified as either gomphodont or sectorial, but those of tritylodontids are distinctive enough that they are usually placed in a separate category distinct from the gomphodont type. Because cynodonts had intensely modified their cheek teeth in some groups, it is difficult to deduce the homologies of individual cusps (and cingula) among different tooth forms. In general, gomphodont teeth are thought to have originated from sectorial teeth by widening of both the crown and the root (e.g., Abdala and Ribeiro 2003). Based on a comparison between the postcanines of *Scalenodon* and *Oligokyphus*, Crompton and Ellenberger (1957) suggested that tritylodontid teeth can be derived from traversodontid teeth. Hopson and Kitching (2001) held the same opinion, so they presumed that cingula occurring on the same side (lingual or labial) of the tooth row are homologous across all cynodonts (e.g., their characters 61 and 62) and that similarly positioned individual cusps are homologous between traversodontids and tritylodontids (e.g., their characters 67 and 69). By contrast, Rowe (1986) used evidence from *Trirachodon* to support the view that gomphodont teeth evolved through the counter-clockwise rotation of teeth in their dentary sockets, possibly to allow more teeth to be packed into the available space. He further proposed that tritylodontid teeth did not evolve through rotation, implying that no individual cusps can be homologized between tritylodontid and gomphodont teeth. In the tritheledontid *Diarthrognathus*, which has transversely widened teeth, all newly erupting teeth are oriented with their long axes parallel to that of the jaw, so that rotation must have occurred later in ontogeny in order to allow the teeth to become functional (Gow 1994). This clearly demonstrated the reality of the rotation mechanism in cynodonts. Because of the conflicting interpretations of homology, we applied characters on cusps only for the same type of teeth, i.e., no hypothetical homology between sectorial and gomphodont teeth, and no assumed correspondence of cusps between tritylodontid and other gomphodont teeth. However, correspondence of cusps is assumed within Gomphodontia excluding Tritylodontidae (diademodontids, trirachodontids, plus traversodontids) following previous works such as Abdala and Ribeiro (2003) and Hopson (2005).

Analyses and results

The data matrix (Appendix II) was analyzed with PAUP *4.0 b10 with a heuristic search using the random addition sequence with 1,000 replicates, the tree bisection-reconnection algorithm in branch-swapping, and all trees saved are themselves input to the branch swapping procedure. All multistate characters were treated as unordered. This analysis resulted in eight most parsimonious trees of 429 steps (Consistency Index=0.49, Retention Index=0.77), the strict consensus of which is illustrated in Fig. 1. The Bremer support values were calculated by a series of manual PAUP converse constraint analyses. When the 21 characters marked in the list with asterisks were ordered, the topology of the most parsimonious trees was the same but the tree length increased to 435 steps. When postcranial characters were excluded, analyses resulted in 24 most parsimonious trees of 386 steps if all characters were unordered (their strict consensus tree shown in Fig. 2) and 48 trees of 391 steps if the 21 characters indicated in the list were ordered. When the selected characters were ordered, the strict consensus tree remained topologically identical to that shown in Fig. 1.

To evaluate the impact of synonymizing *Probelesodon* with *Chiniquodon*, and *Brasilitherium* with *Brasilodon*, these taxa were coded separately and analyzed with other taxa. The results are almost the same as those of the above analysis.

The impact of fragmentary taxa

Some taxa with large porportion of missing data were pruned from the data matrix in some analyses. The number of shortest trees (Table 3) decreases when *Sinognathus* and *Scalenodon hirschoni* are deleted, but does not change upon deletion of *Scalenodon angustifrons* or of the most fragmentary taxon in the analysis, *Adelobasileus*. The number of shortest trees actually increases when either of the incompletely known taxa *Prozostrodon* or *Therioherpeton* is deleted (Table 3). Thus, the quantity of missing data is not completely correlated with the degree of ambiguity; the lack of resolution in the analysis is primarily due to character conflict rather than incomplete information.

The relationships among eucynodont taxa undergo little change after deletion of *Sinognathus*, *Scalenodon hirschoni*,
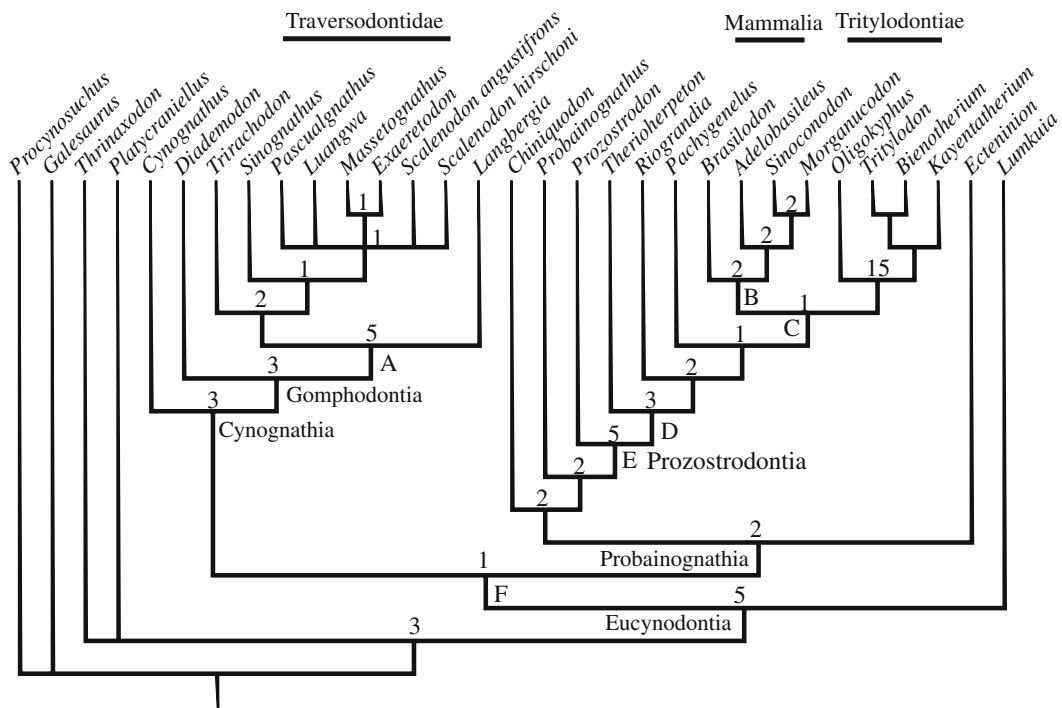
Fig. 1 Strict consensus tree of most parsimonious trees (tree length=429, CI=0.49, RI=0.77) obtained using PAUP4.0b10, with all characters unordered. The number above the node is the decay index of that clade. The unambiguous characters support clades from MacClade 4.08 OSX (Maddison and Maddison 2005) (characters in *bold* indicate CI=1, characters in *italics* are unique, uniform within that clade): A, 18(1), 23(1), 28(1), 35(1), 56(2), 69(1), 74(1), 83(1), 117(1); B, 18(0), **47(1), 50(1)**, 55(1), 94(1),96(0); C, 38(2), **54(1)**, 56 (2), **132(1),138(2);** D, 13(1), 144(1), 145(1); E, 16(1), 82(0),**86(1),** 107(1), **138(1),***139(1), 140(1);* F, 41(1), 48(1), **87(1), 88(1)**; Traver-sodontidae, 83(2), **116(1)**; 111(2) (on 6 of 8 trees); Gomphodontia, 22 (1), 91(1), 92(1), 93(3), 102(2), 112(1), 119(1);Cynodontia, 17(1),(19 (2), 23(2), 24(1),25(1), 97(1),126(1);Tritylodontidae, 1(1), 6(1), 8(1), 11(0), 20(2), 21(0), 22(1), 24(1), 25(1), **45(1)**, 46(1), 52(1), 59(1), 60 (1), 61(1), 62(1), 63(0), *69(3),***78(2),** 79(0), **80(2)**, 81(0), 84(1), 91(1), 93(3), 103(2), 104(2), **106(2)**, 109(2), 112(1), *117(3)*, 118(2), *119(2)*, **127(2)**; Probainognathia, 56(1), 69(1), 70(1), 74(1), 76(2), 77(1); Eucynodontia, *40(1), 46(1)*, 79(1), 81(1), 83(1), 105(1); 42(1), 82(1), *127(1)* (on 4 of 8 trees).
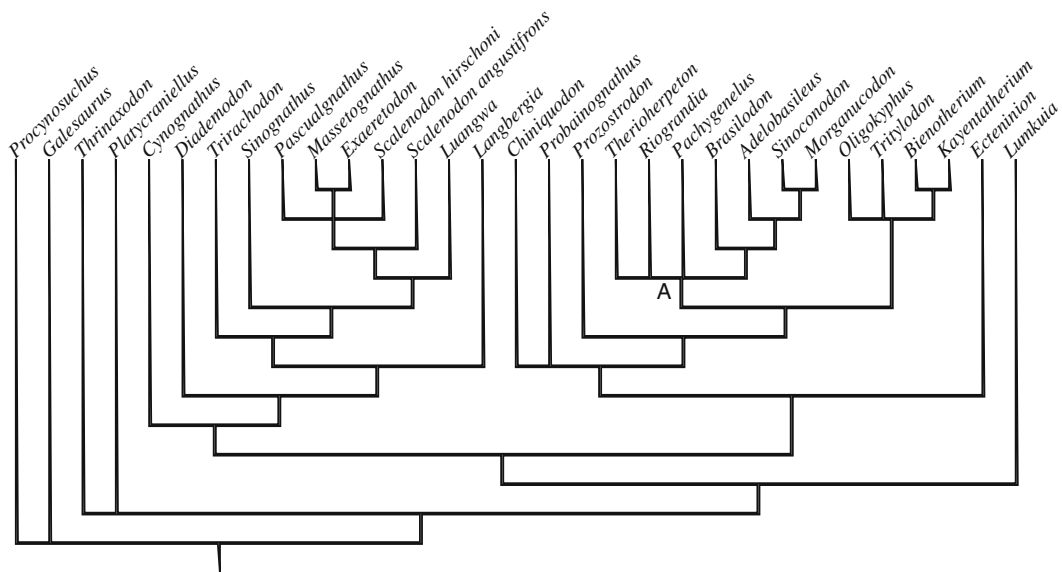
Fig. 2 Strict consensus tree of most parsimonious trees, after excluding postcranial characters. Unambiguous synapomorphies for clade A when all characters are unordered include (*bold* indicates CI=1): **11(1)**; 31(0), **44(1), 46(2), 63(1)**, 75(1), **129(1)** on 12 of 24 MPTs; and 17(2) on other MPTs.

