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Evolutionary trends and the origin of the mammalian lower jaw

Christian A. Sidor

Abstract.—The single bony element forming the lower jaw of living mammals, the dentary, has been interpreted as representing the culmination of a long and gradual evolutionary trend. Numerous fossil nonmammalian synapsids (''mammal-like reptiles'') show varying degrees of enlargement of the dentary and concomitant reduction in the postdentary bones. To quantitatively reexamine patterns of morphological change in the evolution of the mammalian lower jaw, measurement and discrete character data were collected from 322 fossil synapsid mandibles spanning Late Carboniferous through Jurassic time. Measurements confirm that the relative contribution of the dentary increased in theriodont (advanced therapsid) evolution with regard to both stratigraphic and phylogenetic position. However, dentary enlargement and postdentary reduction failed to typify all therapsid subclades. Qualitative characters of the mandible were used to quantify morphological similarity with regard to the early mammal *Morganucodon*. Analyses contrasting stratigraphic and phylogenetic position with mammalian similarity indicate that mandibular evolution was primarily conservative, with only anomodont therapsids evolving substantial morphological novelty. Scaling analyses comparing the area of the dentary and postdentary regions to jaw length uniformly show isometry or slight positive allometry, although cynodont therapsids have a smaller postdentary region than any other therapsid subgroup. These results suggest that body size decreases cannot fully explain the reduction of the postdentary bones. Finally, step size bias was tested as a mechanism for explaining long-term trends. Qualitative data reveal no significant difference in the magnitude of character changes occurring in mammalian and nonmammalian directions.

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Introduction

Mammals are unique among extant vertebrates in possessing a lower jaw (mandible) formed by a single bony element, the dentary. By contrast, the lower jaws of other vertebrates retain a host of postdentary bones (e.g., four to six in most lizards, five in crocodiles and many birds, and typically even greater numbers in fishes). Recorded from rocks dating from over 300 Ma, the mandibles of the earliest nonmammalian synapsids possessed up to seven postdentary bones (Fig. 1), whereas stratigraphically more recent taxa show various stages in the reduction and eventual loss of these bones (Fig. 2) (Romer and Price 1940; Crompton 1963; Allin 1975). The evolutionary fate of the mammalian postdentary bones has been well established; Reichert (1837) used embryological evidence to homologize the incus and malleus of the mammalian middle ear with the quadrate and articular, respectively, of nonmammalian vertebrates. The transformation of several postdentary jaw bones into sound-conducting middle ear bones within synapsids is one of the best-documented examples of a major evolutionary transformation in the vertebrate fossil record (Hopson 1966; Allin 1975; Allin and Hopson 1992; Luo and Crompton 1994). Indeed, synapsid mandibular evolution has come to be regarded as recording a gradual trend whereby enlargement of the dentary occurs at the expense of the postdentary bones (Crompton and Jenkins 1973; Kemp 1982; Hopson 1987). In this study, I use measurement and discrete character data to: (1) quantify the morphological changes that occurred in the evolution of the lower jaw between pelycosaur-grade synapsids and their mammalian descendants, and (2) address several previously proposed hypotheses concerning the nature and magnitude of morphological trends during the first ~100 Myr of synapsid history.

Background to Study Taxa.—Theories of synapsid evolution have traditionally been couched in terms of several adaptive radiations or grades of organization representing successive steps in the mammalian direction. However, a recent proliferation of numerical

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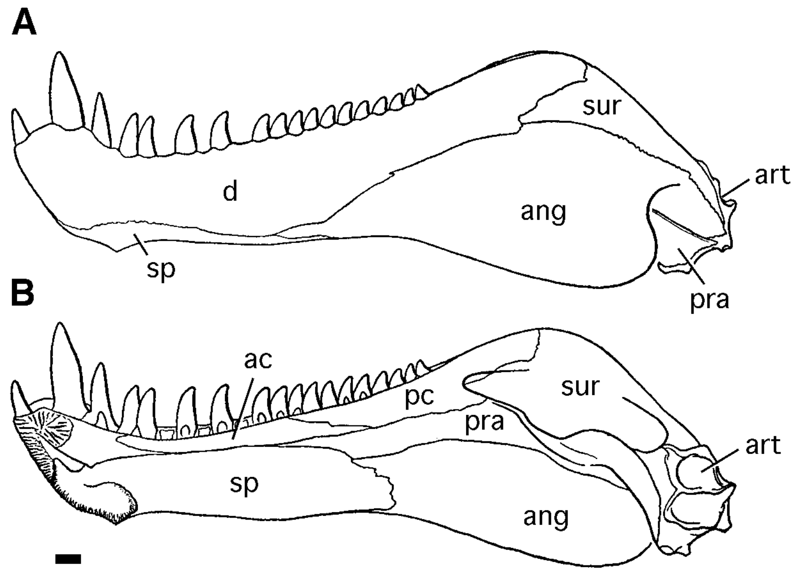

FIGURE 1. The lower jaw of the Late Carboniferous and Early Permian pelycosaur-grade synapsid *Dimetrodon* in lateral (A) and medial (B) views. Scale bar, 1 cm. Anatomical abbreviations: ac = anterior coronoid, ang = angular, art = articular, d = dentary, pc = posterior coronoid, pra = prearticular, sp = splenial, sur = surangular. Illustration modified from Romer and Price 1940.

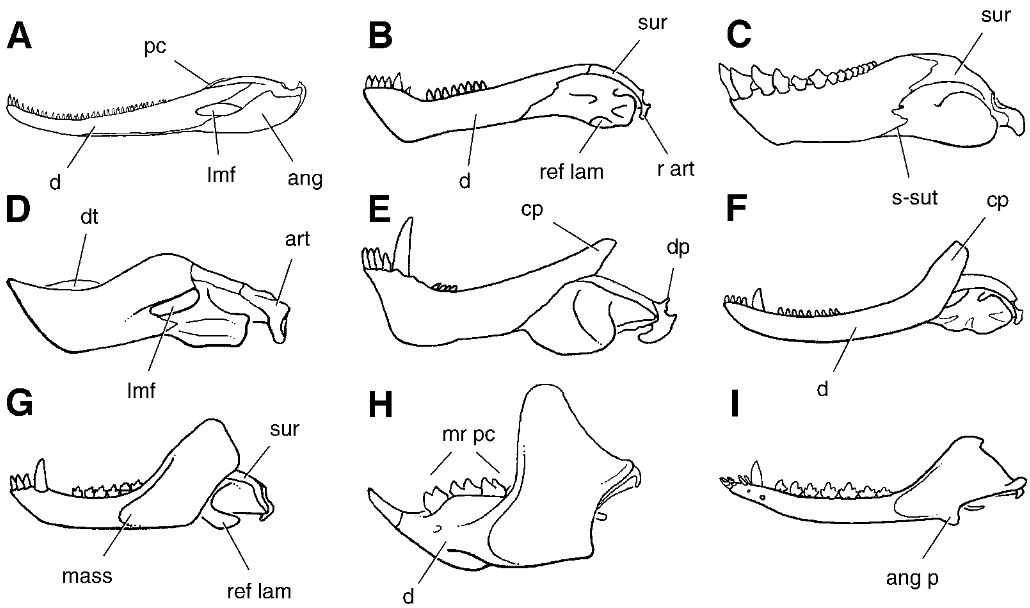

FIGURE 2. Representative synapsid mandibles in lateral view (not to same scale). A, The Late Pennsylvanian and Early Permian ''pelycosaur'' *Ophiacodon*. B, The Late Permian biarmosuchian *Biarmosuchus*. C, The Late Permian tapinocephalid dinocephalian *Ulemosaurus*. D, The Late Permian advanced dicynodont *Diictodon*. E, The Late Permian gorgonopsid *Arctognathus*. F, The Late Permian therocephalian *Ictidosuchoides*. G, The Early Triassic primitive cynodont *Thrinaxodon*. H, The late Early Jurassic or early Middle Jurassic tritylodontid *Bocatherium*. I, The Early Jurassic primitive mammal *Morganucodon*. Anatomical abbreviations: ang = angular, ang p = angular process, art = articular, cp = freestanding coronoid process, d = dentary, dp, dorsal process of the articular; dt = dentary tables, lmf = lateral mandibular fenestra, mass = masseteric fossa, mr pc = multirooted postcanines, pc = posterior coronoid, r art = retroarticular process, ref lam = reflected lamina, s-sut = s-shaped dentary/angular suture, sur = surangular. Illustration sources: Romer and Price 1940 (A), Efremov 1940 (C), and Hopson 1994 (remaining figure parts).

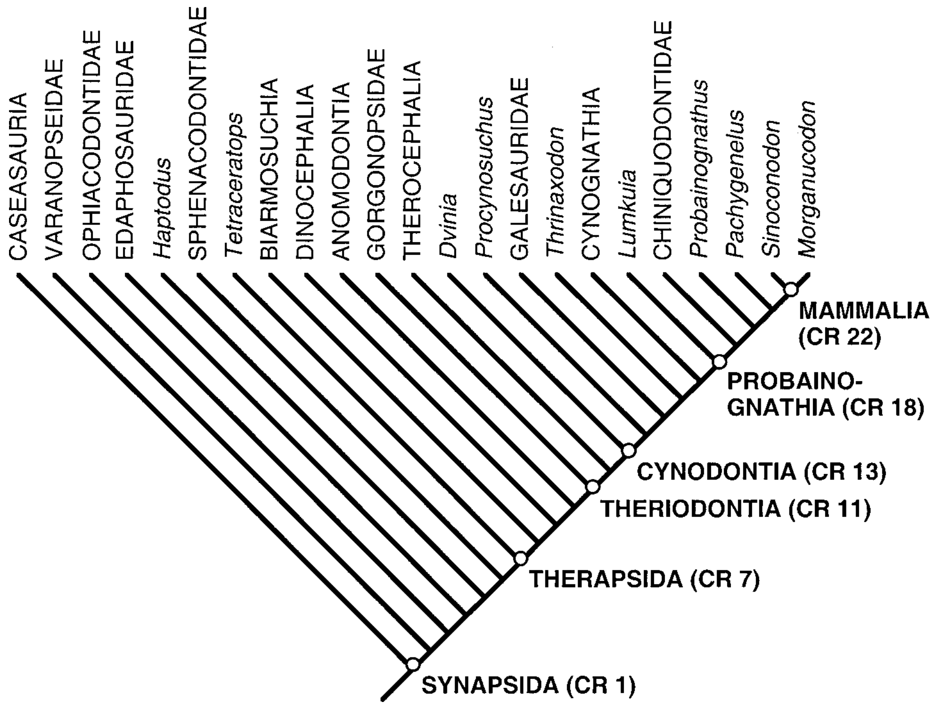

FIGURE 3. Cladogram of higher-level synapsid relationships used herein. This topology is based primarily on those proposed by Reisz (1986) and Sidor and Hopson (1998). See Appendix 1 for cladogram details and Figure 4 for lower-level relationships. This cladogram includes 22 nodes along its spine that define the 22 clade ranks (CR) used in later analyses. For example, taxa included within the Varanopseidae and Galesauridae have CRs of 2 and 15, respectively.

cladistic analyses has contributed greatly to our understanding of synapsid phylogeny (Fig. 3), and regions of broad consensus are gradually emerging (Rubidge and Sidor 2001).

The earliest occurring and phylogenetically most primitive synapsids are the "pelycosaurs" of traditional terminology. These taxa form a paraphyletic series and are primarily known from Upper Carboniferous to Lower Permian rocks in Europe and North America (Reisz 1986) although several taxa persisted into the Middle Permian in Russia and South Africa (Reisz et al. 1998; Modesto et al. 2001). Sphenacodontids, such as the familiar sail-back *Dimetrodon*, are among the most advanced pelycosaur subgroups (Reisz et al. 1992). All more derived synapsids form the clade Therapsida.

All of the major therapsid clades first appear in the fossil record during the Middle and Late Permian (e.g., Biarmosuchia, Dinocephalia, Anomodontia, Gorgonopsia, Therocephalia, and Cynodontia) and—except for dicynodont anomodonts, some advanced therocephalians, and cynodonts—went extinct in this time interval as well. Therapsids taxonomically and ecologically dominated the end-Paleozoic Pangaean landscape and established the first herbivore-based food chains among vertebrates in the terrestrial realm (Olson 1962; King et al. 1989; Reisz and Sues 2000). The presence of several derived features recently led Laurin and Reisz (1990, 1996) to suggest that *Tetraceratops insignis*, from the Early Permian of Texas, is phylogenetically the most primitive therapsid (but see Conrad and Sidor 2001).

Cynodonts are first recorded from Upper Permian strata in southern Africa and Russia and represent the therapsid subclade that includes mammals. Numerous derived features associated with obtaining food and its mastication characterize Cynodontia, including the presence of a fossa for the neomorphic masseter muscle on the lateral surface of the dentary, postcanine teeth with accessory cusps and lingual cingula, and a complete sagittal crest for the origin of temporalis musculature. According to the phylogenetic hypothesis proposed by Hopson (1991b, 1994; Hopson and Kitching 2001), a key dichotomy in cynodont phylogeny occurred with the Triassic divergence of the cynognathian and probainognathian lineages. Terminal cynognathians (tritylodontids) range stratigraphically upwards into the Lower Cretaceous (Tatarinov and Matchenko 1999), whereas terminal probainognathians (mammals) first appear in Upper Triassic or Lower Jurassic rocks and survive until the Recent (Lucas and Luo 1993; Luo 1994).

Vertebrate paleontologists have traditionally defined mammals as possessing a well-formed dentary-squamosal jaw joint (Simpson 1960). Taxa included under this (apomorphy-based) definition include *Morganucodon* and *Kuehneotherium*, although these and other early Mesozoic forms (e.g., *Sinoconodon*) probably possessed a functional quadrate-articular jaw joint as well (Hopson 1991b; Luo and Crompton 1994). More recently, Rowe (1988) and Rowe and Gauthier (1992) have advocated using a crown-group definition for Mammalia, and they have termed the larger clade—including traditional mammals that lie phylogenetically outside the clade bounded by extant forms—Mammaliaformes. My use of Mammalia and of the terms ''mammal'' and ''mammalian'' correspond to traditional usage (see also Luo et al. 2002).