Table 3 The effect of pruning various taxa from data matrix in Appendix II on the most parsimonious trees obtained with phylogenetic analysis

Deleted taxon (taxa)	PM	PI	NT	TL
Sinognathus	33.1	0	6	421
Scalenodon angustifrons	39.3	1.4	8	427
Scalenodon hirchoni	52.4	1.4	2	424
Prozostrodon	52.4	2.1	23	423
Therioherpeton	66.2	2.1	16	427
Adelobasileus	72.4	0	8	424
Prozostrodon plus *Therioherpeton*			220	420

PM percentage of missing characters; *PI* percentage of inapplicable characters; *NT* number of most parsimonious trees after pruning indicated taxa; *TL* length of the parsimonious trees

or *Adelobasileus*. If only the most complete taxa (coded for more than 80% of the characters) are included in the analysis, the result is a subtree of Fig. 1. This agrees with the simulations of Wiens (2003), which also shows that the inclusion of highly incomplete taxa tends to have little impact on the recovered pattern of relationships among more complete ones. However, when *Scalenodon angustifrons* is excluded, a monophyletic Traversodontidae disappears from some trees; when *Prozostrodon* is deleted from the analysis, *Riograndia* and *Pachygenelus* become closer to mammals than tritylodontids in half of the most parsimonious trees (MPTs), and *Chiniquodon* forms a monophyletic clade with *Probainognathus* in some trees. Exclusion of *Therioherpeton* results in a consensus tree similar to Fig. 2.

The impact of selecting taxa

To ascertain the effect of taxon sampling on the eucynodont interrelationships, the composed data matrix (Appendix II) was run following the previous taxon samplings.

Using a sample of taxa similar to that considered by Rowe (1993), and selecting *Pachygenelus* as the representative of Tritheledontidae, and *Oligokyphus* as the representative of Tritylodontidae, two most parsimonious trees are obtained. One tree is almost identical to that obtained by Rowe (1993) (Fig. 3). If *Riograndia* is selected to represent Tritheledontidae, a tree corresponding to that in Fig. 3b is the only recovered. If both *Pachygenelus* and *Riograndia* are used, they form a monophyletic sister clade to *Morganucodon*, but the Fig. 3b topology is otherwise unchanged. These results are unique in the position of *Exaeretodon*: it does not group with *Diademodon* and is closer to *Morganucodon* than is *Probainognathus*. This result will change if any other traversodontid taxon is chosen as representative of the group. When *Massetognathus* or *Scalenodon hirschoni* is selected, this clade shifts to the position indicated by the "X" of Fig. 3b. When any of the other traversodontids is selected, a monophyletic Cynognathia appears on the tree.

Lucas and Luo (1993) selected fewer taxa than Rowe (1993). Based on their sampling, the tree represented in Fig. 4b is obtained regardless of whether *Riograndia*, *Pachygenelus*, or both are used to represent tritheledontids, and this result is stable when any combination of the four tritylodontid species is chosen to represent tritylodontids. When the postcranial characters are excluded, however, *Exaeretodon* groups with tritylodontids. When *Diademodon* is included, the result is nearly the same as that shown in fig. 6.1B of Luo (1994).

Following the sampling of Martinez et al. (1996), selecting *Pachygenelus* as representative of Tritheledontidae and *Oligokyphus* as representative of Tritylodontidae, resulted in two most parsimonious trees. *Massetognathus* is a "wild-card" here, but *Chiniquodon* is closer to *Morganucodon* than *Ecteninion* (Fig. 5). Even if the postcranial characters are excluded, Tritylodontidae is closer to
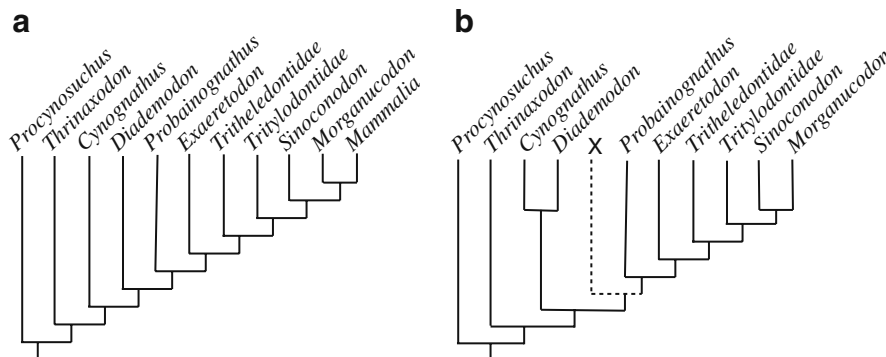
Fig. 3 a Cladogram for Eucynodontia adapted from Rowe (1993: fig. 10.2); **b** the only one or one of two most parsimonious trees obtained from analysis of the data matrix in this paper with all characters unordered using *Riograndia* or *Pachygenelus* and *Riog-* *randia* as representative of Tritheledontidae; "X" indicates the position of *Massetognathus* or *Scalenodon hirschoni* as representative of Traversodontidae.
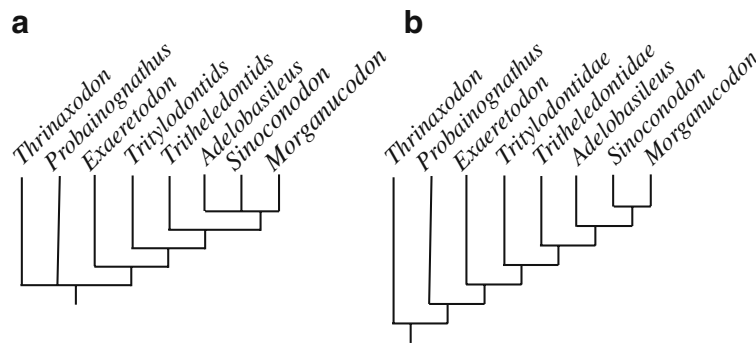
Fig. 4 **a** Cladograms for Eucynodontia adapted from Lucas and Luo (1993: fig. 14); **b** the one most parsimonious tree obtained from analysis of the data matrix in this paper with all characters unordered, selecting *Riograndia*, *Pachygenelus*, or both as representative of Tritheledontidae, and any combination of the four tritylodontid species as representative of Tritylodontidae.

Morganucodon than is Tritheledontidae as in fig. 5 of Martinez et al. (1996).

Using only the taxa considered by Hopson and Kitching (2001), the consensus tree is nearly identical to the tree shown in Fig. 1. Tritylodontidae always groups within Probainognathia, rather than within Traversodontidae, and *Lumkuia* lies in a basal position within Probainognathia in some of the most parsimonious trees.

Including only the taxa used by Bonaparte et al. (2003), results in a shortest tree with the topology shown in Fig. 1, which slightly differs from fig. 21 of Bonaparte et al. (2003). Using the species considered by Bonaparte et al. (2005), also results in trees that are similar to Fig. 1, differing strikingly from fig. 20 of Bonaparte et al. (2005). The relationships among "tritheledontans" and between this group and basal mammals are nearly identical to those obtained by Martinelli et al. (2005) in their analysis of a similar sample of taxa, although relationships among the basal taxa are slightly different (Fig. 6). Depending on the selection of the representative of Traversodontidae, some of the results are similar to fig. 4 of Martinelli and Rougier (2007).

Discussion and Conclusion

Platycraniellus was regarded as more derived than *Thrinaxodon* by Abdala (2007), but the position of *Platycraniellus* is equivocal here. Kemp (1982) defined Eucynodontia as all cynodonts closer to extant mammals than *Thrinaxodon*, so *Platycraniellus* could be a basal member of Eucynodontia.