Data Collection

Taxon Sampling.—Fossil synapsids included in this study range from the earliest-appearing (Late Carboniferous) pelycosaur-grade taxa through some of the most primitive mammals, such as the Early Jurassic genera *Morganucodon* and *Sinoconodon*. In total, 19 ''pelycosaurs,'' six basal therapsids, 13 dinocephalians (including five anteosaurians and eight tapinocephalians), 25 anomodonts, ten gorgonopsians, ten therocephalians, and 25 cynodonts were included. The cynodonts include six non-eucynodonts, 11 cynognathians (including six tritylodontids), and eight probainognathians (including two Mesozoic mammals). All taxa were at the genus level or, in several instances, below.

The stratigraphic range of each taxon was collected from original museum locality information or the literature (e.g., Kitching 1977; Rubidge 1995; Ivachnenko et al. 1997) and then binned into one or more of 18 age ranks (AR) for the purpose of analysis. ARs are non-overlapping stratigraphic bins in an ordered sequence (Gauthier et al. 1988). Importantly, ARs are not necessarily of equal duration; some ARs are equivalent to a single geological formation, whereas others encompass several formations or groups. The goal of this type of binning is a single, resolved sequence of the synapsid fossil record despite its derivation from a variety of widely separated continental deposits (see also Sidor 2001). One major drawback to the AR approach is that gaps in the synapsid record are effectively ignored; time periods lacking synapsid fossils are not represented in the analysis. For example, a major hiatus in the synapsid record occurs between the youngest continental deposits in North America (e.g., the San Angelo and Flowerpot Formations) and the oldest in Russia and South Africa (e.g., Mezen and the *Eodicynodon* Assemblage Zone, respectively) (Lucas and Heckert 2001). This approximately 2-Myr hiatus encompasses much of Roadian time, but is not evident between ARs 6 and 7. Appendix 4 reports the geological formations and vertebrate biozones making up each AR.

From a recent compilation of synapsid cladistic analyses, I also collected phylogenetic inference data, which consisted of each taxon's clade rank (CR) (Gauthier et al. 1988) and the number of branch points from the root of the cladogram (i.e., patristic distance, PD) (Figs. 3, 4). A rationale for this specific arrangement of synapsid relationships is provided in Appendix 1. CR equals the number of branching points a taxon is positioned up the phylogenetic trajectory from Synapsida to Mammalia (Fig. 3). Branching within a terminal taxon on this pectinate tree is not considered. For example, every species within Gorgonopsia has a CR of 11. In contrast, PD measures the total number of nodes passed from the root of the cladogram to the taxon in question because branching within side-branches is taken into account. Only when a singleton attaches directly to the primary spine of the cladogram (e.g., *Tetraceratops* or *Dvinia*) are CR and PD equal.

Data were collected from study of fossil specimens at the following institutions: Albany Museum, Grahamstown, South Africa; American Museum of Natural History, New York; Field Museum of Natural History, Chicago; Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; National Museum of Natural History, Washington, D.C.; University of California Museum of Paleontology, Berkeley; Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Johannesburg; National Museum, Bloemfontein; South African Museum, Cape Town; Transvaal Museum, Pretoria; The Natural History Museum, London; Museum of Zoology, University of Cambridge, Cambridge, United Kingdom; Oxford University Museum, Oxford; Paleontological Institute, Moscow; Bayerische Staatssammlung für Paläontologie und Historische Geologie, Munich; Humboldt Museum für Naturkunde, Berlin; and Institut und Museum für Geologie und Paläontologie, Tübingen. Only four taxa were coded exclusively from the literature: *Bienotheroides wanhsienensis*, *Ecteninion lunensis*, *Probelesodon sanjuanensis*, and *Sinoconodon* sp. (Sun 1984; Crompton and Luo 1993; Martinez and Forster 1996; Martinez et al. 1996).

Qualitative Data.—I used 82 qualitative characters to describe morphological variation within the synapsid mandible. These characters included 22 pertaining to the dentary and 41 to the postdentary bones, six general shape features, and 13 dentition-related features. The last set specifically did *not* include characters describing the morphology of the dentition itself (such as cusp patterns). Rather, these characters focused on dental features manifesting themselves on the form of the lower jaw itself (e.g., whether or not the teeth were set in sockets). Many of the characters and character states were taken from previous cladistic analyses of synapsid relationships. Characters, character state descriptions, and literature references are presented in Appendix 2. The corresponding taxon/character data matrix is in Appendix 3.

The data matrix in Appendix 3 was converted to a taxon/taxon similarity matrix using the Simple Matching Coefficient (S_{SM}) (Sokal and Sneath 1963), which is equal to the number of characters for which two taxa match divided by the number of characters for which they could possibly match (in order to accommodate missing or inapplicable characters). Appendix 4 contains the final line in the similarity matrix, which compares the early mammal *Morganucodon* with every other taxon.

Quantitative Data.—Two areas and four linear measurements constitute the quantitative data set (Fig. 5). The area of the dentary and postdentary bones was calculated by digitizing their respective outlines in NIH Image. Synapsid mandibles were oriented *norma lateralis*, and then the following measurements were taken parallel to the long axis of the jaw: (1) jaw length, measured from the anteriormost point on the dentary to the midpoint of the craniomandibular joint; (2) dorsal length of the dentary, measured from the anterior tip of the dentary to the sutural contact between the dentary and surangular along the dorsal margin of the mandible; (3) ventral length of the dentary, measured from the anterior tip of the dentary to the sutural contact between the dentary and angular along the ventral margin of the mandible; and (4) perpendicular to the previous measurements, height of the coronoid region, equal to the distance from the mandibular joint to the dorsalmost point on the lower jaw. Measurements under 200 mm were taken with digital calipers and recorded to the nearest one-tenth millimeter. Measurements over 200 mm were taken with a measuring tape and recorded to the nearest half-millimeter. Raw data are presented in Appendix 5.

From the six original variables, four ratios were calculated: (A) the relative position of the dentary/surangular suture, calculated as the ratio of measurement (2) to measurement (1), (B) the relative position of the dentary/angular suture, calculated as the ratio of measurement (3) to measurement (1); (C) the relative height of the coronoid process, calculated as the ratio of measurement (4) to measurement (1); and (D) the relative area of the

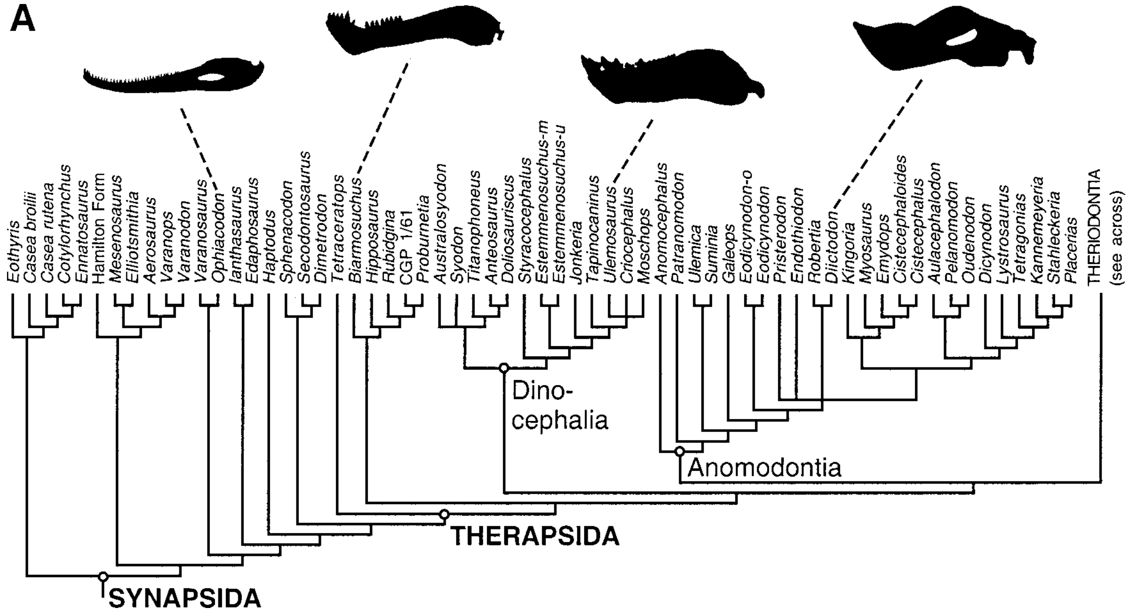

FIGURE 4. Cladogram of lower-level relationships among synapsids used herein. Appendix 1 includes a rationale for this specific topology. A taxon's patristic distance (PD) is calculated as the number of nodes passed from the base of this cladogram. For example, the ophiacodontids *Varanosaurus* and *Ophiacodon* each have a PD of 4. The most primitive cynodont, *Dvinia*, has a PD of 13 and illustrates the fact that singleton taxa attaching directly to the spine of the cladogram have PD and clade ranks (CR) of equal value. PDs for each terminal taxon are given in Appendix 4. CGP 1/61 refers to a new burnetiamorph housed in the collections of the Council for GeoSciences, Pretoria (Sidor 2000). SAM-PK-K9954 refers to a new galesaurid housed in the South African Museum, Cape Town (Sidor and Smith in press). Hamilton Form refers to a new, primitive varanopseid (Reisz and Dilkes 2003). "*Estemmenosuchus-m*" refers to *E. mirabilis*, "*Estemmenosuchus-u*" to *E. uralensis*, "*Probelesodon-lew.*" to *P. lewisi*, and "*Probelesodon-san.*" to *P. sanjuanensis*.

dentary, calculated as the area of the dentary divided by the total area of the lower jaw. Measurements were originally collected from 764 mandibles (Sidor 2000: App. 6.1). Of these, 322 lower jaws preserved at least two measurements and were used to calculate mean values for each taxon for each of the four dentary ratios (Appendix 5). For the purpose of summarizing changes in all four ratios, each taxon's *dentary index* (DI) was calculated as the average of the four ratios when each was standardized to have a mean of zero and unit variance. Appendix 4 contains the four original ratios and the summary DI, in addition to each taxon's first and last appearances (in ARs), CR, and PD. Because of fossil incompleteness, not every taxon has a complete set of measurements and so could not be included in all analyses.

Measurement-based Analyses

Stratigraphic Results.—Figure 6A summarizes the results of the measurement-based analyses. The dentary index (DI) is plotted on the abscissa, with increasingly positive values indicating an overall larger contribution of the dentary to the composition of the lower jaw. Although only the DI is depicted, the four individual dentary ratios show similar patterns (Table 1). The ordinate represents the stratigraphic distribution of each taxon in ARs. Significant, positive correlation between the two axes corresponds to a preferential positioning of dentary relative sizes through time.

The pattern depicted in Figure 6A confirms that the earliest-occurring, pelycosaur-grade taxa had the relatively smallest dentaries and largest complement of postdentary bones, and that the latest-occurring synapsids (e.g., tritylodontids and mammals) had mandibles that were almost exclusively formed by the dentary. Importantly, both the maximum and average dentary size increased over time in this study sample. However, it is interesting to note that several late-occurring synapsids retained relatively small dentaries.

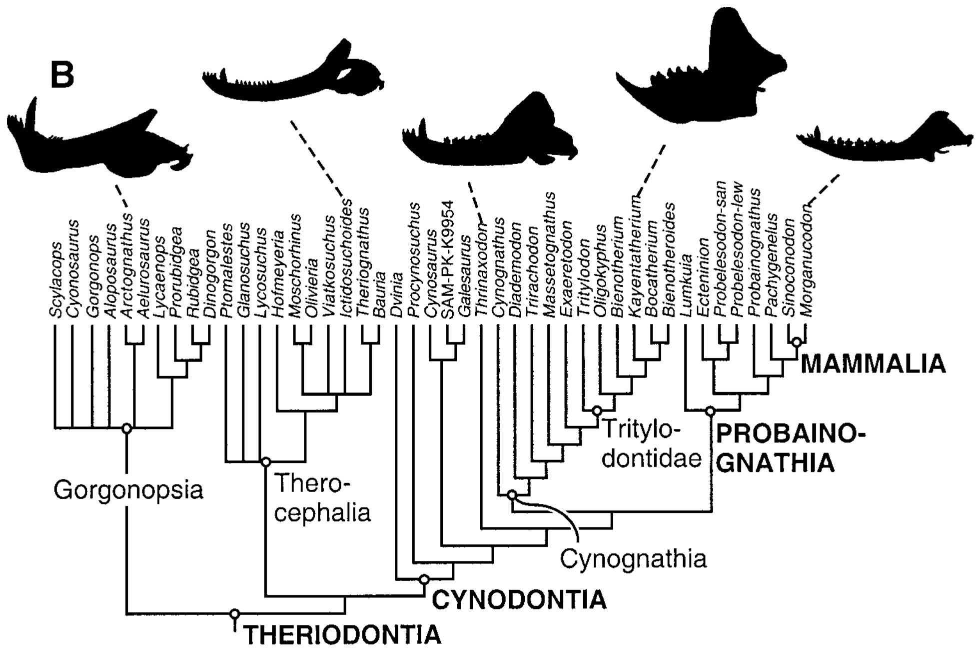

FIGURE 4. Continued.