Eucynodontia is a robust clade with a Bremer support value of 5, and is supported by six unambiguous characters. Four of the most parsimonious trees have three additional unambiguous synapomorphies. A dichotomy within most species of Eucynodontia also is recovered here, although the membership of each branch differs slightly from what previous analyses have proposed. *Lumkuia* is a basal eucynodont. This possibility was implicit in the cladograms of Martinelli et al. (2005), in which *Lumkuia* forms a trichotomy with cynognathians and probainognathians. This position contrasts with proposals by Hopson and Kitching (2001) and Abdala (2007) that *Lumkuia* is a basal probainognathian. Cynognathia (not including Tritylodontidae) has a Bremer support value of 3, and seven
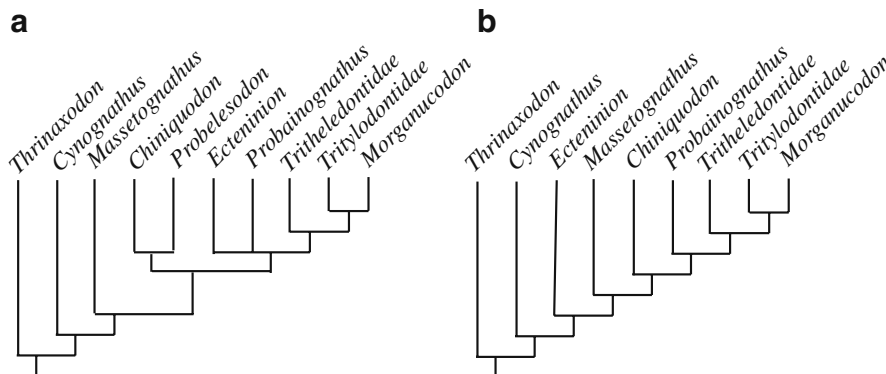
Fig. 5 **a** Cladograms for Eucynodontia cited from Martinez et al. (1996: fig. 5); **b** One of two most parsimonious trees obtained from analysis of the data matrix in this paper with all characters unordered, selecting *Pachygenelus* as representative of Tritheledontidae and *Oligokyphus* as representative of Tritylodontidae.
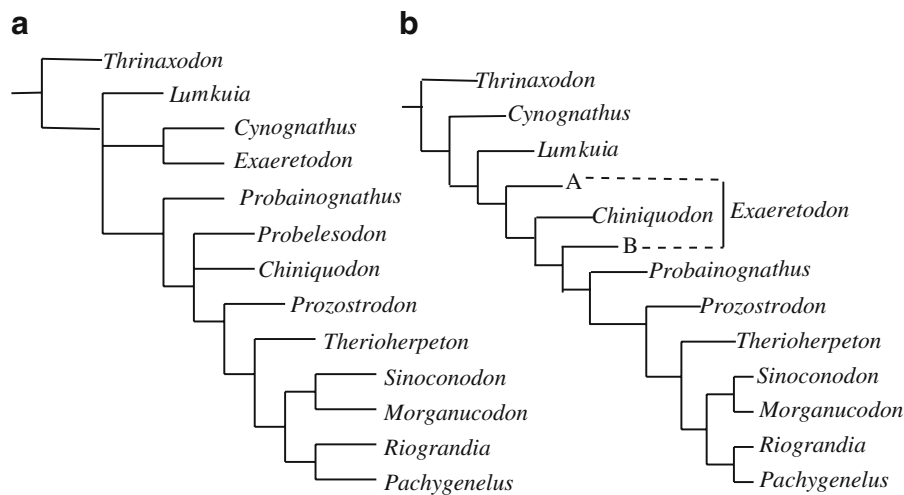
Fig. 6 **a** Cladograms for Eucynodontia adapted from Martinelli et al. (2005: fig. 12); **b** two most parsimonious trees obtained from the analysis selecting 12 taxa from the data matrix of this paper, with all characters unordered; *Exaeretodon* is a "wild-card" taxon, with position at either A or B.

unequivocal synapomorphies, while Probainognathia has a support value of 2 and six unequivocal synapomorphies.

Hopson first proposed a sister relationship between *Cynognathus* and gomphodonts (Hopson and Barghusen 1986; Hopson 1991); Hopson 1991). This relationship is corroborated here. Gomphodontia emerged as a natural group in the tree of Hopson and Kitching (2001). Hopson (1991) proposed a basic pattern of ((Diademodontidae, (Trirachodontidae, Traversodontidae))); essentially the same pattern was recovered here, although a monophyletic Trirachodontidae was absent. Tritylodontidae was thought to be derived from traversodontids (Hopson 1991; Hopson and Kitching 2001), but it was found to be closely related to mammals here. The species of Trirachodontidae used in our analysis showed considerable variation in skull morphology, but they may form a monophyletic group in an analysis including more dental characters. The detailed relationships among these groups will be discussed elsewhere.

Recovered relationships within Probainognathia in our hypotheses were slightly different from those suggested by Hopson and Kitching (2001). The position of *Ecteninion* varies in different studies: it was originally proposed to be a cynodont more derived than *Chiniquodon* (Martinez et al., 1996), a basal probainognathian (Hopson and Kitching 2001; Martinelli and Rougier 2007), or the sister taxon of cynognathians (Abdala 2007). The present analysis placed *Ecteninion* at a basal position within Probainognathia.

Probainognathus is placed closer to mammals than is *Chiniquodon* in most studies, e.g., Martinez et al. (1996), Hopson and Kitching (2001), Abdala (2007), and Martinelli and Rougier (2007); this relationship is absent only in the trees of Bonaparte et al. (2003, 2005) and Martinelli et al. (2005).

Clade E is a stable clade in all results. It includes "tritheledontans", tritylodontids, and mammals. This clade

is more inclusive than Mammaliamorpha of Rowe (1988), and is named as Prozostrodontia here. This group is defined as the least inclusive clade containing *Prozostrodon brasiliensis*, *Tritylodon langaevus*, *Pachygenelus monus*, and *Mus musculus*. Salient synapomorphies of this clade include the reduction of the prefrontal, postorbital, and postorbital bar, presence of sphenopalatine foramen (convergently appearing in traversodontids), unfused dentary symphysis, posterior extension of sagittal crest at the same level as the posteriormost part of the lambdoidal crest, neural spines of posterior thoracic vertebrae posterodorsally inclined, convex iliac blade, reduced posterior iliac spine, acetabular notch on ischium, and lesser trochanter located near the level of femoral head on the medial surface of the femoral shaft.

Tritheledonta is not monophyletic, because as defined by Kemp (2005) it excludes mammals, which contrast with the result of the present analysis. Furthermore, Tritheledonta remains non-monophyletic, even if mammals are not considered, in the cladogram of Abdala (2007) and in the present study. Hence, Tritheledonta in its original meaning cannot be used as a formal taxonomic name. The monophyly of Tritheledontidae has never been seriously doubted; it has been supported in those analyses that have tested it by including multiple tritheledontids (Martinelli et al. 2005; Martinelli and Rougier 2007). The monophyly of Tritheledontidae (*sensu* Martinelli and Rougier 2007) cannot be tested in this study. *Riograndia* does not group with *Pachygenelus* in Fig. 1, but a monophyletic Ictidosauria (*sensu* Martinelli and Rougier 2007) appeared in 12 of the 24 most parsimonious trees recovered when the postcranial characters were excluded. There is only one unambiguous synapomorphy for *Riograndia* plus *Pachygenelus* [93(1)], but nine possible synapomorphies for this clade. The possibil-

ity of a monophyletic Ictidosauria (*sensu* Martinelli and Rougier 2007) cannot be excluded, and needs additional testing.

Pachygenelus is more closely related to mammals than *Prozostrodon* in all most parsimonious trees recovered in this study, and closer to mammals than *Therioherpeton* in most of the trees. This result agrees with the findings of Martinelli et al. (2005) and Martinelli and Rougier (2007), but differs from those of Bonaparte et al. (2005) and Sidor and Hancox (2006).

In all most parsimonious trees, *Brasilodon* falls between other non-mammalian cynodonts and Mammalia, and all four species of tritylodontids used in our analysis group together as a robust monophyletic clade that is supported by 34 unequivocal characters. Even though Tritylodontidae is consistently more closely related to mammals than *Prozostrodon*, the position of Tritylodontidae varies under different character sets. It appears as the sister taxon of *Brasilodon* plus mammals using all characters (Fig. 1), but is found to be the sister taxon of a grouping that includes most "tritheledontans" if postcranial characters are excluded (Fig. 2). Abdala (2007) did not include postcranial characters in his matrix, but tritylodontids form a clade with *Pachygenelus* in his tree.

The impact of fragmentary taxa

In general, incompletely known taxa are usually associated with a large number of equally parsimonious cladograms and poorly resolved consensus trees that fail to reveal strictly supported relationships (Gauthier 1986; Wilkinson 2003). This is not true in the present analysis. Thus, it is clear that the proportion of missing characters for a particular taxon should not be used as a criterion for its inclusion or exclusion within an analysis (Kearney and Clark 2003; Wilkinson 2003). Taxa with the most missing features in this study are the basal traversodontid *Scalenodon angustifrons*, basal prozostrodontians *Prozostrodon* and *Therioherpeton*, and the basal mammaliaform *Adelobasileus*. Basal members of clades are likely to have an important impact on phylogenetic analysis, and should generally be included in the analysis even if they are known only from fragmentary material.

The impact of selecting taxa

In summary, the results of previous analyses are partly congruent with the most parsimonious trees found in this study. Because these simulated analyses mentioned above were based on our data matrix, their different results should be due to taxon sampling. When taxa are poorly sampled, the phylogenetic trees obtained are not reliable.

Different hypothesis and supporting characters

Tritylodontidae-mammals-Traversodontidae relationship

Alternative hypotheses regarding the relationships of these taxa conflict mainly in the placement of tritylodontids, which are sometimes within Cynognathia (including Traversodontidae) and sometimes within Probainognathia. In this data set, the placement of tritylodontids within Cynognathia requires an extra 14 steps if multistate characters are treated as unordered.

The placement of tritylodontids within Cynognathia rather than Probainognathia is supported by many characters (Table 4). Most of these characters are related to either the zygomatic arch or the postcanine teeth, and their presence in both cynognathians and tritylodontids may be a result of convergent adaptation to a herbivorous diet.