Table 1 displays the results of a series of analyses that examine evolutionary patterns within several synapsid subclades. These analyses show that a significant positive correlation between DI and AR is nearly uniformly present in those clades encompassing mammals (e.g., Synapsida, Therapsida, Theriodontia, Cynodontia). Probainognathia is the exception to this pattern, but this may be due to the relatively few intervals that this clade spans. In contrast, clades not encompassing mammals (i.e., side branches such as anomodonts) generally have nonsignificant correlations. This crucial disagreement suggests that only the ancestral lineage leading to mammals (i.e., along the backbone of the cladogram) shows a consistent dentary enlargement (see below), and that clades budded off from this line retained their ancestral proportions but did not systematically continue the trend. It is worth noting that pelycosaur-grade synapsids show little indication of directionality, even though they span seven long intervals (ARs 1–7; Late Carboniferous to early Middle Permian, or approximately 35 Myr) and represent the primitive morphotype from which all subsequent change was derived.

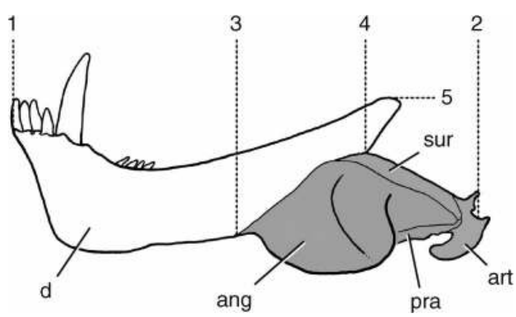

FIGURE 5. Lower jaw of the gorgonopsid *Arctognathus* in lateral view illustrating the five landmarks and two areas measured for this study. Landmarks included (1) the anteriormost tip of the dentary, (2) the midpoint of the jaw joint, (3) the anteriormost contact between the angular and dentary along the ventral margin of the lower jaw, (4) the anteriormost contact between the surangular and dentary along the dorsal surface of the lower jaw, and (5) the dorsalmost point on the coronoid eminence or process. The measurements taken between these landmarks are described in the text. The dentary is unshaded, whereas the area of the postdentary bones is shaded. Anatomical abbreviations as in Figure 1. Figure modified from Kemp 1982.

Phylogenetic Results.—Figure 6B plots the relationship between DI and each taxon's cladogram position, as measured by CR (see Table 2 for complete results). It is clear from this graph that the degree to which a synapsid clade shares ancestry with mammals has a strong, positive relationship with that clade's average dentary size. However, when the inferred primitive condition for each consecutive clade is highlighted (filled circles), this point does not consistently reside in the left tail of that clade's range of DI values. This position suggests that diversification within each synapsid subclade expanded the range of DI values but did not uniformly increase the relative contribution of the dentary.

Directionality within subclades is more fully considered in Figure 6C (and Table 3), which contrasts the number of branch points separating each taxon from the root of the cladogram (patristic distance; PD) with its DI. Because stratigraphic and phylogenetic position show a strong relationship in synapsids (Sidor and Hopson 1998), Figure 6C is very similar to 6A. Taxa diverging relatively early (i.e., with low PDs) tend to have small dentaries, whereas phylogenetically more derived taxa show a wider range of values. The expanding range of values observed at high PDs can be attributed to the persistence of small-dentaried anomodonts (plus signs) with theriodonts (filled circles) that consistently enlarge the dentary. However, just as with the stratigraphic analyses, the individual theriodont subclades that lack mammals as a subgroup lack a corresponding trend (Table 3). Again, this suggests that increasing the dentary size was not a universal feature of synapsid evolution.

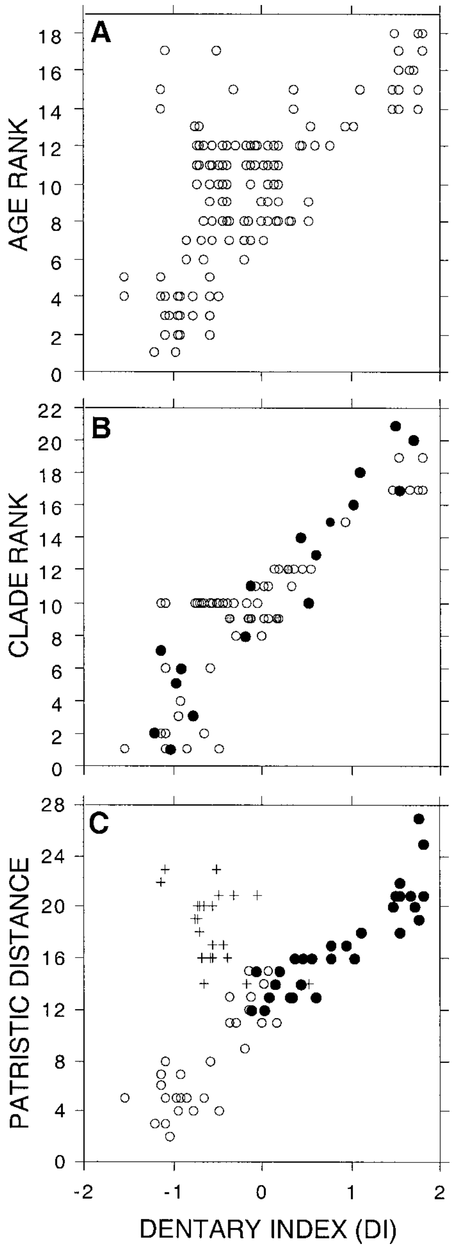

FIGURE 6. Contribution of the dentary to the lower jaw in synapsid evolution. (A) compares the stratigraphic range (measured in Age Ranks) to each fossil synapsid's dentary index (DI). The DI is computed as the average score of the four original dentary ratios when each is scaled to a mean of zero with unit variance. Low DIs correspond to mandibles with relatively small dentaries and low coronoid regions, whereas high DIs correspond to the opposite. In (B), filled circles represent the inferred primitive condition at each clade rank. Grayed circles indicate the two most primitive members for clades with no single most primitive taxon. The following taxa were used in these cases: *Ianthasaurus* for edaphosaurids (Modesto 1995), *Syodon* and *Styracocephalus* for dinocephalians (Rubidge 1994; Rubidge and van den Heever 1997), *Patranomodon* (in A) or *Ulemica* for anom-

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odonts (Rubidge and Hopson 1996), *Cyonosaurus* for gorgonopsids (Sigogneau 1970), *Ptomalestes* and *Glanosuchus* for therocephalians (Hopson and Barghusen 1986), and *Sinoconodon* for mammals (Luo 1994). A strong trend for increasing the dentary's overall contribution to the composition of the mandible is present among the primitive members of each consecutively more advanced clade. Interestingly, however, the most primitive member of each subgroup does not tend to be positioned at the low end of its group's distribution, suggesting that a within-subclade evolution does not display the same pattern. In (C), open circles are stem taxa, plus signs are anomodonts, and filled circles are theriodonts. Theriodonts show the strongest relationship between PD and each of the four dentary size measurements whereas anomodonts consistently display none. Note that the variance in DI observed in anomodonts in (C) is collapsed in to a single horizontal line in (B). Statistics for (A), (B), and (C) are in Tables 1, 2, and 3, respectively.

TABLE 1. Results of Spearman rank correlation tests for lower jaw measurements versus stratigraphic range (in age ranks). ''Pelycosaurs'' are not a clade, but they are included here to represent the early portion of synapsid evolution. All other subgroups represent clades. Only first appearances were used in this analysis (mean taxon duration = 1.6 age ranks). The test statistic (Rho) and *p*-value are corrected for ties in this and subsequent Tables. ns* $p = 0.0570$.

Subgroup	Area		Dorsal		Ventral		Coronoid		DI	
	Rho	*p*	Rho	*p*	Rho	*p*	Rho	*p*	Rho	*p*
Synapsida	0.77	<0.0001	0.42	<0.0001	0.61	<0.0001	0.55	<0.0001	0.64	<0.0001
''Pelycosaurs''	0.29	ns	0.24	ns	0.26	ns	−0.08	ns	0.14	ns
Therapsida	0.61	<0.0001	0.41	0.0005	0.52	<0.0001	0.35	0.0040	0.46	0.0003
Dinocephalia	0.41	ns	−0.11	ns	0.49	ns	−0.06	ns	0.39	ns
Anomodontia	−0.02	ns	0.11	ns	−0.30	ns	−0.19	ns	−0.33	ns
Theriodontia	0.86	<0.0001	0.79	<0.0001	0.82	<0.0001	0.47	0.0055	0.89	<0.0001
Gorgonopsidae	−0.46	ns	−0.14	ns	−0.66	0.0475	0.78	ns*	−0.53	ns
Therocephalia	0.25	ns	0.22	ns	0.01	ns	0.11	ns	0.64	ns
Cynodontia	0.83	<0.0001	0.74	0.0012	0.65	0.0027	0.29	ns	0.81	0.0008
Cynognathia	0.64	ns	0.20	ns	0.27	ns	0.32	ns	0.52	ns
Tritylodontidae	−1.00	ns	0.36	0.0008	0.50	ns	−0.40	ns	−1.00	ns
Probainognathia	0.99	0.0275	0.50	ns	0.36	ns	−0.55	ns	0.36	ns

Character-based Analyses

The six measurements used above can provide only a limited view of morphological changes occurring within synapsid mandibular evolution. Potentially more informative is quantifying morphological similarity with reference to an exemplar primitive mammal (*Morganucodon*, in this case) using discrete characters (Appendix 4). Phenetic similarity is an appropriate metric to use in this case because the convergent acquisition of a certain phenotype pertains to net, rather than total, morphological change (Foote 1996). As with the measurement-based analyses, significantly positive correlations between the degree of similarity to mammals and stratigraphic or phylogenetic position would support the hypothesis of a morphological trend toward gaining mammal-like features, whereas nonsignificant correlations would refute it. Furthermore, negative correlations correspond to increasing dissimilarity; i.e., the morphological modifications experienced by a clade's lower jaw consistently distance it from the mammalian position in morphospace.

Stratigraphic and Phylogenetic Results.—Figure 7 and Table 4 contain the principal results of the discrete character-based analyses, which are remarkably similar to those based on measurements (compare with Fig. 6). This similarity implies that both data sets are capturing a common signal from synapsid evolution. When compared with stratigraphic position (Fig. 7A), Late Carboniferous and Early Permian pelycosaur-grade synapsids begin with approximately 60% of their (comparable) lower-jaw characters matching the condition in *Morganucodon* (AR 1–6). By the middle of Late Permian times (AR 9), however, therapsid diversification expanded this range of values, with anomodonts becoming increasingly *dissimilar* to mammals, and theriodonts becoming increasingly similar (presumably through synapomorphy). The ''increase in variance'' pattern continued until the demise of anomodonts in the Late Triassic (AR 17), whereby only the advanced cynodonts (i.e., the right tail of the distribution) remained. As with the measurement-based results, subclades encompassing mammals typically show signifi-

TABLE 2. Results of Spearman rank correlation tests for lower jaw measurements versus inferred phylogenetic position in clade ranks (CR). All taxa except ''pelycosaurs'' and ''non-theriodonts'' represent clades. ns* $p = 0.0601$.

Subgroup	Area		Dorsal		Ventral		Coronoid		DI	
	Rho	*p*	Rho	*p*	Rho	*p*	Rho	*p*	Rho	*p*
Synapsida	0.89	<0.0001	0.54	<0.0001	0.78	<0.0001	0.64	<0.0001	0.82	<0.0001
''Pelycosaurs''	0.05	ns	−0.34	ns	−0.03	ns	0.22	ns	0.17	ns
Therapsida	0.83	<0.0001	0.57	<0.0001	0.78	<0.0001	0.49	<0.0001	0.74	<0.0001
''Non-theriodonts''	0.68	<0.0001	−0.38	0.0060	0.13	ns	0.44	<0.0019	0.37	0.0099
Theriodontia	0.88	<0.0001	0.87	<0.0001	0.90	<0.0001	0.25	ns	0.91	<0.0001
Cynodontia	0.56	<0.0001	0.81	0.0004	0.48	0.0237	−0.09	ns	0.67	0.0055
Probainognathia	0.75	ns	0.84	ns*	0.09	ns	−0.81	0.0327	0.21	ns

cant correlations between AR and the degree of similarity to mammals, whereas side-branches often do not (Table 4).

Figure 7B compares the degree of mammal mandibular similarity against each taxon's CR, with the inferred primitive condition at each point highlighted. An increasingly mammal-like lower jaw is expected to correlate with higher CRs, given that some of the features used in this analysis have been proposed as synapomorphies diagnosing higher-level synapsid clades. An interesting result is the relatively low degree of divergence (i.e., range of values) from the presumed ancestral condition at each CR (filled circles). Only anomodonts, and in particular their derived dicynodont subclade (e.g., Fig. 2D), show substantial morphological divergence. Although I attempted to be as exhaustive as possible in my character selection, doubtless additional characters could be discovered and affect this low degree of subclade morphological divergence.

Presuming that the characters used herein are an unbiased sample from the total pool of possible lower-jaw characters, an interesting pattern emerges: except for caseasaurs (CR 1), the inferred primitive condition at each CR lies at the mammal-like (right-hand) tail for non-theriodonts (CRs 2–10), shifts to an intermediate value within gorgonopsians and therocephalians (CRs 11 and 12), and then lies on the non-mammal-like (left-hand) end for cynodonts onward (CRs 13–22). This implies that morphological change within each subclade went from being primarily divergent, within non-cynodonts, to convergent, within cynodonts (but see below). It is also worth noting that discontinuities between the inferred ancestral condition between adjacent CRs could indicate gaps in the fossil record, if synapsid evolution was predominantly monotonic (Sidor and Hopson 1998), or variation in the rate of character acquisition, if taxon sampling probabilities were relatively constant (Sereno et al. 1999).

Figure 7C plots the number of inferred branch points from the root of the cladogram to each terminal taxon (PD) against the degree to which each taxon's lower jaw is similar to that of *Morganucodon*. Taxa positioned near the base of the tree (with low PDs) hover around

TABLE 3. Results of Spearman rank correlation tests for lower jaw measurements versus inferred degree of phylogenetic advancement based on the number of branch points passed from the root of the cladogram (PD). All taxa except ''pelycosaurs'' represent clades. Only first appearances were used in this analysis (mean taxon duration = 1.6 intervals). ns* $p = 0.0668$, ns** $p = 0.0845$, ns*** $p = 0.0738$.

Subgroup	Area		Dorsal		Ventral		Coronoid		DI	
	Rho	*p*	Rho	*p*	Rho	*p*	Rho	*p*	Rho	*p*
Synapsida	0.65	<0.0001	0.15	ns	0.38	0.0002	0.48	<0.0001	0.44	<0.0001
''Pelycosaurs''	0.01	ns	−0.13	ns	−0.17	ns	0.44	ns	0.07	ns
Therapsida	0.39	0.0016	0.04	ns	0.17	ns	0.23	0.0512	0.07	ns
Dinocephalia	−0.55	ns	−0.21	ns	−0.13	ns	0.77	0.0210	0.34	ns
Anomodontia	−0.13	ns	−0.06	ns	−0.37	ns	−0.13	ns	−0.25	ns
Theriodontia	0.87	<0.0001	0.82	<0.0001	0.84	<0.0001	0.50	0.0031	0.90	<0.0001
Gorgonopsidae	0.48	ns	0.29	ns	−0.31	ns	0.08	ns	0.26	ns
Therocephalia	0.19	ns	0.38	ns	−0.10	ns	0.17	ns	0.73	ns***
Cynodontia	0.85	0.0003	0.69	0.0027	0.63	0.0029	0.36	ns	0.27	0.0371
Cynognathia	0.57	ns	0.17	ns	0.21	ns	0.38	ns	0.46	ns
Tritylodontidae	−1.00	ns	1.00	ns	0.50	ns	−0.11	ns	−1.00	ns
Probainognathia	0.82	ns*	0.77	ns**	0.45	ns	−0.62	ns	0.89	ns

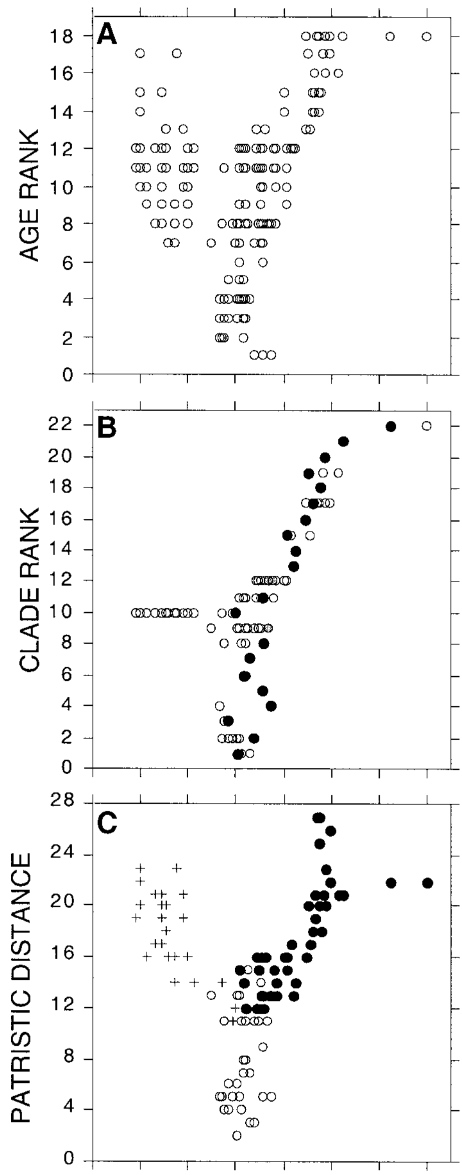

FIGURE 7. Plots comparing the degree of phenetic similarity with the early mammal *Morganucodon* for each taxon against its stratigraphic position (A) and phylogenetic position (B, C). Points highlighted in (B) correspond to the same taxa as in Figure 6B, except that *Anomocephalus* (Modesto et al. 1999) was used in place of *Patranomodon*. See Table 4 for details of correlation statistics.

a mammal mandibular similarity of 60%, whereas anomodonts and nonmammalian theriodonts expand this range by roughly 20% in negative and positive directions, respec-

TABLE 4. Results of Spearman rank correlation tests comparing the overall similarity of each taxon's lower jaw with that of the early mammal *Morganucodon*, to stratigraphic position (AR) and two measures of phylogenetic position (CR and PDR). All taxa except ''pelycosaurs'' represent clades. The clade rank comparison can only be made for those taxa encompassing mammals. ns* $p = 0.0953$.

	Age rank		Clade rank		Patristic distance	
Subgroup	Rho	*p*	Rho	*p*	Rho	*p*
Synapsida	0.43	<0.0001	0.64	<0.0001	0.16	ns
''Pelycosaurs''	−0.218	ns	0.20	ns	0.04	ns
Therapsida	0.49	<0.0001	0.77	<0.0001	0.13	ns
Dinocephalia	−0.19	ns	—	—	−0.55	0.0087
Anomodontia	−0.33	ns	—	—	−0.37	ns
Theriodontia	0.80	<0.0001	0.93	<0.0001	0.83	<0.0001
Gorgonopsidae	−0.33	ns	—	—	−0.09	ns
Therocephalia	−0.27	ns	—	—	−0.33	ns
Cynodontia	0.63	0.0026	0.81	0.0001	0.69	0.0009
Cynognathia	0.18	ns	—	—	0.46	ns
Tritylodontidae	−0.10	ns	—	—	−0.41	ns
Probainognathia	0.63	ns*	0.87	0.0211	0.87	0.0221

tively. Thus, prior to the early mammal *Sinoconodon*, the lower jaws of advanced nonmammalian cynodonts such as *Probainognathus* maintained substantial differences from those of early mammals. This plot most clearly depicts the Y-shaped pattern hinted at in several other graphs (compare Figs. 6A,C and 7A,C), where anomodonts and theriodonts morphologically diverge from one another after an early phase of nondirectionality within more basal synapsids. The gap between the branches of the Y is due to the relatively low diversity and short temporal duration of the clades with intermediate similarity values (viz. gorgonopsians and therocephalians).

Scaling Patterns

Synapsids diversified into an impressive array of body sizes and presumed ecologies during the Permian and Triassic. However, the possibility that changes in body size were important factors in the reduction of the postdentary bones has received scant attention in the literature. Instead, most analyses have focused on the detailed morphology of several exemplar taxa assumed to be phylogenetically close to the line leading toward mammals (Allin 1975).

Figure 8A compares dentary area and total jaw length for the 160 synapsids with both measurements (Appendix 5). A line with a slope of two indicates isometry in this case because an area is being plotted against a linear measurement. A reduced major axis regression (RMA) indicates that synapsids as a whole conform to this expectation (slope = 2.031 ± 0.101). Furthermore, various synapsid subgroups show either near isometry or slight positive allometry (Table 5).

Figure 8B plots postdentary area against total jaw length for 154 fossil synapsids. In contrast to the dentary area results, the RMA regression for Synapsida is significantly greater than isometry (slope = 2.617 ± 0.180). However, this apparent allometry is due to the mixing of two regressions. When synapsids are subdivided into cynodonts and non-cynodont components, both of these groups show a relationship between postdentary area and jaw length that is indistinguishable from isometry (slopes of 2.174 ± 0.184 and 2.108 ± 0.180, respectively). However, the cynodont regression is offset below that of all other synapsids, indicating that this group had a proportionally more gracile postdentary region. See Table 6 for complete results.

Step-Size Analysis

The analyses presented above show a complicated pattern of results but do not address the underlying mechanisms by which trends could develop. One such mechanism could be a bias in step size (Fisher 1986; McShea 1994; Wagner 2000b). For example, even if dentary increases and decreases were equally likely to occur during the course of synapsid evolution, if increases were twice the magnitude of decreases, then the dentary would be predicted

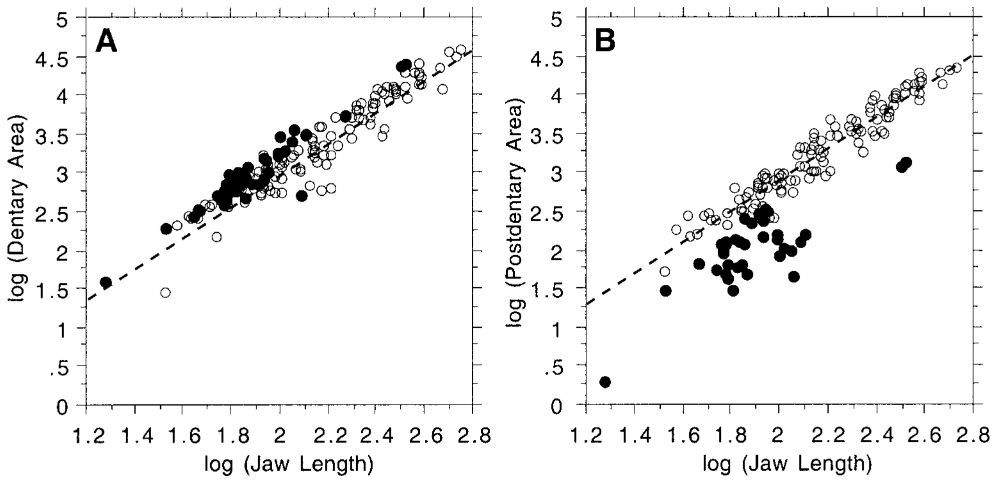

FIGURE 8. Scaling patterns between dentary area (A) and postdentary area (B) against jaw length. Filled circles denote cynodonts, whereas open circles denote non-cynodont synapsids. Dashed line indicates isometric scaling (slope = 2). Regressions for most synapsid subgroups either are indistinguishable from isometry or show slight positive allometry. See Tables 5 and 6 for regression results.

to enlarge over time. The possibility that unequal degrees of mammalian versus nonmammalian morphological change brought about a trend for an increasingly mammalian lower jaw is examined below.

Methods.—To address the hypothesis of step-size bias with the discrete character data, I used MacClade (Maddison and Maddison 1992) to contrast the number of internodal character state changes leading to each pair of sister taxa at every CR along the spine of the cladogram in Figure 3. For example, at CR 7 (Therapsida) between three and ten character-state changes (depending on optimization) occur along the branch to *Tetraceratops*, whereas six to nine occur along the branch to CR 8. If evolution along the mammalian line typically produced larger than average changes, then we might expect the number of character-state changes between CRs to be consistently larger than between CR nodes and side branches.

These comparisons are based on the premise that morphological changes occurring between consecutive nodes on this cladogram produce increased similarity to mammals (because they are synapomorphic), whereas changes accumulated on the side-branches (i.e., toward the individual terminal taxa)

TABLE 5. Log-log regressions of dentary area and jaw length in synapsids. Regressions for all of these synapsid subgroups are either isometric (slope = 2) or slightly positively allometric. The slope and intercept are based on reduced major-axis regression. The 95% confidence limit (CL) and correlation coefficient (r^2) are estimates based on the results of simple linear regressions. All slopes are significantly different from zero for at least $p < 0.05$ level.

Subgroup	Slope ± CL	Intercept	r^2	n
Synapsida	2.031 ± 0.101	−0.991	0.900	160
''Noncynodont''	2.116 ± 0.100	−1.221	0.909	120
''Pelycosaurs''	2.313 ± 0.105	−1.918	0.903	23
Biarmosuchia	2.203 ± 0.120	−1.523	0.928	7
Dinocephalia	1.915 ± 0.110	−0.695	0.917	13
Anomodontia	2.040 ± 0.102	−0.940	0.981	52
Gorgonopsidae	2.193 ± 0.113	−1.386	0.979	10
Therocephalia	2.304 ± 0.108	−1.594	0.936	15
Cynodontia	2.249 ± 0.103	−1.266	0.901	40

TABLE 6. Log-log regressions of postdentary area and jaw length in synapsids. Regressions for all of these synapsid subgroups are either isometric (slope = 2) or slightly positively allometric. The slope and intercept are based on reduced major axis regression. The 95% confidence limit (CL) and correlation coefficient (r^2) are estimates based on the results of simple linear regressions. All slopes are significantly different from zero for at least $p < 0.05$ level.

Subgroup	Slope ± CL	Intercept	r^2	n
Synapsida	2.617 ± 0.180	−2.540	0.818	154
''Noncynodont''	2.108 ± 0.180	−1.325	0.926	118
''Pelycosaurs''	2.198 ± 0.188	−1.521	0.875	23
Biarmosuchia	2.472 ± 0.215	−2.107	0.810	7
Dinocephalia	1.900 ± 0.198	−0.806	0.854	12
Anomodontia	2.046 ± 0.182	−1.127	0.969	52
Gorgonopsidae	2.232 ± 0.202	−1.701	0.941	10
Therocephalia	2.068 ± 0.195	−1.430	0.878	14
Cynodontia	2.177 ± 0.184	−2.086	0.643	36

TABLE 7. Mammalian versus nonmammalian step-size contrasts. The 21 clade ranks (CR) are derived from the cladograms in Figures 3 and 4. ''Mammal'' refers to the number of character state changes occurring between consecutive CRs (e.g., between CR 1 and CR 2). ''Non-mammal'' refers to the number of character state changes occurring between a particular node and the terminal taxon attaching to it (e.g., between the node at CR 7 and *Tetraceratops*). Minimum and maximum numbers of character state changes were computed in MacClade (Maddison and Maddison, 1993). In order to calculate the maximum character state changes, polychotomies in Figure 5 were arbitrarily resolved. Results of a Wilcoxon signed rank test indicate no significant difference in the sign or magnitude of mammalian versus nonmammalian changes for either the minimum or maximum of discrete changes ($p = 0.7405$).