Sues (1985) listed 11 characters as possible synapomorphies supporting the inclusion of tritylodontids within Cynognathia. Some of his characters are ambiguous. For example, his character 5, lack of the ectopterygoid, is problematic because this bone is also absent in both *Probainognathus* and prozostrodontians. Similarly, his character 7, ventral margin of the basicranium distinctly sigmoid, is not developed in traversodontids to the same degree as in tritylodontids. Most traversonodontids in fact have a relatively flat basisphenoid. Even in *Exaeretodon*, the basisphenoid is far less sigmoid than in tritylodontids, so that the presence of a sigmoid basisphenoid is best considered as an apomorphy of Tritylodontidae. The condition of the basicranial process of the prootic is unclear in basal probainognathians. If *Oligokyphus* exemplifies the ancestral condition of tritylodontids, characters 10 and 11

Table 4 Characters supporting tritylodontids within Cynognathia

6(1)	Maxillary platform lateral to the tooth row
17(1)	Zygomatic arch high
22(1)	Posteroventral process of jugal high
24(1)	Squamosal groove for external auditory meatus deep
25(1)	Posterior extension of the squamosal dorsal to squamosal sulcus in zygomatic arch well developed
57(1)	Nerve $V_{2\&3}$ exit via two foramina between prootic and epipterygoid
91(1)	Posteriorly directed power stroke during occlusion for mandibles
92(1)	Bilateral, interdigitating occlusion between multiple cusps on each postcanine tooth
93(3)	One or two transverse and crescentic wear facets on multiple cusps
102 (2)	Upper postcanines bucco-lingually expanded
112 (2)	Upper postcanines bear multiple cusps in multiple rows

of Sues are perhaps not synapomorphies for this group because of the presence of anapophysis (Kühne 1956: fig. 45) and the absence of expanded apices on neural spines in *Oligokyphus*.

If tritylodontids are constrained to form a monophyletic clade with traversodontids, the sister taxon of tritylodontids is found to be *Exaeretodon*, not *Scalenodon hirschoni* as suggested by Hopson and Kitching (2001). The following characters support the relationship of tritylodontids plus *Exaeretodon*: 7(1), 52(1), 84(1), 118(2), 125(0), and 133(1). Meanwhile, only three of them unequivocally support the postulated sister-group relationship between *Exaeretodon* and tritylodontids: 52(1), space for trigeminal ganglion partially floored by prootic; 84(1), angle of dentary close to jaw joint; and 118(2), upper tooth series extends posteriorly beyond anterior border of subtemporal fenestra.

A close relationship between tritylodontids and traversodontids was originally proposed mainly on postcanine morphology (Crompton and Ellenberger 1957; Crompton 1972). Most of the dental characters used by Hopson and Kitching (2001) are included in the current list, although a few characters on cusp pattern are excluded because the homologies of the cusps cannot be ascertained. In previous studies, postcranial characters typically played a key role in supporting a close relationship between tritylodontids and the tritheledontids-mammals clade, to the exclusion of traversodontids (abbreviated as: Tri-M/Tra) (Kemp 1983). The present analysis persists in placing tritylodontids within Probainognathia even when postcranial characters are excluded (Fig. 2), requiring three additional steps in order to place tritylodontids within traversodontids for the data set without postcranial characters.

The cranial characters that support Tri-M/Tra mainly come from the orbital region, the palatal complex, the prootic, and the quadrate, including 10(1), 12(1), 13(1), 14(2), 15(2), 37(1), 38(2), 39(1), 49(1), 51(1), 54(1), 58(2), 59(1), 60(1), 61(1), 62(1), 64(1), 65(1), 71(1), 73(1), 74(1), 75(1), 76(3), 77(1), 83(3), and 86(1). The completely divided roots of the postcanines constitute a potential synapomorphy for Tri-M/Tra. Postcranial characters that support Tri-M/Tra include 120(1), 121(1), 122(1), 123(1), 131(1), 132(1), 138(2), 139(1), 140(1), 141(1), 142(1), 143(1), 144(1), and 145(1). On balance, the postcranial skeleton of tritylodontids can be regarded as more mammal-like than that of traversodontids.

Sues and Jenkins (2006) questioned the value of postcranial characters as synapomorphies for Tri-M/Tra, citing Luo (1994: 104) for support. However, Luo (1994) discussed the relationships of tritylodontids with mammals compared with tritheledontids rather than traversodontids, and is therefore not directly relevant. According to Sues and Jenkins (2006), "most of the alleged postcranial similarities are only superficial in nature" and "certain

mammal-like features of the postcranial skeleton of the Tritylodontidae (e.g., large, ossified olecranon process) appear to represent autapomorphies for this group and thus are not useful for determining its phylogenetic relationships". In discussing the relationships of Tritylodontidae, Sues (1985) argued that autapomorphic features should not be emphasized in the context of phylogenetic analysis. Cladistic analysis proceeds by identifying similarities between potentially homologous structures in different taxa. Accepting hypotheses of primary homology only when structures are comparable in minute detail would reduce most anatomical data to lists of uninformative autapomorphies. Although the coding of characters is still an art, workers attempt to maintain a consensus that avoids dismissing too many structures as autapomorphic. Most postcranial characters used in the present study have been widely accepted by different scholars.

A predominantly preacetabular iliac blade has evolved in *Exaeretodon* (Bonaparte 1963), *Therioherpeton* (Bonaparte and Barberena 2001), Tritylodontidae (Sues and Jenkins 2006), and *Morganucodon* (Jenkins and Parrington 1976). Even if a posterior process is present in Tritylodontidae, it nevertheless lies entirely anterior to acetabulum. Even differences in the lesser trochanter of the femur were emphasized by Sues and Jenkins (2006), but these osteological details do not obviate the fact that the gross body plan of tritylodontids is unquestionably more mammal-like than is the body plan of basal cynodonts. We believe that the postcranial characters listed are well established as synapomorphies for Tri-M/Tra.

Identifying the mammal sister-group and Tritylodontidae–Tritheledontidae–mammals relationship (TTMR) and the impact of *Brasilodon*

Traditionally, the two predominant hypotheses relating to the sister-group of mammals have been the tritylodontid-mammal hypothesis (TYMH) and the tritheledontid-mammal hypothesis (TRMH). Each of these alternatives is supported by a large number of putative synapomorphies and contradicted by a substantial amount of opposing anatomical evidence. Luo (1994) analyzed the support for each hypothesis in detail, and showed that it is difficult to conclusively choose between them on the basis of available evidence. These two hypotheses have different implications for the phylogenetic transformations of important mammalian characters. Although no consensus on TTMR can be easily obtained, new findings have shed additional light on the problem of identifying the sister taxon of mammals. *Brasilodon* from Rio Grande do Sul, Brazil, shares more synapomorphies with mammals than does any other non-mammalian cynodont. *Brasilodon* has been recovered as the sister taxon of mammals in all subsequent cladograms

that have included it, provided that *Adelobasileus* is accepted as a basal mammal (Bonaparte et al. 2003, 2005; Abdala 2007; Martinelli and Rougier 2007; this paper).

In their first paper, Bonaparte et al. (2003) listed a number of features as derived characters shared by *Brasilodon* (including *Brasilitherium* in this paper) and morganucodontids but not recorded in other cynodonts (Table 5). Subsequently, they recognized additional derived characters in *Brasilodon*, such as delayed postcanine tooth replacement and the presence of a differentiated promontorium. In this paper, some unambiguous and equivocal synapomorphies are recognized for *Brasilodon* and mammals (Table 6). As recognized by Bonaparte et al. (2003), *Brasilodon* is not directly ancestral to any known mammal. *Brasilodon* has some striking autapomorphies, such as postcanine morphology more complex than *Sinoconodon*, a long stapedial process from the anterior rather than the posterior side of the neck on the quadrate ["STPQ" in fig. 1 of Bonaparte et al. (2005)] (Luo 2007). The monophyly of *Adelobasileus*, *Sinoconodon*, and *Morganucodon* can be recognized even when only a subset of the available mammalian characters are used in this data matrix.

The present study does not conclusively resolve the problem of TTMR. Luo (1994) listed the synapomorphies for each hypothesis. The following paragraphs present alternative interpretations of some of these characters, and present the possible synapomorphies found in this study.

For the orbital region, Luo (1994) listed four characters as synapomorphies shared by tritylodontids and mammals. However, all four characters are invalid or at least problematic. A large ascending process of the palatine and orbitosphenoid contributing to the orbital wall is present not only in tritylodontids but also in *Prozostrodon*, *Therioherpeton* (Bonaparte and Barberena 2001: figs. 1, 9), *Riograndia* (Soares, 2004), and *Brasilodon* (Bonaparte et al., 2005: fig. 14). Among tritylodontids, the palatine participates in the subtemporal border of the orbit only in *Kayentatherium*; the state of this character is unclear in *Oligokyphus* based on the original reconstruction of Kühne (1956: text-fig. 18). In the holotype of *Bienotherium* (personal observation), the palatine is close to the subtemporal border but does not not participate in it. Young

(1947) did not illustrate a clear border between the palatine and the pterygoid. In *Tritylodon* (BP/1/4778), Brink (1988) showed different states on the two sides of the skull. Luo (1994) also listed "separate orbital openings for greater and lesser palatine nerves". However, the homology of the formina for the greater and lesser palatine nerves is hard to understand in tritylodontids and mammals. Within Tritylodontidae, two separated foramina are known only in *Kayentathrium* (Sues 1986); it is unclear whether this condition is shared by other genera.

Luo (1994) believed that the tritheledontid mandible moved dorsomedially in occlusion, whereas Luo et al. (2001; Character 74 in appendix) considered the direction of occlusion to be orthal.