CR	Mammal $Char_{min/max}$	Non-mammal $Char_{min/max}$
1	0/2	0/2
2	1/1	1/3
3	2/6	3/6
4	3/6	0/4
5	1/5	0/2
6	1/6	1/6
7	3/10	6/9
8	0/1	1/3
9	1/5	2/4
10	1/1	4/7
11	2/4	6/8
12	3/6	1/3
13	0/0	1/2
14	1/5	3/6
15	1/2	0/0
16	4/5	2/2
17	2/4	0/1
18	2/6	1/2
19	1/4	0/3
20	4/10	2/6
21	5/10	2/7

should produce increased dissimilarity. One shortcoming of this type of analysis is that it only uses the first possible comparison at each CR (i.e., changes occurring on the first internode in either direction) and thereby disregards subsequent (i.e., more deeply nested) changes within each sister clade.

Results.—Wilcoxon sign-rank tests found no significant difference between the number of character changes in mammalian and nonmammalian directions (Table 7, Fig. 9). This result was the same regardless of whether minimum or maximum numbers of character-state changes were used.

Discussion

The hypothesis that disparate groups of synapsids independently acquired mammal-like characteristics has a long pedigree (Olson 1944, 1959, 1962; Romer 1965; Simpson 1959). However, some examples of ''convergence'' probably arose from the taxonomic framework accepted at that time—one that recognized paraphyletic and polyphyletic grades of organization (Hopson 1994). The application of cladistic methods to synapsid systematics has dispelled some cases of morphologic homoplasy as unnecessary when viewed from the standpoint of total character congruence (Hopson and Barghusen 1986; Rowe 1986; Kemp 1988b). Here, I have readdressed the oft-noted observation that the size of the dentary increased during the course of synapsid evolution. Both quantitative and discrete data indicate that a lower jaw of increasingly mammalian cast was a prevalent feature of premammalian synapsid evolution (Fig. 10), but finer scales of phylogenetic resolution yield more complex patterns.

In Theriodontia and its subordinate clades that encompass mammals, the pattern of both measurements and similarity values is suggestive of a driven trend (in that both the minimum and maximum values steadily increase). Thus, the measurement results accord well with Allin's (1975) hypothesis that reduction of the postdentary bones improved high-frequency hearing in these taxa and was therefore selectively advantageous. However, corresponding directionality is not apparent within the ''side-branch'' clades (Tables 1–4), which suggests that a common driving force is doubtful. In the most extreme case, anomodonts show the exact opposite trend: *decreasing* dentary size and *increasing* their lower jaw's distinctiveness from that of mammals. This suggests either that high-frequency hearing was not important to anomodonts or that selection for this feature was not exclusively molding mandibular evolution in this group.

The specialized structure of the anomodont mandible is an interesting exception to another result of these analyses—the relative scarcity of divergent lower-jaw morphologies among synapsid side-branches. Although there are certainly some features that are autapomorphic for the clades that do not encompass mammals (e.g., the extremely slender dentary of varanopseids, the near-vertical

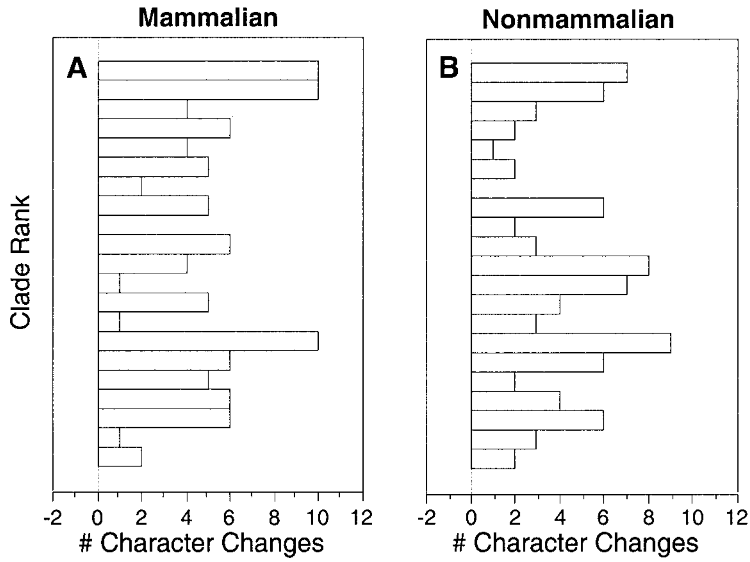

FIGURE 9. Step-size comparisons contrasting the maximum and minimum number of character-state changes along the phylogenetic trajectory toward mammals (mammalian) versus those made toward side-branches (nonmammalian). The vertical axis represents clade rank (CR). The final 21 comparisons were made for discrete characters. A and B display the maximum number of discrete character changes in mammalian and nonmammalian directions, respectively. See text and Table 7 for details.

ridge on the reflected lamina of gorgonopsians, or the elongate angular process of the dentary in some advanced cynognathians), no one synapsid subgroup amasses more than a few such specializations, except for the anomodonts. Importantly, this lack of mandibular autapomorphy indicates that the acquisition of only a few mammalian characters would be sufficient to drive an apparent trend toward a mammal-like jaw.

Disruptive Patterns.—The Y-shaped pattern of dentary size and mammalian similarity (Figs. 6, 7) that emerged from several analyses is strikingly similar to that of disruptive selection within modern populations (i.e., when selection acts against intermediates and favors morphological extremes). Foote (1993) showed that blastoids exhibit a similar disruptive pattern, but he suggested that if a bias against intermediates were present, then its explanation would require investigation at finer scales. In the case of synapsids, the lack of intermediates is due to the early extinction of gorgonopsians and therocephalians, compared with the relatively long-lived anomodont and cynodont clades.

Combining Methods.—Both stratigraphy- and phylogeny-based methods have been used to examine patterns of morphological change in fossil lineages (Gingerich 1976; Benton 1990; McShea 1994; Wagner 1996). Importantly, the potential weaknesses of either approach might be overcome by using both methods in a study. For example, if cladistic estimates of synapsid phylogeny have been led astray by rampant homoplasy, then the stratigraphic distribution of the taxa may yield a more informative measure of relatively primitive and derived taxa. Conversely, if the fossil record does not accurately portray the first appearances of synapsids because preservation rates vary widely, then phylogenetic measures might yield a more reliable sequence of branching events. The concordant results found in this study suggest that the synapsid fossil record is relatively well sampled and that the cladistic hypothesis of synapsid relationships presented here is in line with the distribution of fossil finds (Sidor and Hopson 1998).

Conclusions

The prevalence of homoplasy in synapsid evolution has been a hotly contested topic (Kemp 1988a; Rowe 1988; Hopson 1991a). Hopson (1994: p. 212) suggested that although

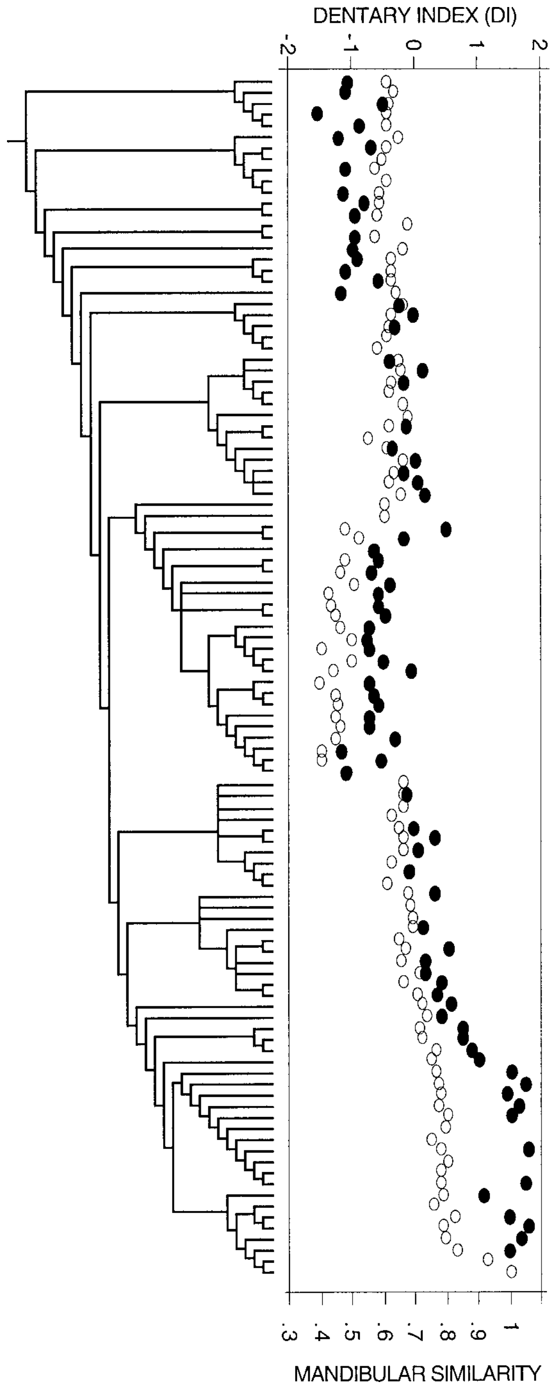

FIGURE 10. Changes in dentary size and mammal mandibular similarity plotted against a cladogram of synapsid relationships. DI values are denoted by filled ellipses (left axis) and similarity values by hollow ellipses (right axis).

"[t]he polyphyletic origin of mammals is no longer a tenable hypothesis. . . this is not to say that parallelism and convergence have not been significant aspects of pre-mammalian synapsid evolution."

The present study supports the following main conclusions:

1. The lack of a well-supported phylogeny has exaggerated previous estimates of morphological convergence or parallelism in the synapsid fossil record. The hypothesis of multiple therapsid groups arising independently from pelycosaur-grade ancestors (e.g., Olson 1962; Boonstra 1972) necessitated rampant homoplasy and are now considered untenable (Rubidge and Sidor 2001). Certain lower jaw characteristics and proportions are better viewed as broadly distributed synapomorphies indicative of common ancestry.
2. Despite the striking differences between the lower jaws of basal synapsids (i.e., "pelycosaur") and mammals, mandibular evolution within synapsids was predominantly conservative. Except for dicynodont anomodonts, most therapsid subclades do not acquire substantial morphological novelty in their lower jaw structure.
3. The area of the dentary and postdentary regions scales either isometrically or with slight positive allometry when compared with jaw length. This suggests that body-size trends are not sufficient to drive the reduction of the postdentary bones in synapsid evolution. Importantly, when compared with other synapsid subgroups, cynodonts are characterized by smaller-than-predicted postdentary areas.
4. Selection acting to decrease the size of the postdentary bones, and thereby improving high-frequency hearing, is still the most tenable mechanism for the evolution of the mammalian lower jaw (Allin 1975; Allin and Hopson 1992). However, this mechanism by itself has difficulty explaining the converse pattern in anomodont therapsids (i.e., decreasing the size of the dentary and increasing the size of the postdentary bones).

These conclusions, in combination with

those of recent studies on long-term patterns of epipodial (Hopson 1995) and cranial (Sidor 2001) evolution, suggest that morphological trends within synapsids should be reinvestigated within a quantitative and phylogenetic framework.

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Literature Cited

Allin, E. F. 1975. Evolution of the mammalian middle ear. Journal of Morphology 147:403–438.

Allin, E. F., and J. A. Hopson. 1992. Evolution of the auditory system in Synapsida (''mammal-like reptiles'' and primitive mammals) as seen in the fossil record. Pp. 587–614 *in* D. B. Webster, R. R. Fay, and A. N. Popper, eds. The evolutionary biology of hearing. Springer, New York.

Angielczyk, K. D. 2001. Preliminary phylogenetic analysis and stratigraphic congruence of the dicynodont anomodonts (Synapsida: Therapsida). Palaeontologia Africana 37:53–79.

Battail, B. 1991. Les Cynodontes (Reptilia, Therapsida): une phylogénie. Bulletin du Muséum National d'Histoire Naturelle 13:17–105.

Benton, M. J. 1990. Reptiles. Pp. 279–300 *in* K. J. McNamara, ed. Evolutionary trends. Belhaven, London.

Berman, D. S., R. R. Reisz, J. R. Bolt, and D. Scott. 1995. The cranial anatomy and relationships of the synapsid *Varanosaurus* (Eupelycosauria: Ophiacodontidae) from the Early Permian of Texas and Oklahoma. Annals of the Carnegie Museum 64: 99–133.

Bonaparte, J. F. 1962. Descripción del cráneo y mandibula de *Exaeretodon frenguellii*, Cabrera, y su comparación con Diademodontidae, Tritylodontidae y los cinodontes sudamericanos. Publicaciones del Museo Municipal de Ciencias Naturales de Mar del Plata ''Lorenzo Scaglia'' 1:135–202.

Boonstra, L. D. 1972. Discard the names Theriodontia and Anomodontia: a new classification of the Therapsida. Annals of the South African Museum 59:315–338.

Brinkman, D. 1981. The structure and relationships of the dromasaurs (Reptilia: Therapsida). Breviora 465:1–34.

Clark, J. M., and J. A. Hopson. 1985. Distinctive mammal-like reptile from Mexico and its bearing on the phylogeny of the Tritylodontidae. Nature 315:398–400.

Cluver, M. A., and G. M. King. 1983. A reassessment of the relationships of the Permian Dicynodontia (Reptilia, Therapsida) and a new classification of dicynodonts. Annals of the South African Museum 91:195–273.

Conrad, J., and C. Sidor. 2001. Re-evaluation of *Tetraceratops insignis* (Synapsida: Sphenacodontia). Journal of Vertebrate Paleontology 21:42A.

Crompton, A. W. 1963. The evolution of the mammalian jaw. Evolution 17:431–439.

———. 1972. Postcanine occlusion in cynodonts and tritylodontids. Bulletin of the British Museum (Natural History) Geology 21:30–71.

Crompton, A. W., and F. Ellenberger. 1957. On a new cynodont from the Molteno Beds and the origin of the tritylodontids. Annals of the South African Museum 44:1–14.