The pterygoplatine ridges include a middle ridge and intermediate ridges. The middle ridge is absent in *Pachygenelus* (Allin and Hopson 1992: fig. 28.4H) and *Riograndia* (Soares 2004); the middle ridge is present and reaches the basisphenoid in most tritylodontids, including *Bienotherium* (Young 1947: fig. 3), *Tritylodon* (BP/1/4778), and *Yunnanodon* (Luo 2001: fig. 1), but not *Bienotheroides* (Sun 1984: fig. 4); and the same condition is present in *Brasi1odon* (Bonaparte et al. 2005: fig. 11, UFRGS-PV 0929T), *Adelobasileus* (Lucas and Luo 1993: fig. 9), *Sinoconodon* (Crompton and Luo 1993: fig. 4.10), and *Morganucodon* (Kermack et al. 1981: fig. 98). The presence of a middle pterygoplatine ridge [character 38(2)] optimizes as a synapomorphy for tritylodontids and mammals. The intermediate ridges extend posteriorly to the anterior border of the basisphenoid in both tritheledontids (*Pachygenelus* and *Riograndia*) and basal mammals, but not tritylodontids. The description of this character in Luo's (1994) table 6.2 is not entirely correct; the character should be given as "intermediate pterygopalatine ridges reach basisphenoid". This character is correlated with the width of the anterior part of the basisphenoid [44], as intermediate pterygopalatine ridges only can extend to the basisphenoid if the basisphenoid is broad.

Character 75(1), round dorsal margin of the dorsal plate of the quadrate, was found to be a synapomorphy of tritheledontids and mammals by Luo (1994) and also in the present analysis. However, despite that tritylodontids primitively have a peg-like dorsal process, such as in *Oligokyphus* (Kühne 1956; Luo and Crompton 1994), the rounded margin also occurs convergently in some derived tritylodontids, such as *Kayentatherium* (Luo and Crompton 1994: fig. 9) and *Bienotherium* (CUP 2241).

The putative synapomorphies shared by tritheledontids and mammals found in this study also include: moderate expansion of the braincase in the parietal region [11(1)], presence of an interpterygoid vacuity in the adult [31(0)], and basisphenoid wing (parasphenoid ala) much shorter and overlapping prootic pars cochlearis (cochlear housing) [46(2)]. The potential synapomorphies shared by tritylodontids and mammals are

Table 5 Synapomorphies of *Brasilodon* and morganucodontids from Bonaparte et al. (2003)

Reduced postdentary bones

Low position of Meckelian groove

Presence of three anteriorly directed lower incisors

Canines reduced to near the size of the last incisor

Presence of cusp g in lower postcanines

Greatly reduced mandibular symphysis

Expansion of braincase in parietal region

Table 6 Synaptomorphies of *Brasilodon* and mammals recognized in this study

	Unambiguous	Equivocal
18	(0)	Anteroventral corner of zygomatic arch lying at same level as postcanine line
3	(0)	Snout longer than temporal region
47	(1)	Basioccipital overlapping medial side of promontorium
57	(2)	Nerve $V_{2\&3}$ exiting via separate foramina, some enclosed by anterior lamina of prootic (petrosal)
50	(1)	Promontorium present
55	(1)	Presence of foramen and passage of prootic sinus on lateral trough
94	(1)	Four upper incisors present
100	(1)	Lower canine reduced
96	(0)	Incisors small
119	(1)	Delayed postcanine tooth replacement

fusion of the prootic and the opisthotic at early ontogenetic stage [49(1)], presence of foramen "X" (Rougier et al. 1992) in the posterior part of the lateral flange of the prootic [54(1)], lateral flange vascular canal present for route of the venous drainage exiting from the back of the cavum epiptericum [56(2)] (Crompton and Luo 1993), and completely divided postcanine roots [106, 107] (modified in advanced tritylodontid *Bienotheroides* (Cui and Sun 1987; Luo 1994)).

Most postcranial characters offer equal support to the TRMH and TYMH interpretations, rather than unequivocally favoring TYMH. Only two postcranial characters favor TYMH: absence of an ectepicondylar foramen in the humerus [132(1)] and presence of the longitudinal ridge dividing the lateral surface of iliac blade into dorsal and ventral portions [138(2)]. However, the result would change if the postcranial skeleton of *Adelobasileus* and *Sinoconodon* were shown to differ from that of *Morganucodon*. Only one known postcranial character, elongation of the scapula between the acromion and glenoid, supports TRMH more strongly than TYMH.

These character conflicts impede resolution of the interrelationships within Mammaliamorpha. One possibility for overcoming this problem is to recover more information from known taxa, whereas another is to discover new basal taxa within the clade. For example, *Prozostrodon* and *Therioherpeton* are undoubtedly important taxa in this context, but they are so fragmentary (more than 50% missing data), that more information on their morphology is essential if their potential for helping to elucidate phylogenetic relationships is to be realized.

As stated by Bonaparte et al. (2005), mammalian characters emerged in a mosaic fashion across different non-mammalian cynodont clades appearing alongside persistent primitive features. Diagnostic characters of Mammalia include the presence of craniomandibular joint comprising of dentary condyle and squamosal glenoid, the presence of a petrosal promontorium, the extensive development of a petrosal floor for the cavum epiptericum, the presence of a separate tympanic aperture for the prootic canal, the separation of the hypoglossal foramen from the jugular foramen, and the presence of four lower incisors (Luo et al. 2002). These authors also included the loss of the thickened rim of the fenestra vestibuli in their diagnosis, but this formulation of the character differs from that given in the work they cited (Lucas and Luo 1993). The character should be changed to "loss of the basisphenoid contribution to the thickened ring of the fenestra vestibuli". An incipient dentary/squamosal joint may exist in tritheledontids, although this was doubted by Gow (1981). The promontorium is the most distinctive feature of the mammalian basicranium (Rowe 1988; Wible 1991; Luo 1994; Luo et al. 2002), but this feature also occurs in *Adelobasileus* (Lucas and Luo 1993) and *Brasilodon* (Bonaparte et al. 2005). A distinctive cochlear canal is discovered in the tritylodontid *Yunnanodon* (Luo 2001). The space for the trigeminal ganglion is partially floored by the prootic in *Exaeretodon* (Bonaparte 1966), *Bienotherium* (Hopson 1964), and *Tritylodon* (Gow 1986). A separate tympanic aperture for the prootic canal also occurs in *Probainognathus* and *Massetognathus* (Wible and Hopson 1995). The hypoglossal foramen is completely separated from the jugular foramen in *Riograndia* (UFRGS-PV 0833T), *Brasilodon* (UFRGS-PV 0628T, Bonaparte et al. 2005: fig. 7), and *Tritylodon* (personal observation on Hopson's collection), but is positioned on the sidewall of the jugular foramen in *Oligokyphus* (Crompton

1964: fig. 2). Four lower incisors are also found in *Prozostrodon* (Bonaparte and Barberena 2001).

In conclusion, the monophyly of Eucynodontia is confirmed in this study, although the results differ slightly from those of previous analyses with respect to the composition of both Cynognathia and Probainognathia. Pruning highly incomplete taxa has little effect on the inferred pattern of relationships among the more complete taxa, although this pattern can change according to the inclusion or exclusion of basal fragmentary taxa. Taxon sampling of the current data matrix shows that taxon sampling was poor in some previous studies, implying that their results are not reliable.

Two major unresolved questions in cynodont phylogenetics are whether tritylodontids are more closely related to mammals or to traversodontids, and whether tritylodontids or tritheledontids are closer to mammals. Analyses of possible synapomorphies support a relatively close relationship between mammals and tritylodontids, to the exclusion of traversodontids, but do not clearly indicate whether or not tritheledontids are closer to mammals than are tritylodontids.

Appendix I: List of Morphological Characters

The following abbreviations are used to identify authors that previously used a particular character in data matrices: R, (Rowe 1988); W, (Wible 1991); WH, (Wible and Hopson 1993); LL, (Lucas and Luo 1993); L, (Luo 1994); LC, (Luo and Crompton 1994); M, (Martinez et al. 1996); H, (Hopson and Kitching 2001); LCS, (Luo et al. 2001); B, (Bonaparte et al. 2003); S, (Sidor and Smith 2004); MA, (Martinelli et al. 2005), BO, (Bonaparte et al. 2005); SH, (Sidor and Hancox 2006); A, (Abdala 2007). The number following the abbreviation indicates the position of the character in the author's matrix. Italics indicate that the definition of the character provided by the previous author(s) differs from that provided here. Asterisk indicates that the polarity of the character differs, or current states are part of the original states. A pound sign (#) preceding the character definition indicates that the character is ordered in some analyses.

Rostrum

1. #Premaxillary extranasal process: absent or with very little exposure (0); large but not contacting nasal (1); contacting nasal (2). [R2, *W36*, L82, M14, A1]
2. Septomaxilla facial process: long, extending far beyond posterior border of external naris (0); short, almost limited in external naris (1). [*S1, A2*]
3. #Snout in relation to temporal region: longer (0); subequal (1); shorter (2). [A11]
4. Position of paracanine fossa in relation to upper canine: anteromedial (0); medial or posteromedial (1); anterior (2); paracanine fossa absent (3). [A14*]
5. Premaxilla: does not form (0) or does form (1) posterior border of incisive foramen. [M19, H1, B21, BO27, MA24, *A13*]
6. Maxillary platform lateral to tooth row: absent (0); present (1). [M15, H77, BO15, *A23*]
7. Maxilla: excluded from (0) or participates in (1) border of subtemporal fenestra. [R15, W14, *L62*, M16, A21]

   Skull roof

8. Profile of skull roof (relationship of sagittal crest with part of skull roof just anterior to it): nearly flat (0); remarkably concave (1); convex (2). [*S7, A65*]
9. Parietal foramen: present (0); absent (1). [R8, W12, LL34, L64, M31, H7, B24, BO34, MA28, A7]
10. Interparietal (postparietal) in adult: separate bone (0); absent or fused with other bones (1). [R21, W15, *LL36*, M34]
11. #Lateral expansion of braincase in parietal region: absent (0); moderate (1); well developed (2). [*L67, M33*]

12. Sagittal crest: does not (0) or does (1) extend posteriorly to reach or closely approach the posterior-most part of the lambdoidal crest.

Orbital region

13. Prefrontal: present (0); absent (1). [R4, W1, M28, H3, B22, BO30, MA25, A4]

14. #Postorbital: present and forms postorbital bar (0); present but does not form postorbital bar (1); absent (2). [R7, W2, LL33, L55, M29, H5, B23, B40, BO31, BO32, MA 50, A6]

15. #Palatine: does not meet frontal (0); meets frontal but neither element contributes significantly to medial orbit wall (1); meets frontal and both elements contribute significantly to medial orbit wall (2). [R6, R31, W17, W37, L56, L60, M24, M30, H23, B29, BO46, MA38, A63]

16. Sphenopalatine foramen: absent (0); present (1). [L57, M26]

Zygomatic arch

17. Dorsoventral height of zygomatic arch as a proportion of skull length: moderately deep (10~18%) (0); very deep (>18%) (1); slender (<10%) (2). [R16, W40, L54, M39, H18, S5, BO40, MA33, A69]

18. Anteroventral corner of zygomatic arch: lies at same level as (0) or lies significantly higher than (1) postcanine line.

19. Infraorbital process: absent (0); suborbital angulation between maxilla and jugal (1); descending process of jugal (2). [M18, H21, H41, A25, B38, BO29, BO44, MA36, MA46, A70]

20. #Maximum dorsal extent of zygomatic arch: below middle of orbit (0); above middle of orbit but below upper border (1); above upper border of orbit (2). [H19]

21. Maximum posterior extent of jugal along zygomatic arch: near quadratojugal notch of squamosal (0); near squamosal glenoid (1); receding from glenoid (2). [L28]

22. Posteroventral process of jugal: low, forming less than half the height of the zygomatic arch (0); high, forming more than half the height of the zygomatic arch. [H20, BO43, A71]

23. Width of temporal fossa: greatest near middle (0); constant or nearly constant along its length (1); strongly increasing toward the posterior end (2). [H39, BO42, MA44, A74]

24. Squamosal groove for external auditory meatus: an incipient depression (0); deep (1). [M55, H22, B28, S18, BO45, MA37, A73]

25. Posterior extension of squamosal, dorsal to squamosal sulcus in zygomatic arch: incipient (0); well developed (1) [A72]

26. Notch separating lambdoidal crest from zygomatic arch: shallow (0); deep, V-shaped (1). [H43, S17, BO55, A75]

Palatal complex

27. Palatine: excluded from subtemporal border of orbit (0); participates in subtemporal border by displacing pterygoid posteriorly (1). [L58]

28. Vomer exposure in incisive foramen (at anterior ends of maxillae on palate): present (0); absent (1). [M21]

29. Vomer: with (0) or without (1) vertical septum extending posteriorly beyond level of secondary palate. [SH65]

30. Ectopterygoid: present, but does not contact maxilla (0); present and contacts maxilla (1); absent (2). [R32, H9, S15, A20]

31. Interpterygoid vacuity between pterygoid flanges: present (0); absent (1) in adults. [M27, H10, B25, BO35, MA29, A25]

32. Secondary palatal plate on maxilla: does not extend to midline (0); extends to midline (1). [H12, S11, A16]

33. Secondary palatal plate on palatine: does not extend to midline (0); extends to midline (1). [H13, S12, A16]

34. Osseous secondary palate: terminates well anterior to last upper postcanine tooth (0); terminates near or well posterior to last upper postcanine tooth (1). [R30, W16, L68, M23, LCS40, H14, B26, BO36, MA30, A18]

35. #Osseous secondary palate: terminates anterior to (0), at approximately the level of (1), or posterior to (2) anterior border of orbit. [H15, B27, BO38]

36. Anteroposterior extent of osseous secondary palate: 45% of skull length or less (0); more than 45% of skull length (1). [A17]

37. Contribution of palatine to osseous secondary palate: short (less than 1/3 anteroposterior length of osseous secondary palate) (0); long (greater than 1/3) (1) [M22, H40, B37, BO53, MA45, A19]

38. Middle of pterygoid: smooth (0); bears a boss (1); bears a distinct median crest (2). [LL12, L71, A26]

39. Nasopharyngeal roof posterior to transverse process of pterygoid: narrow, deep, forms a ventral keel (0); flat, minimum width greater than half width of transverse process of pterygoid (1).

40. Quadrate ramus of pterygoid: present (0); absent (1). [R38, W47, LC10, M40, H30, B34, BO52, S20, MA43, A30]

41. Quadrate articulation with quadrate ramus of epipterygoid: absent (0); present (1). [LC11, M53, A31]

Basicranium and lateral wall of braincase

42. Frontal-epipterygoid contact: present (0), absent (1). [R39, W48, L61, H35*, S24*, A64*]

43. Epipterygoid ascending process at level of trigeminal foramen: greatly expanded (0); moderately expanded (1). [H32*, B35*, A67*]

44. Anterior part of basisphenoid: narrow (0); wide, and width greater than half width of transverse process of pterygoid (1). [L69, LCS44]

45. Parasphenoid ala (basisphenoid wing): at same level as basicranium (0); ventrally expanded below basicranium (1). [H17, BO39, MA32, A29]

46. #Parasphenoid ala: long, bordering fenestra vestibuli (0); slightly shorter and excluded from fenestra vestibuli, but overlapping entire prootic pars cochlearis (a part of the petrosal) (1); much shorter and overlapping prootic pars cochlearis (2); basisphenoid does not overlap prootic pars cochlearis (3). [R40, W49, L74, M41, M49, LCS37, A28]

47. #Extent of basioccipital overlap on pars cochlearis: covers entire pars cochlearis (0); covers medial side of promontorium (1); no overlapping (2). [LCS38]

48. Internal carotid foramina in basisphenoid: present (0); absent (1). [R42, W50, WH23, LL14, L72, M45, H26, B31, BO48, MA40, A27]

49. Prootic and opisthotic: separate (0); fused at early ontogenetic stage to form petrosal (=periotic) (1). [R51, W5, WH29, L34, BO56, A37]

50. Promontorium: absent (0); present (1). [R52, W6, LL1, L35, LCS9, BO57, A35]

51. Internal auditory meatus: open (0); walled (1). [R53, W7, WH12, L39, M47, H36, B36, A38]

52. #Space for trigeminal ganglion (semilunar ganglion): open ventrally (0); partly floored by prootic (1); completely floored by prootic (2). [W54, A34]

53. Lateral trough floor anterior to tympanic aperture of prootic canal and/or primary facial foramen: absent (0); present (1). [R49, LL6, L43, M44, LCS 15*]

54. Vascular foramen in posterior part of lateral flange (Foramen "X" of Rougier et al. 1992: 205): absent (0); present (1). [LL30, L53, M43, LCS29]

55. Foramen and passage of prootic sinus in lateral trough: absent (0); present (1). [R50, W28, LL3, L45, MA49, BO58, A36]

56. Route of venous drainage from back of cavum epiptericum: only vascular groove on lateral flange (0); absent (1); vascular canal on lateral flange (foramina on lateral surface) (2). [W53, WH22, H27]

57. #Maxillary and mandibular branches (V_{2+3}) of trigeminal nerve exit: via single foramen between prootic and epipterygoid (0); via two foramina between prootic and epipterygoid (1); via separate foramina, some enclosed by anterior lamina of prootic (petrosal) (2). [L50, M48, H28, B33 BO51, S27, MA42, A66]

58. Pterygoparoccipital foramen: squamosal does not contribute to enclosure of foramen (0); squamosal contributes to enclosure of foramen (1); open as a notch (2). [LL23, L51]

59. Lateral flange of prootic: lacks vertical component (0); includes vertical component, so that flange is L-shaped and forms vertical wall adjacent to pterygoparoccipital foramen. [L52, LCS25]

60. Anterior part of paroccipital process: lateral aspect covered by squamosal (0); lateral aspect exposed due to dorsal withdrawal of squamosal (1). [L47, LCS22]

61. Hyoid (stapedial) muscle fossa on paroccipital process: absent (0); present (1). [R55, W56, WH35, LL7, L40, M59, LCS32, MA48, BO61, A39]

62. Paroccipital process: undifferentiated (0); differentiated into a posterior process and a bulbous anterior process (1); differentiated into mastoid and quadrate processes (2). [R56, W18, L46, L47, M50, LCS21, LCS30, BO66, A44*]

63. Fenestra rotunda and jugular foramen: confluent (0); completely and widely separated (1). [R60, W29, LL10, L42, M46, HK42, LCS33, B39, BO60, A41]

64. Paroccipital process: does not contact quadrate (0); contacts quadrate (1). [R19, W41, M52, H29, A33]

Occipital region

65. Paroccipital process in base of posttemporal fossa: absent (0); present (1). [H24, A45]

66. Tabular: present (0); absent (1). [R22, LL19, L80, LCS 47]

67. Relationship of hypoglossal foramen (condylar foramen) with jugular foramen: confluent or sharing a depression (0); at least one foramen completely separated from jugular foramen (1). [LL11*, L75*, M51*, LCS39*, BO65]

68. Shape of occipital condyles (in lateral view): bulbous (0); ovoid to cylindrical (1). [LL15, L77, LCS51]

Craniomandibular joint

69. Rotation of dorsal plate relative to trochlear axis of quadrate: small (less than 10 degrees) (0); about 45 degrees (1); around 90 degrees (2); parallel to trochlear axis (3). [L30, LC1]