Crompton, A. W., and N. Hotton. 1967. Functional morphology of the masticatory apparatus of two dicynodonts (Reptilia, Therapsida). Postilla 109:1–51.

Crompton, A. W., and F. A. Jenkins Jr. 1973. Mammals from reptiles: a review of mammalian origins. Annual Review of Earth and Planetary Sciences 1:131–155.

Crompton, A. W., and Z. Luo. 1993. Relationship of the Liassic mammals *Sinoconodon*, *Morganucodon oehleri*, and *Dinnetherium*. Pp. 30–44 *in* F. S. Szalay, M. J. Novacek, and M. C. McKenna, eds. Mammal phylogeny: Mesozoic differentiation, multituberculates, monotremes, early therians, and marsupials. Springer, New York.

Efremov, I. A. 1940. *Ulemosaurus svijagensis* Riab.—ein Dincephale aus den Ablagerurgen des Perm der UdSSR. Nova Acta Leopoldina 9:155–205.

Fisher, D. C. 1986. Progress in organismal design. Pp. 99–117 *in* D. M. Raup and D. Jablonski, eds. Patterns and processes in the history of life. Springer, Berlin.

Foote, M. 1993. Contributions of individual taxa to overall morphological variation. Paleobiology 19:403–419.

———. 1996. Evolutionary patterns in the fossil record. Evolution 50:1–11.

Gauthier, J., A. Kluge, and T. Rowe. 1988. Amniote phylogeny and the importance of fossils. Cladistics 4:105–209.

Gingerich, P. D. 1976. Paleontology and phylogeny: patterns of evolution at the species level in Early Tertiary mammals. American Journal of Science 276:1–28.

Grine, F. E. 1997. Dinocephalians are not anomodonts. Journal of Vertebrate Paleontology 17:177–183.

Hopson, J. A. 1965. Tritylodontid therapsids from Yunnan and the cranial morphology of *Bienotherium*. Ph.D. dissertation. University of Chicago, Chicago.

———. 1966. The origin of the mammalian middle ear. American Zoologist 6:437–450.

———. 1987. The mammal-like reptiles: a study of transitional fossils. American Biology Teacher 49:16–26.

———. 1991a. Convergence in mammals, tritheledonts, and tritylodonts. Journal of Vertebrate Paleontology 11:36A.

———. 1991b. Systematics of the nonmammalian Synapsida and implications for patterns of evolution in synapsids. Pp. 635–693 *in* H.-P. Schultze and L. Trueb, eds. Origins of the higher groups of tetrapods: controversy and consensus. Comstock, Ithaca.

———. 1994. Synapsid evolution and the radiation of non-eutherian mammals. Pp. 190–219 *in* D. B. Prothero and R. M. Schoch, eds. Major features of vertebrate evolution. Paleontological Society, Knoxville, Tenn.

———. 1995. Patterns of evolution in the manus and pes of nonmammalian therapsids. Journal of Vertebrate Paleontology 15:615–639.

———. 1999. Therapsids. Pp. 1256–1266 *in* R. Singer, ed. Encyclopedia of paleontology. Fitzroy Dearborn, Chicago.

Hopson, J. A., and H. Barghusen. 1986. An analysis of therapsid relationships. Pp. 83–106 *in* N. Hotton, P. D. MacLean, J. J. Roth, and E. C. Roth, eds. The ecology and biology of the mammal-like reptiles. Smithsonian Institution Press, Washington, D.C.

Hopson, J. A., and J. W. Kitching. 1972. A revised classification of cynodonts (Reptilia; Therapsida). Palaeontologia Africana 14:71–85.

———. 2001. A probainognathian cynodont from South Africa and the phylogeny of nonmammalian cynodonts. Bulletin of the Museum of Comparative Zoology 156:3–35.

Huelsenbeck, J. P. 1991. When are fossils better than extant taxa in phylogenetic analysis? Systematic Zoology 40:458–469.

Ivachnenko, M. F., V. K. Golubev, Y. M. Gubin, N. N. Kalandadze, I. V. Novikov, A. G. Sennikov, and A. S. Rautian. 1997. Permskie i Triasovye tetrapody Vostochnoi Evropy (Permian and Triassic tetrapods of Eastern Europe). Geos, Moscow.

Kemp, T. S. 1982. Mammal-like reptiles and the origin of mammals. Academic Press, New York.

———. 1983. The relationships of mammals. Zoological Journal of the Linnean Society 77:353–384.

———. 1988a. Haemothermia or Archosauria? The interrelationships of mammals, birds and crocodiles. Zoological Journal of the Linnean Society 92:67–104.

———. 1988b. Interrelationships of the Synapsida. *In* M. J. Benton, ed. The phylogeny and classification of the tetrapods, Vol. 2. Mammals. Systematics Association Special Volume 35B:1–22. Clarendon, Oxford.

Kermack, D. M., F. Mussett, and H. W. Rigney. 1973. The lower jaw of *Morganucodon*. Zoological Journal of the Linnean Society 53:87–175.

King, G. M. 1988. Anomodontia. Pp. 1–174 *in* P. Wellnhofer, ed. Encyclopedia of paleoherpetology, Part 17C. Gustav Fischer, Stuttgart.

King, G. M., B. W. Oelofsen, and B. S. Rubidge. 1989. The evolution of the dicynodont feeding system. Zoological Journal of the Linnean Society 96:185–211.

Kitching, J. W. 1977. The distribution of the Karroo vertebrate fauna, Memoir 1. Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Johannesburg.

Laurin, M. 1993. Anatomy and relationships of *Haptodus garnettensis*, a Pennsylvanian synapsid from Kansas. Journal of Vertebrate Paleontology 13:200–229.

Laurin, M., and R. R. Reisz. 1990. *Tetraceratops* is the oldest known therapsid. Nature 345:249–250.

———. 1996. The osteology and relationships of *Tetraceratops insignis*, the oldest known therapsid. Journal of Vertebrate Paleontology 16:95–102.

Lucas, S. G., and A. B. Heckert. 2001. Olson's gap: a global hiatus in the record of Middle Permian tetrapods. Journal of Vertebrate Paleontology 21:75A.

Lucas, S. G., and Z. Luo. 1993. *Adelobasileus* from the Upper Triassic of West Texas: the oldest mammal. Journal of Vertebrate Paleontology 13:309–334.

Luo, Z. 1994. Sister-group relationships of mammals and transformations of diagnostic mammalian characters. Pp. 98–128 *in* N. C. Fraser and H.-D. Sues, eds. In the shadow of the dinosaurs: early Mesozoic tetrapods. Cambridge University Press, New York.

Luo, Z., and A. W. Crompton. 1994. Transformation of the quadrate (incus) through the transition from non-mammalian cynodonts to mammals. Journal of Vertebrate Paleontology 14:341–374.

Luo, Z., and X.-C. Wu. 1995. Correlations of vertebrate assemblage of the Lower Lufeng Formation, Yunnan, China. Pp. 83–88 *in* A. Sun and Y. Wang, eds. Sixth symposium of Mesozoic terrestrial ecosystems and biota, short papers. China Ocean Press, Beijing.

Luo, Z., Z. Kielan-Jaworoska, and R. L. Cifelli. 2002. In quest for a phylogeny of Mesozoic mammals. Acta Palaeontologica Polonica 47:1–78.

Maddison, W. P., and D. R. Maddison. 1992. MacClade 3.0.8a: interactive analysis of phylogeny and character evolution. Sinauer, Sunderland, Mass.

Martinez, R. N., and C. A. Forster. 1996. The skull of *Probelesodon sanjuanensis*, Sp. Nov., from the Late Triassic Ischigualasto Formation of Argentina. Journal of Vertebrate Paleontology 16:285–291.

Martinez, R. N., C. L. May, and C. A. Forster. 1996. A new carnivorous cynodont from the Ischigualasto Formation (Late Triassic, Argentina), with comments on eucynodont phylogeny. Journal of Vertebrate Paleontology 16:271–284.

McShea, D. W. 1994. Mechanisms of large-scale evolutionary trends. Evolution 48:1747–1763.

Modesto, S. P. 1995. The skull of the herbivorous synapsid *Edaphosaurus boanerges* from the Lower Permian of Texas. Palaeontology 38:213–239.

Modesto, S. P., B. S. Rubidge, and J. Welman. 1999. The most basal anomodont therapsid and the primacy of Gondwana in the evolution of the anomodonts. Proceedings of the Royal Society of London B 266:331–337.

Modesto, S., C. A. Sidor, B. S. Rubidge, and J. Welman. 2001. A second varanopseid skull from the Upper Permian of South Africa: implications for Late Permian 'pelycosaur' evolution. Lethaia 34:249–259.

Olson, E. C. 1944. The origin of mammals based on the cranial morphology of the therapsid suborders. Geological Society of America Special Paper 55:1–136.

———. 1959. The evolution of mammalian characters. Evolution 13:344–353.

———. 1962. Late Permian terrestrial vertebrates, U.S.A. and U.S.S.R. Transactions of the American Philosophical Society 52:1–224.

Parrington, F. R. 1955. On the cranial anatomy of some gorgonopsids and the synapsid middle ear. Proceedings of the Zoological Society of London 125:1–40.

Reichert, C. 1837. Über die Visceralbögen der Wirbeltiere im Allgemeinen und deren Metamorphosen bei den Vögeln und

Säugetieren. Müllers Archiv für Anatomie, Physiologie und wissenschaftliche Medizin 1837:120–222.

Reisz, R. R. 1986. Pelycosauria. Pp. 1–102 *in* P. Wellnhofer, ed. Encyclopedia of paleoherpetology, Part 17A. Gustav Fischer, Stuttgart.

———. 1988. Two small reptiles from a Late Pennsylvanian quarry near Hamilton, Kansas. Kansas Geological Survey Guidebook 6:189–194.

Reisz, R. R., and D. W. Dilkes. 1995. A small varanopseid (Synapsida: Eupelycosauria) from the uppermost Carboniferous (Upper Pennsylvanian) of Kansas. Journal of Vertebrate Paleontology 15:49A.

———. 2003. *Archaeovenator hamiltoni*, a new varanopid (Synapsida: Eupelycosauria) from the Upper Carboniferous of Kansas. Canadian Journal of Earth Sciences 40:667–668.

Reisz, R. R., and H.-D. Sues. 2000. Herbivory in Late Paleozoic and Triassic terrestrial vertebrates. Pp. 9–41 *in* H.-D. Sues, ed. Evolution of herbivory in terrestrial vertebrates. Cambridge University Press, New York.

Reisz, R. R., D. S. Berman, and D. Scott. 1992. The cranial anatomy and relationships of *Secodontosaurus*, an unusual mammal-like reptile (Synapsida: Sphenacodontidae) from the Early Permian of Texas. Zoological Journal of the Linnean Society 104:127–184.

Reisz, R. R., D. W. Dilkes, and D. S. Berman. 1998. Anatomy and relationships of *Elliotsmithia longiceps* Broom, a small synapsid (Eupelycosauria: Varanopseidae) from the Late Permian of South Africa. Journal of Vertebrate Paleontology 18:602–611.

Renaut, A. J. 2000. A re-evaluation of the cranial morphology and taxonomy of the Triassic dicynodont genus *Kannemeyeria*. Ph.D. dissertation. University of the Witwatersrand, Johannesburg.

Romer, A. S. 1965. Possible polyphylety of the vertebrate classes. Zoologische Jahrbuch 92:143–156.

———. 1969. The Chañares (Argentina) Triassic reptile fauna V. A new chiniquodontid cynodont, *Probelesodon lewisi*: cynodont ancestry. Breviora 333:1–24.

———. 1970. The Chañares (Argentina) Triassic reptile fauna VI. A chiniquodontid cynodont with an incipient squamosal-dentary jaw articulation. Breviora 344:1–18.

Romer, A. S., and L. I. Price. 1940. Review of the Pelycosauria. Geological Society of America Special Paper 28:1–538.

Rowe, T. 1986. Osteological diagnosis of Mammalia, L. 1758, and its relationship to extinct Synapsida. Ph.D. dissertation. University of California, Berkeley.

———. 1988. Definition, diagnosis, and the origin of Mammalia. Journal of Vertebrate Paleontology 8:241–264.

———. 1993. Phylogenetic systematics and the early history of mammals. Pp. 129–145 *in* F. S. Szalay, M. J. Novacek, and M. C. McKenna, eds. Mammal phylogeny: Mesozoic differentiation, multituberculates, monotremes, early therians, and marsupials. Springer, New York.

Rowe, T., and J. Gauthier. 1992. Ancestry, paleontology, and the definition of the name Mammalia. Systematic Biology 41:372–378.

Rubidge, B. S. 1991. A new primitive dinocephalian mammal-like reptile from the Permian of southern Africa. Palaeontology 34:547–559.

———. 1994. *Australosyodon*, the first primitive anteosaurid dinocephalian from the Upper Permian of Gondwana. Palaeontology 37:579–594.

———. 1995. Biostratigraphy of the Beaufort Group (Karoo Series), South Africa. Government Printer, Pretoria.

Rubidge, B. S., and J. A. Hopson. 1996. A primitive anomodont therapsid from the base of the Beaufort Group (Upper Permian) of South Africa. Zoological Journal of the Linnean Society 117:117–139.

Rubidge, B. S., and C. A. Sidor. 2001. Evolutionary patterns among Permo-Triassic therapsids. Annual Review of Ecology and Systematics 32:449–480.

Rubidge, B. S., and J. A. van den Heever. 1997. Morphology and systematic position of the dinocephalian *Styracocephalus platyrhinus*. Lethaia 30:157–168.

Rybczynski, N. 2000. Cranial anatomy and phylogenetic position of *Suminia getmanovi*, a basal anomodont (Amniota: Therapsida) from the Late Permian of Eastern Europe. Zoological Journal of the Linnean Society 130:329–373.