70. Contact facet on posterior side of dorsal plate of quadrate: flat or convex (0); concave (1). [L29, LC2, M56]

71. Trochlear condyles of quadrate: lateral condyle larger than medial condyle (0); medial condyle at least as large as lateral condyle (1). [LC3]

72. Shape of trochlea of quadrate: cylindrical (0); trough-shaped (1). [LC4]

73. #Lateral margin of dorsal plate of quadrate: straight (0); flaring posteriorly (1); flaring and rotated posteromedially (2). [LC5]

74. #Medial margin of dorsal plate of quadrate: straight (0); flaring anteriorly (1); flaring and rotated anterolaterally (2). [LC6]

75. Dorsal margin of dorsal plate of quadrate: with a pointed dorsal process ("dorsal angle") (0); rounded (1) [L31, LC7]

76. #Lateral notch and neck of quadrate (separating lateral margin of contact facet from trochlea): lateral notch absent or poorly developed (0); lateral notch developed, separating lateral margin of contact facet from lateral end of trochlea (1); lateral notch broader, separation of lateral margin of contact facet from trochlea wider, lateral margin shifted medially (2); neck developed, displacing contact facet away from trochlea (3). [L32, LC8]

77. Articulation of quadrate with squamosal: via an anteriorly open and concave recess in the squamosal (0); anteriorly open squamosal recess is absent (1); quadrate having little or no contact with the squamosal (2). [WH7, LC12, M54, H31, A61]

78. Articulation of quadrate with stapes: via broad recess on medial margin and medial end of trochlea (0); stapedial contact restricted to medial end of trochlea (1); via projection from medial margin of dorsal plate (2); via medial vertical ridge on neck of quadrate (3); via projection from neck of quadrate (4). [R20, W42, L33, LC14]

79. Craniomandibular articulation: quadrate/articular (0); primarily quadrate/articular, secondarily surangular/squamosal (1); incipient dentary/squamosal (2); primarily dentary/squamosal (3). [R66, R67, W9, W60, L23, L24, M60, H25, LCS 70, B30, S19, BO26, MA39, A59]

80. Craniomandibular articulation: around dorsoventral level of postcanine line (0), much lower than postcanine line (1); much higher than postcanine line (2). [L25, A60].

81. Squamosal articular surface for mandible: absent (0); formed by small and medially or anteromedially facing facet (1); wide glenoid cavity directed approximately ventrally (2). [L26, B19, BO37, MA22, A58]

Mandible

82. Dentary symphysis: unfused (0); fused (1). [R68, W10, L19, LCS56, H44, B17, S34, BO21, MA21, A62]

83. #Lateral crest of dentary: absent (0); incipient (1); moderately developed (2); strongly projecting (3). [A48]

84. Angle of dentary: close to anteroposterior position of postorbital bar (0); close to jaw joint (1). [A55]

85. Anteroposterior position of dorsal contact between dentary–surangular, relative to postorbital bar and jaw joint: around midway between these landmarks (0); closer to jaw joint (1). [H48, A56]

86. Inner side of coronoid process (including coronoid bone): relatively thin (0); mediolaterally thick (1). [M66, H50, A52]

87. Splenial: large and deep, reaches ventral border of dentary (0); thin splint covering dentary groove (1). [M64]

88. #Postdentary bones: large, including tall surangular (0); angular, surangular, and prearticular medium in height and lying in dentary groove (1); single gracile rod in postdentary trough (2). [R74*, W59*, M65*, H49*]

89. Posterior extent of reflected lamina of angular: greater than 1/2 distance from angle of dentary to jaw joint (0); less than l/2 this distance (1). [H51]

90. #Reflected lamina of angular in lateral view: spoon-shaped plate bearing slight depressions (0); hook-like lamina (1); thin process (2) [M62, H52, S44, A57*]

91. Mandibular movement during occlusion inferred from wear facets: orthal movement during power stroke (0); posteriorly directed power stroke (1); moderate rotation along longitudinal axis during power stroke (2). [R79, W62, L2, LCS74*, B2, BO2]

Dentition

92. Postcanine occlusion: no consistent pattern of contact between upper and lower tooth rows (0); bilateral, interdigitating occlusion between multiple cusps (1); precise unilateral occlusion (2) [R84, R86, W33, L1, L14, M8, LCS 73, LCS 81, B1, BO1, MA1, A88]

93. Wear facets on postcanines: absent (0); simple longitudinal facet present on crown (1); main cusp bears two distinct facets (2); multiple cusps each bear one or two transverse and crescentic facets (3). [L17, B16, MA19, BO20]

94. Number of upper incisors: five or more (0); four (1); three or less (2). [R81, W63, L5, M1, H53, B3, S45, BO3, MA3, A76]

95. Number of lower incisors: four or more (0); three (1); two or less (2). [L5, M2, H54, B4, S46, BO4, MA4, A78]

96. Incisors: all small (0); some or all large (1). [H56, B5, B6, BO5, MA5, MA6, MA7, A79]

97. Incisor cutting margins: smoothly ridged (0); serrated (1); denticulated (2). [H55, A80]

98. Distinct diastema between upper incisor and canine: present (0); absent (1). [A82]

99. Upper canine: large (0); small (height <10% of skull length) (1); absent (2). [L6, H57, A84]

100. Lower canine: large (0); small (1); absent (2). [L6, H58, A85]

101. Canine serrations: absent (0); present (1). [H59*, A86*]

102. Upper postcanine: sectorial, lacking cingulum or with incipient lingual cingulum (0); sectorial, with well-developed lingual cingulum (1); bucco-lingually expanded (2). [L13, M5, M9, H60, H62, A7, S51, S55, B10, BO8, A90]

103. #Single-cusped tooth as anteriormost postcanine: present in juveniles and adults (0); present only in juveniles (1); absent (2).

104. #Gomphodont tooth as posteriormost postcanine: absent (0); absent in juveniles but present in adults (1); present in both juveniles and adults (2). [H80]

105. Main cusps of posterior postcanine teeth: not strongly curved (0); strongly curved (1). [S52, A91]

106. Upper postcanine roots: single (0); divided into two longitudinally aligned roots (1); multiple roots (more than two) (2). [R88, W65, W66, L9, M6, LCS77, B8, BO6, MA9, A96]

107. Lower postcanine roots: single (0); divided (1). [R88, W65, L9, M7, B8, BO6, MA9, A95]

108. Buccal (external) cingulum on sectorial upper post-canines: absent (0); present (1). [R85, H61, B9, BO7, MA10, A92]

109. Transverse crest in upper postcanines: absent (0); present with two cusps (1); present with three or more cusps (2) [H63, A93]

110. Position of transverse row of upper postcanines: midcrown (almost to posterior margin) (0); on anterior half of crown (1); at posterior margin of crown (no posterior cingulum) (2). [H64*]

111. Central cusp of transverse row of upper postcanines: absent (0); midway between buccal and lingual cusps (1); closer to lingual cusp (2). [H65]

112. Alignment of main cusps of upper postcanines: single longitudinal row (0); multiple cusps in multiple rows (1). [L13, LCS78]

113. Contacts between adjacent lower postcanines: simple, with no interlocking (0); distal cuspule of anterior molar fits into embayment between cusps of succeeding molar (1). [L11, B14, BO18]

114. Number of cusps in transverse row of lower postcanines: two (0); three or more (1). [H73]

115. Lingual cingulum on lower postcanine: present (0); vestigial or absent (1) [L12, LCS80, B11, B12, BO9, BO10, S56, A94]

116. Lower posterior basin: absent (0); present (1). [H75]

117. Axis of posterior part of maxillary tooth row: directed lateral to subtemporal fossa (0); directed toward center of fossa (1); directed toward medial rim of fossa and diverged curved (2); directed toward medial rim of fossa and straight (3). [R80, M12, H78, B13, MA17, MA20, BO14, BO16, BO17, A87]

118. Posterior end of upper tooth row: below orbit and anterior to subtemporal fenestra (0); anterior to orbit (1); posterior to anterior border of subtemporal fenestra (2). [H79, A76]

119. Postcanine replacement pattern: alternating (0); delayed (1); sequential addition of postcanines, no replacement (2). [L7, H81, LCS89, B7]

Postcranial skeleton

120. Vertebral centra: amphicoelous (0); platycoelous (1). [R108, H101, B51, BO78, MO61]

121. Axial centrum: cylindrical (0); depressed (1). [R98]

122. Dens: absent or vestigial (0); strongly developed (1) [R99]

123. Posterior thoracic vertebrae (or mid-dorsal vertebrae): neural spines nearly vertical or slightly inclined (0) or strongly inclined (1). [R102]

124. Anapophysis: absent (0); present (1).

125. Expanded costal plates on dorsal ribs: absent (0); present (1). [H82]

126. The ridge on lumbar costal plates overlapping preceding rib: absent (0); present (1). [H83]

127. #Acromion process: absent (0); weakly to moderately developed (1); strongly developed and close to level of glenoid (2). [R115*, H85*]

128. Scapular constriction below acromion: absent (0); present (1). [H86]

129. Scapular elongation between acromion and glenoid: absent (0); present (1). [H87, B41, BO68, MO51]

130. Procoracoid contribution to glenoid fossa: present (0); barely present or absent (1). [R116, H88, B42, BO 71, MO52]

131. Procoracoid contact with scapula: longer than coracoid contact (0); equal to or shorter than coracoid contact (1). [H89, B43, BO72, MO53]