Sereno, P. C., A. L. Beck, D. B. Dutheil, H. C. E. Larsson, G. H. Lyon, B. Moussa, R. W. Sadleir, C. A. Sidor, D. J. Varricchio, G. P. Wilson, and J. A. Wilson. 1999. Cretaceous sauropods from the Sahara and the uneven rate of skeletal evolution among dinosaurs. Science 286:1342–1347.

Sidor, C. A. 2000. Evolutionary trends and relationships within the Synapsida. Ph.D. dissertation. University of Chicago, Chicago.

———. 2001. Simplification as a trend in synapsid cranial evolution. Evolution 55:1419–1442.

Sidor, C. A., and J. A. Hopson. 1998. Ghost lineages and ''mammalness'': assessing the temporal pattern of character acquisition in the Synapsida. Paleobiology 24:254–273.

Sidor, C. A., and R. M. H. Smith. In press. A new galesaurid (Therapsida: Cynodontia) from the Early Triassic of South Africa. Palaeontology.

Sigogneau, D. 1970. Révision systématique des gorgonopsiens Sud-Africains. Cahiers de Paléontologie, Paris.

Simpson, G. G. 1959. Mesozoic mammals and the polyphyletic origin of mammals. Evolution 13:405–414.

———. 1960. Diagnosis of the classes Reptilia and Mammalia. Evolution 14:388–392.

Sokal, R. R., and P. H. A. Sneath. 1963. Principles of numerical taxonomy. W. H. Freeman, San Francisco.

Sues, H.-D. 1985. The relationships of the Tritylodontidae (Synapsida). Zoological Journal of the Linnean Society 85:205–217.

Sun, A. 1984. Skull morphology of the tritylodont genus *Bienotheroides* of Sichuan. Scientia Sinica 27:970–984.

Tatarinov, L. P., and E. N. Matchenko. 1999. A find of an aberrant tritylodont (Reptilia, Cynodontia) in the Lower Cretaceous of the Kemerovo region. Paleontological Journal 33:422–428.

van den Heever, J. A. 1994. The cranial anatomy of the early Therocephalia (Amniota: Therapsida). Universiteit van Stellenbosch Annale 1994/1:1–59.

Wagner, P. J. 1996. Contrasting the underlying patterns of active trends in morphologic evolution. Evolution 50:990–1007.

———. 2000a. The quality of the fossil record and the accuracy of phylogenetic inferences about sampling and diversity. Systematic Biology 49:65–86.

———. 2000b. Rate heterogeneity in shell character evolution among lophospiroid gastropods. Paleobiology 27:290–310.

Watson, D. M. S., and A. S. Romer. 1956. A classification of therapsid reptiles. Bulletin of the Museum of Comparative Zoology 114:37–89.

Appendix 1

Higher-Level Relationships

Sidor and Hopson (1998) presented the most recent analysis of higher-level synapsid relationships, and their analysis was chosen as the baseline cladogram for this compilation. Not surprisingly, Sidor and Hopson's results largely conform to the topology previously put forward by Hopson and Barghusen (1986) and Hopson (1991b, 1994). Where they overlap, the Sidor and Hopson analysis corroborates the results of Reisz (1986) and Laurin (1993), with regard to the basal pelycosaur-grade taxa. The remainder of higher-level pelycosaur relationships was adopted from Reisz (1986). Higher cynodont relationships are discussed below.

Rowe (1986, 1988) and Gauthier et al. (1988) proposed a phylogenetic arrangement for synapsids that differs from that adopted here in terms of (1) the position of varanopseids relative to caseasaurs and ophiacodontids, (2) the position of anomodonts (dicynodonts in their terminology) relative to gorgonopsians, and (3) higher cynodont relationships. The position of varanopseids has since been resolved by Reisz et al. (1998), although Modesto et al. (2001) dispute the position of *Elliotsmithia* (a viewpoint upheld here). The position of Anomodontia within the therapsid tree has been surprisingly labile (Gauthier et al. 1988; King 1988; Rubidge and Sidor 2001). Indeed, the grouping that combines anomodonts and theriodonts (Neotherapsida sensu Hopson 1999) was supported by relatively few characters in Sidor and Hopson's (1998) analysis. Grine (1997) has demonstrated that at least one of the proposed anomodont sister-groupings, that with dinocephalians (Watson and Romer 1956; King 1988), is unsupported. I have chosen to maintain anomodonts in the position advocated by Sidor and Hopson (1998), but it is important to note that advancing them one clade rank (as proposed by Gauthier et al. 1988) has a negligible effect on the overall results presented in the text.

Nonmammalian cynodont systematics still lack consensus, but most phylogenetic hypotheses fall into one of three camps. The first supports the traditional view that tritylodontids are derived from a lineage of gomphodont cynodonts with transversely expanded cheek teeth, whereas mammals arose from a lineage with a persistently sectorial dentition (Crompton and Ellenberger 1957; Crompton 1972; Hopson and Kitching 1972, 2001; Sues 1985; Hopson 1991b). The second contends that most gomphodonts (i.e., diademodontids, trirachodontids, and traversodonts) form a clade, but that tritylodontids are distinct and more closely related to mammals (and possibly tritheledonts) (Kemp 1982, 1983). The final permutation completely dissolves the tooth-type dichotomy and intersperses gomphodont with non-gomphodont taxa as successive mammal outgroups (Rowe 1993). Battail (1991) groups gomphodonts and tritylodontids but suggests that mammals evolved from a *Thrinaxodon*-grade ancestor, a hypothesis unlike that any of the previous workers.

Hopson and Kitching (2001) have provided the most recent investigation of the higher cynodont problem. Their results support the traditional hypothesis and also have the benefit of the most extensive taxon sampling—an important factor in accurately reconstructing phylogenies (Huelsenbeck 1991; Wagner 2000a). Thus, it stands as the most current understanding of cynodont phylogeny, and I have used Hopson and Kitching's (2001) cladogram here. Placing tritylodontids as the sister taxon to mammals has little effect on the overall pattern of results.

Lower-Level Relationships

Less effort has been devoted to understanding lower- (i.e., genus-) level relationships within nonmammalian synapsids. Among pelycosaur-grade synapsids, I have followed the lower-level relationships put forward by Modesto et al. (2001), Berman et al. (1995), Modesto (1995), Laurin (1993), and Reisz et al. (1992) for varanopseids, ophiacodontids, edaphosaurids, *Haptodus*, and sphenacodontoids, respectively. ''Hamilton Form'' refers to KUVP 12483, a specimen described by Reisz (1988) as a small reptile, and then later by Reisz and Dilkes (1995, 2003) as the most primitive varanopseid. *Tetraceratops* was positioned between sphenacodontids and traditional therapsids (Laurin and Reisz 1996), although the poor preservation of the sole, holotypic specimen makes a confident acceptance of this placement problematic (Conrad and Sidor 2001).

Hopson and Barghusen (1986) were the first to propose that taxa such as *Biarmosuchus*, *Hipposaurus*, and *Ictidorhinus* were among the phylogenetically most primitive therapsids. They did not, however, attempt to resolve the relationships among these taxa, and no work has been published since. The cladistic topology used here is based on the results of Rubidge and Sidor (unpublished data).

I based dinocephalian interrelationships on the published analyses of Hopson and Barghusen (1986), Rubidge (1991, 1994), and Rubidge and van den Heever (1997). Although *Ulemosaurus*, *Criocephalus*, and *Moschops* have been proposed to form a clade more derived than *Tapinocaninus* (Rubidge 1991), their precise relationships have not yet been proposed in print. The topology for these tapinocephalids, depicted in Figure 4, is based on my unpublished cladistic analyses.

The discovery in recent years of new, primitive anomodonts has prompted several investigations into the early evolution of this clade (Rubidge and Hopson 1996; Modesto et al. 1999; Rybczynski 2000). Within anomodonts, dicynodont interrelationships have been examined by Cluver and King (1983), King (1988), and Angielczyk (2001). For the purpose of this analysis, I have used the basal anomodont topology of Modesto et al. (1999), which recognizes a clade of Russian venyukovioids (e.g., *Ulemica* + *Suminia*), but is otherwise similar to that of Rubidge and Hopson (1996) and, earlier, Hopson and Barghusen (1986). Among dicynodonts, most analyses have yielded fairly congruent results; conflicting opinions as to the position of *Diictodon*/*Robertia*, *Pristerodon*, and *Endothiodon* have been represented by an unresolved basal trichotomy in Figure 4.

Gorgonopsian interrelationships have yet to be examined within the cladistic paradigm. The topology used here is based on the evolutionary scheme put forth by Sigogneau (1970). Similarly, except for van den Heever's (1994) work on relatively primitive forms, knowledge of therocephalian systematics has been at a standstill since Hopson and Barghusen's (1986) initial treatment. The relationships used here therefore come directly from these two sources.

As discussed above, the cynodont relationships used here are based on the results of Hopson and Kitching's (2001) most recent analysis. However, several taxa included here were not included in Hopson's analysis. *Cynosaurus* and a new genus housed in the South African Museum (SAM-PK-K9954) are grouped with *Galesaurus* on the basis on their possession of galesaurid synapomorphies (Sidor and Smith in press). Tritylodontid interrelationships are based on the findings of Clark and Hopson (1985), with further resolution provided by Luo and Wu (1995).

Appendix 2

The following is a list of the characters and character states used in this analysis. Following the last character state for each character is a citation for previous uses of the character in the literature. An asterisk following a citation means that the character definition has been modified or that an additional character state(s) has been added. Citations are in the form: (author: character number), except for those of Hopson and Barghusen (1986), which are (author:table.clade.character number), and King (1988), which are (author:suite.character number). Abbreviations for authors are as follows: B, Berman et al. (1995); GKR, Gauthier et al. (1988); HB, Hopson and Barghusen (1986); K, King (1988); M, Modesto (1995); MRW, Modesto et al. (1999); R, Rowe (1988); SH, Sidor and Hopson (1998); S, Sidor (2001).

1. Dentary symphysis: unfused (0), fused (1) (HB:1.6.2; HB: 4.42.2; SH:81; MRW:33; S:25).
2. Ventral protuberance on the anterior portion of the dentary: absent (0), present, obscuring symphysis in lateral view (1).
3. Depth of anterior ramus of dentary: moderate to deep (0), extremely slender (1).
4. Shape of anterior portion of dentary: tapering continuation of posterior regions (0), dorsoventrally deepened compared with posterior portions (1), or beak shaped (2). (HB:2.21.1; SH:79*)
5. Inclination of the anterior portion of the dentary: nearly horizontal (0), tipped anterodorsally producing procumbency (1), or strongly recurved (2).
6. Boss on lateral surface of dentary (dentary shelf of King 1988): absent (0), present (1). (K:E.12; MRW:34)
7. Large boss positioned halfway along ventral margin of dentary: absent (0), present (1).
8. Posterodorsal edge of dentary thickened into laterally overhanging shelf: absent (0), present (1).
9. Pit along tooth row formed to receive upper canine: absent (0), present (1).
10. Occlusal surface has parallel ridges bounding median groove (longitudinal dentary groove or sulcus of Crompton and Hotton 1967): absent (0), present (1). (K:J.1*; K:C′.2*)
11. Angle between coronoid eminence/process to long axis of jaw: less than 70 degrees (0), greater than 80 degrees (1).
12. Dentary coronoid region: basically flat (0), convex eminence (1), forms distinct freestanding coronoid process (2). (HB: 1.7.1*; GKR:92*; SH:80*; B:61*)
13. Coronoid region dorsal extent: below middle of orbit (0), in upper half of orbit (1), extends above orbit (2). (GKR:97*; SH:86*)
14. Coronoid process extends posteriorly beyond level of jaw articulation: absent (0), present (1).
15. Dentary masseteric fossa: absent (0), present (1). (HB:1.6.7*; HB:1.11.1*; GKR:88; SH:82)
16. Dentary masseteric fossa extent: high on coronoid region (0), extends to lower border of dentary (1). (HB:4.38.1; SH: 83)
17. Dentary possesses a freestanding, posteriorly directed (angular) process along its posterior margin: absent (0), present but small (1), present and elongate (2). (GKR:89*)
18. Dentary articular process: absent (0), present as posterior eminence (1), present as a distinct process (2). (GKR:96*; SH:87*)
19. Dentary boomerang or banana shaped: absent (0), present (1). (HB:3.25.1)
20. Dentary—angular suture runs smoothly anteroventrally (0), or S-shaped (1).
21. Dentary tables: absent (0), present (1). (K:E.3*; K:L.1*; K: D′.3*)
22. Direction of angular process: posterior (0), ventral (1).
23. Splenial: present (0), absent (1). (S:26*)
24. Splenial symphysis: unfused (0), fused (1). (S:26*)
25. Mandibular symphysis: dentary and splenial (0), dentary only (1). (B:58)
26. Splenial appearance: visible near symphysis in lateral view (0), visible between dentary and angular in lateral view (1), or not visible in lateral view (2). (B:59*; SH:90*)
27. Splenial with triangular dorsal process in symphysial region: absent (0), present (1).
28. Splenial pinches out dentary anteriorly at symphysis: absent (0), present (1). (M:22*; B:59*)
29. Angular distinct (0), or at least partially fused to adjacent postdentary bones (1). (S:27*)
30. Ventral margin of angular: rounded (0), keeled (1). (GKR: 98; B:60)
31. Angular reflected lamina: absent (0), present (1). (HB:1.1.1; GKR:102; SH:95)
32. Angular reflected lamina shape: flat and platelike (0), or ringlike (1). (GKR:103*; SH:99*)
33. Angular reflected lamina posterior emargination: short (0), long with free dorsal margin (1), long but lacking free dorsal margin (2). (HB:1.2.5*; HB:1.8.9*; SH:96*)
34. Angular reflected lamina with pattern of radiating ridges and grooves: absent (0), present (1). (SH:98*)
35. Angular reflected lamina with near vertical ridge: absent (0), present (1). (HB:1.8.10)
36. Lateral surface of angular with a thickened region (boss) adjacent to dentary: absent (0), present (1). (HB:2.13.1)
37. Ventral margins of angular and dentary confluent (0) or angular offset dorsally from that of dentary (1). (HB:1.9.9*; GKR:93*; SH:84)
38. Reflected lamina of angular lies far anterior to jaw articulation: absent (0), present (1). (HB:1.8.8; SH:97*)
39. Posteroventral margin of lateral surface of angular supports large boss: absent (0), present (1).
40. Angular anterior ramus extends anteriorly to level of jaw symphysis: absent (0), present (1).
41. Surangular: present (0), absent (1). (S:28*)
42. Surangular distinct (0), or at least partially fused to adjacent postdentary bones (1). (S:28*)
43. Surangular abuts (0) or dorsally overrides (1) the dentary along dorsal margin of lower jaw.
44. Lateral surface of surangular with fossa for lateral slip of adductor mandibulae externus: absent (0), present (1).
45. Surangular vertical lamina lateral to articular: absent (0), or present (1). (MRW:37)
46. Surangular participation in craniomandibular joint: absent (0), present as articular recess or fossa (1), or as condylar process (2). (HB:4.42.1*)
47. Surangular position: exposed laterally (0), confined medially (1).
48. Articular distinct (0), or at least partially fused to prearticular (1). (S:30*)
49. Articular-prearticular complex at least partially fused to surangular: absent (0), present (1). (S:29*; S:30*)
50. Dorsolateral surface of articular forms lateral shelf: absent (0), present (1).
51. Articular bone with prominent posterolateral process (dorsal process of Parrington 1955), which contacts the posterior surface of the quadrate above the lateral condyle: absent (0), present (1). (HB:1.8.6)
52. Level of jaw articulation: set below dentary tooth row (0), roughly at level of dentary tooth row (1), or above dentary tooth row (2). (M:15*)
53. Shape of articular glenoid: elongate oblique troughs (0), screw-shaped hinge (1), elongate flat plate (2), elongate convex curve (3), non-screw-shaped hinge (4), longitudinal troughs (5). (HB:2.21.8*; SH:101*)