132. Ectepicondylar foramen in humerus: present (0); absent (1). [R124, H90, B44, BO73, MO54]

133. Olecranon process of ulna: unossified or poorly ossified (0); well ossified (1). [*R128, H91, B45, MO55*]

134. Number of phalanges present in manual digit III: four (0); three (1). [H92]

135. Number of phalanges present in manual digit IV: four (0); three (1). [H93]

136. Dorsal profile of ilium in lateral view: strongly convex (0); straight to concave (1). [R130, H96, B48, BO75]

137. Length of anterior process of ilium anterior to acetabulum: less than 1.5 times diameter of acetabulum (0); greater than 1.5 times diameter of acetabulum (1). [H94*, B46*, BO74, MO56*]

138. Lateral surface of iliac blade: concave or nearly flat (0); convex (1); divided by longitudinal ridge into dorsal and ventral portions (1). [*R131*]

139. Posterior iliac spine: robust and extends beyond acetabulum (0); small nub that lies entirely anterior to acetabulum (1). [R132, *R133*]

140. Cotyloid (acetabular) notch: lies between ischial and iliac parts of acetabulum, but mainly on ilium (0); lies entirely on ischium, between acetabular facet and pubic process (1). [*R134*]

141. Diameter of obturator foramen: less than or equal to that of acetabulum (0): greater than that of acetabulum (1). [*R139*]

142. Head of femur: rounded and predominantly in plane of shaft (0); subspherical and inflected dorsally (1). [R141]

143. Greater trochanter of femur: continuous with femoral head (0); separated from femoral head by distinct notch (1). [R143, H98, B49, BO76, MO59]

144. Lesser trochanter: on ventromedial surface of femoral shaft (0); on medial surface of femoral shaft (1). [R144*, H100, B50, BO77, MO60]

145. Lesser trochanter: far distally from femoral head (0); near level of femoral head (1). [BO80, MO63]

Appendix II. Data Matrix

Distribution of the character-states for the characters listed in Appendix I among 31 taxa considered in this analysis. A=0&1, B=1&2, a=0/1, b=1/2, ?=unknown, dash=inapplicable

```
Character blocks (tens/ones):
            1          1111111112 2222222223 3333333334 4444444445 5555555556 6666666667 7777777778 8888888889 9999999990 1          1111111111 1111111111 1111111111 1111111111 1111
            1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 12345

Procynosuchus delaharpeae     0000000100 0000000000 0000000000 0000000000 0000000000 0000000000 0001A00000 0000000000 0000000100 0000000100 000000000- -00-000000 0000000-0  0000000000 0000000000 00000
Galesaurus planiceps          0100000000 0000100001 0000100000 1000000000 0000000000 0000000000 0000000000 0010000000 0001100100 000110-100 000010000- -00-100000 0001100??? 0001100?0  ?00?20??00 00000
Thrinaxodon liorhinus         01A0000000 0000000000 0000000000 1110000000 0000000000 0000000000 0000000000 0010010100 0001100011 0001000000 010000000- -00-100000 0001100-0  0001100-0  0000000000 00000
Platycraniellus elegans       0110000000 0000000001 0000000001 0100000000 ?000000000 ?000000000 0000000000 1017?10100 0001?0?100 0001?0?0?? 000000000- -0?-0?000? ???????0?? 0001100?0  0000000000 ?0000
Cynognathus crateronotus      0000000000 0000001021 0021100000 1110000101 1100010100 ?000000000 0000100000 1110010110 1120101000 100010000- -00-100100 0000110000 0000111000 0001100100 ?????????  ?????
Diademodon tetragonus         A000000000 0000001022 0121110001 1110000001 1100010100 00000A0000 0000000000 1110010110 1120101000 1200100010 1200100010 0100?00010 0001111000 0001100000 0001110000 00000
Trirachodon berryi            1100100A0  0000001121 0111110100 1110100201 1100010100 0000021000 0000000011 0110020110 1110101112 1211100020 1211100020 1101010?0? ?701111000 000?777000 000?777000 ?????
Sinognathus gracilis          1020?10010 0000??1101 001111071? 1?1010?001 1000010100 ?????????  007000?011 011102010 113200000  0270700720 0270700720 1100?20201? ???717???? ?????????  ?????????  ?????
Langbergia modisei            0010000000 0000000121 0111110100 1110100001 1000010170 ?200010170 0000000001? 011102110 113101000  1200100020 1200100020 1101001012 ???717???? ?????????  0007710000 00000
Pascualgnathus polanskii      1020?10010 0000001122 0121110111? 1110100001 ?200010?00 ?270272000 007?070?0? ?120100110 132100000  02b000-11  02b000-11  0100-12010 ??71101?70 ??71101?70 0007?10000 00000
Luangwa drysdalli             ?700?1000? 0000010121 001111????  1110?00001 ?270010100 0000??2?00 007?70??0? ?120100110 131101000  12bb000-20 12bb000-20 2100-12010 ?771101100 ?771101100 0077?11000 00000
Massetognathus pascuali       0111110010 0000001101 0111110112 1110200001 0000121100 0000121100 0000000011 0110020110 1131102111 0210000-22 0210000-22 0100-12010 0000101101 0000101101 0007?11000 00000
Exaeretodon argentinus        0011111010 0000111121 0121110112 1101A0001  0100021100 0100021100 0000000071 017??20110 1312110101 02b0000-12 02b0000-12 0100-12210 0000000101 0000000101 0017111000 00000
Scalenodon angustifrons       ?710?7000  0000??1101 0121117???? ?1101?0?71 ?000021100 ?000021100 0000?0007? 0?77?07?a0 1131101000 12bb000-20 12bb000-20 2100-12010 ?????????  ?????????  ?????????  ?????
"Scalenodon" hirschoni        ???0010???  ??0001?1?? ???1110112 11017070?  0?700?7771 ?????7?170 007?07?771 ?17?07?a?  1132210010 02b0000-22 02b0000-22 2100-12010 ?????????  ?????????  ?????????  ?????
Chiniquodon theotonicus       1110101010 0000101011 000000101B 111211001  0000010000 0000010000 0000000071 ?017?71110 1120101112 000010000- 000010000- -00-100000 ?700001101 ?700001101 0001110000 ?0000
Lumkuia fuzzi                 ?710001010 0000?70000 000000?212 010100101  0100001010 ?000001000 0000000000 010100012  1120100012 000010000- 000010000- -00-100007 ??7?0012?? ??7?0012?? ??????????  ?????
Ectenion lunensis            0010?00210  0000200000 00000?1a   110000201  1100010100 ?100010100 0000000011 0011021110 0011100011 1a0010000- 1a0010000- -00-?00000 ?221?71107 ?221?71107 ?0?????0?? ?????
Probainognathus jenseni      0110100210  0000100101 1000010112 111101001  1100100000 0000110000 0000000011 0011021110 2100101112 010000000- 010000000- -00-001100 007000110? 007000110? ??0?011000 ?0000
Prozostrodon brasiliensis    11?0102??   ?70121?1?? ?????????11? ?111121???  ?????????  ?????????  ?????????  ?????????  0000000000 110000000- 110000000- -00-001000 ?77000???? ?77000???? ?0??11111  10000
Therioherpeton cargnini      ?????0?21?   1122212100 1122212100 ?111??????  ?????????  ?????????  ?????????  ?????????  000???????  ?0?0?0000- ?0?0?0000- -00-?00000 ?71?00???? ?71?00???? ?????11111 ?????
Riograndia guaibaensis       0113101211   1122211?1? 011121011  011121011  0000010200 ?000010200 0010000121 102?137???  0012110011 00b000000- 00b000000- -00-101007 ??1?00???? ??1?00????  ?????11111 10011
Pachygenelus monus           2013101211   1122212100 1000000112 011121011  1000010200 1000010200 0010000121 1022131320 1022131320 001000010- 001000010- -00-002001 ?70001111  ?70001111  1017?11111 11111
Brasilodon quadrangularis    a00??01211   1122212000 1000?00?12 011121?211 1000010200 ?0?7122207 0011101121 1022131320 1022131320 001000010- 001000010- -01-001007 ??70001117 ??70001117 ?11??????? ?????
Tritylodon longaevus         102-111111   0112211102 0011110112 110211211  1101021211 1101021211 1101101031 1022031202 1132210-22 -222-21-2- -222-21-2- 1100-03221 ?????22101 ?????22101 11??11211  ?1111
Oligokyphus major            b??-1111?1    0112??1102 0101107172 ?1??21????  1101027211 1101027211 1101100031 0022031202 1132110-22 -222-21-2- -222-21-2- 1100-03221 1110022101 1110022101 111?911211 11111
Bienotherium yunnanense      102-111111    0112211172 01?1110112 110211211  0000110110 1107027011 117110?031 ?222131702 1132110-22 -222-21-2- -222-21-2- 1100-03221 ?????72107 ?????72107 ?11??????1 11111
Kayentatherium wellesi       102-1111?    0112211102 0111111112 010211211  0000110110 1101021211 117110?031 1022131202 1132110-22 -222-21-2- -222-21-2- 1100-03227 1110002101 1110002101 171111121? ?1111
Adelobasileus cromptoni      ?????07??    212?2?????  ?????????  0?????211  000102101  ?211122100 00101110?? ?????????  ?????0????  ?????0???? ?????0???? ?0?71?????  ?????????  ?????????  ?????????  ?????
Sinoconodon rigneyi          0002?01011    2112212000 1000?01?12 111121211  0011031011 ?211122210 1110101?0? ?????07?30 2001000001 001001110- 001001110- -00-101017 001001110  001001110  ?????????  11111
Morganucodon oehleri         0?02?01011    2112212000 2?00001111 111121211  0011032011 1211122201 1211111121 1022132430 2210000001 011001110- 011001110- -01-001011 1111001111 1111001111 11??11211  11111
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