54. Articular surface of lower jaw slopes steeply posteroventrally: absent (0), present (1). (HB:1.6.3)
55. Articular glenoid expanded anteroposteriorly: absent (0), present (1). (HB:2.21.8)
56. Prearticular with (0), or without (1) lateral exposure posteriorly. (MRW:39)
57. Prearticular teeth: absent (0), present (1).
58. Anterior coronoid: present (0), absent (1). (HB:1.6.10*; K:A.4; GKR:100; SH:89; MRW:48; S:31*)
59. Anterior coronoid teeth: absent (0), present (1).
60. Posterior coronoid: present (0), absent (1). (S:32*)
61. Posterior coronoid exposed on lateral surface of lower jaw: absent (0), present (1).
62. Posterior coronoid dentition: absent (0), present (1).
63. Posterior coronoid mediolaterally thickened: absent (0), present (1). (SH:92)
64. Lateral mandibular fenestra: absent (0), present (1), present as a small foramen (2). (HB:1.6.4*; K:A.6*; GKR:87*, SH:64*; SH:94*; B:57*; MRW:36*)
65. Lateral mandibular fenestra bordered by dentary, angular, and surangular (0), or dentary and angular (1). (HB:1.6.4*; HB:3.24.2*; SH:64*)
66. Dentary-squamosal: not in contact (0), articulating (1) (HB: 4.51.1; GKR:91)
67. Position of postdentary bones: broadly exposed laterally (0), narrow and in medial groove (1). (SH:88*)
68. As indicated by wear facets, mandibular movement: primarily orthal (0), with medial component (1), with strong longitudinal component (2). (R:79*; K:E.6; MRW:40*)
69. Foramen present between prearticular, angular, and splenial on medial surface of lower jaw: absent (0), present (1), or present between angular and prearticular (2).
70. Number of dentary teeth: zero (0), one to ten (1), 11 to 20 (2), 21 to 30 (3), 31 or greater (4). (SH:112*)
71. Dentary tooth row: absent (0), single (1), double or multiple (2).
72. Dentary tooth row set at lateral margin of dentary (0), or more medially (1).
73. Terminal lower tooth: absent (0), present and subequal in size to remaining teeth/precanines (1), present and enlarged compared with remaining teeth/precanines (2). (HB:2.18.1*; HB:4.50.2*; SH:107*)
74. Position of anteriormost dentary tooth: terminal (0), nonterminal (1), absent (2).
75. Number of lower incisors: zero (0), one or two (1), three (2), four (3), five or greater (4), undefined owing to lack of lower caniniform (5). (SH:103*)
76. Lower canine: absent (0), incisiform/postcaniniform (1), present (2). (HB:1.6.6*; HB:2.17.2*)
77. Posteriormost dentary tooth: visible in lateral view (0), or obscured by dentary coronoid process (1).
78. Medial surface of lower jaw with large crushing plates: absent (0), present (1). (M:19*)
79. Tooth roots: undivided (0), divided (1). (HB:4.51.3; GKR: 118*; SH:117*)
80. Postcanine tooth implantation: subthecodont (0), thecodont (1). (SH:121)
81. Lower canine passes external to lateral border of maxilla: absent (0), present (1). (HB:2.15.2)
82. Lower postcanine tooth row (and/or incisors) passes medial to lower canine: absent (0), present (1). (HB:2.15.4)

Appendix 3 follows

Appendix 3

The following is the data matrix for the qualitative characters of lower jaw shape. Information regarding characters and character states is provided in Appendix 2. Taxa arranged as in Figure 4. ''?'' denotes missing data and ''n'' denotes that a character is inapplicable for that taxon. Electronic copies of this matrix are available upon request.

Taxon	1 1234567890	1111111112 1234567890	2222222223 1234567890
Eothyris parkeyi	0000000000	00000n0000	0n00000000
Casea broilii	0000000000	00000n0000	0n00000000
Casea rutena	0000000000	00000n0000	0n00000000
Cotylorhynchus romeri	0000000000	00000n0000	0n00000100
Ennatosaurus tecton	0000000000	00000n0000	0n00000100
Hamilton Form	0010000000	00000n0000	0n0012000?
Mesenosaurus romeri	0010000000	00000n0000	0n00020000
Elliotsmithia longiceps	?010000000	00000n000?	0n??????00
Aerosaurus wellesi	0010000000	00000n0000	0n00120000
Varanops brevirostris	0010000000	00000n0000	0n00000000
Varanodon agilis	0010000000	00000n0000	0n00000000
Varanosaurus acutirostris	0010000000	00000n0000	0n00120001
Ophiacodon spp.	0000000000	00000n0000	0n00020001
Ianthasaurus hardestii	0????00000	01000n0000	0n??????01
Edaphosaurus spp.	0000000000	01000n0000	0n00000101
Haptodus garnettensis	0000000000	01000n0000	0n00000001
Sphenacodon spp.	0001000000	01000n0000	0n00000001
Secodontosaurus obtusidens	0000000000	01000n0000	0n00100001
Dimetrodon spp.	0001000000	01000n0000	0n00000001
Tetraceratops insignis	0000000000	01000n0000	0n0000000?
Biarmosuchus tener	0001000000	01000n0000	0n00020001
Hipposaurus spp.	0001000100	01000n0100	0n00020001
Rubidgina augusticeps	0001000100	01000n0100	0n00020001
CGP 1/61	0001000100	01000n0001	0n00020001
Proburnetia viatkensis	0000001100	01000n0001	0n000200?1
Anteosaurus magnificus	0001000?00	01000n0000	0n00?20001
Titanophoneus potens	0001000000	01000n0000	0n00020001
Doliosauriscus yanshinovi	0001000000	01000n?001	0???????01
Australosyodon nyaphuli	0001000?00	01000n0?0?	0n00020001
Syodon efremovi	0001000000	01000n0000	0n00020001
Styracocephalus platyrhynchus	0001000?00	01000n0001	0n0011000?
Estemmenosuchus uralensis	0001000000	01000n0000	0n00000001
Estemmenosuchus mirabilis	0001011000	01000n0001	0n000??001
Jonkeria ingens	0001000000	01000n0001	0n00020001
Tapinocaninus pamelae	0000000000	01000n0001	0n00020001
Criocephalus vanderbyli	0000000000	01000n0001	0n00020001
Ulemosaurus svijagensis	0000000000	01000n0001	0n00020001
Moschops spp.	0000000000	01000n0001	0n00020001
Anomocephalus africanus	??00000000	0100100?00	0n?????00?
Patronomodon nyaphulii	??0??00000	00000n0000	0n0?00??01
Ulemica spp.	0100011010	0100100001	0n000n1001
	1		1
Suminia getmanovi	0000010000	0100100001	0n0002?001
Galeops whaitsi	0000000000	01000n0000	0n0002??01
Eodicynodon oosthuizeni	0002210001	01000n0001	1n01001101
Eodicynodon oelofseni	1002210000	01000n0000	0n010011?1
Pristerodon sp.	1002210001	01000n0001	0n01001101
Endothiodon uniseries	1002211001	0000100001	0n01001101
Diictodon spp.	1002210000	01000n0001	1n01001001
Robertia broomiana	1002210000	01000n0000	1n010????1
Myosaurus gracilis	1002210000	00000n0001	0n0?02?001
Emydops sp.	1002210001	00000n000?	0n010????1
Cistecephalus microrhinus	1002210001	01000n0000	0n01001101

Appendix 3. Extended.

3333333334 1234567890	4444444445 1234567890	5555555556 1234567890	6666666667 1234567890	7777777778 1234567890	88 12
0nnnn00n00	00000?00n0	0150010??0	1000n000?3	1010510000	nn
0nnnn00n00	00000000n0	005001???0	?000n000?2	1010510000	nn
0nnnn00n00	00000?00n0	00500100?0	??00n000??	101??10000	?n
0nnnn00n00	00100000n0	00500101n0	1000n00022	1010510000	nn
0nnnn00n00	00000000n0	0050011000	0000n00022	1010510000	nn
0nnnn00n00	0000000??0	01?0010??0	1000n000?4	1010510000	nn
0nnnn00n00	00100000n0	01500101n0	0000n00003	1010510000	nn
0nnnn00n00	00100?0??0	?1???1????	???0n000?2	1010510000	nn
0nnnn00n00	00100000n0	0150010000	1?00n00023	1010500000	nn
0nnnn00n00	00?0?00??0	0150010???	???0n000??	???????00?	?n
0nnnn00n00	00100000n0	0150010??0	1000n00003	1010510000	nn
0nnnn00n00	00100000n0	0150010??0	1001000024	1010510000	nn
0nnnn00n00	00100000n0	0150010000	1001000024	1010510000	nn
0nnnn00n00	00000000n0	0150010???	???0n000??	10????0000	?n
0nnnn00n00	00000000n0	0050111010	0100n00213	1010510100	0n
0nnnn00n00	00000000n0	0210010000	0100n00003	1010120000	0n
1000000000	00000000n0	0110000000	1000n00003	1010120000	00
1000000000	00100000n0	0210000000	1000n00004	1010510000	nn
1000000000	00000000n0	0010000000	1000n00003	1010120000	00
????00?10	00100000n0	020001????	???0n000?2	1010510000	nn
1011000000	0000?00??0	10100????0	0000n000?2	1010320000	00
1011000000	0000100??0	1010000???	???0n000?2	1010320000	00
1011000000	00001000n0	10100001n0	0000n000?2	1010220000	00
				3	
1011?00000	00?0?00??0	10100001n0	?000n000?2	1010?20000	00
10?1000000	00001?00n?	?0100?0???	???0n000??	1010?20000	00
101?010000	0??0??0???	?0????????	???0n000??	1020320000	00
1010010000	00101000n0	00100001n0	0??0n00012	1020320000	00
1???10??0	0010??0???	?????????0	0??0n000?2	1020320000	00
1010000000	00?0?000n0	00100?0??0	?000n000?2	1020220000	00
1010000000	00101000n0	00100101n0	0??0n00012	1020320000	00
????00?00	0000??0???	?0????0??0	0000n00??2	10?0320000	?0
1010000000	000100???	00?00????0	0??0n00023	1120320000	11
1010000000	00000?0???	?0100??1n?	???0n000?3	1120320000	11
1010000000	00001000n0	00100101n0	0000n00023	1120320001	11
1010000000	00001000n?	00?00?01n1	nnn0n000?2	1020320001	10
1010000000	00001000n0	00100001n1	nnn0n00022	1020??0001	n0
1010000000	00101000n0	00100101n1	nnn0n00012	1020510001	n0
1010000000	00001000n0	00100101n0	0000n000?2	1020510001	n0
????????0?	0001?000??	?0????????	???1?000?1	1010510?01	nn
101100010?	0??01000n0	00100001n0	?001100001	10???10001	nn
1011000000	00011000n1	00210101n0	0001100002	2120511000	nn
1011000000	00011000n0	00311001n0	0001100212	1120510000	nn
101??00100	00001000n0	00311001n1	nnn1000201	10n1510001	nn
1011000101	00001?0100	00311101n1	nnn10002?1	11n1510000	nn
101?000100	0??01?0??1	00311?0???	???1?002?1	11n1510000	nn
1011000100	0000000101	00311101n1	nnn1000201	11n1510000	nn
10110?0101	0010000101	??311001n1	nnn10002?1	11n1511000	nn
			2	2	
1011000101	01000001?1	00311101n1	nnn11002?0	0n0200n0nn	nn
101100010?	0?00??0??1	00311?????	???00002?1	11n1511000	nn
			1		
101?00010?	00000001?1	01311?01n1	nnn1?00200	0n0200n0nn	nn
101100010?	0??0??01?1	00311?????	???11002?1	11n1511000	nn
1011000101	0000000101	00311101n1	nnn1000200	0n0200n0nn	nn
			1		

Appendix 3. Continued.

	1	1111111112	2222222223
Taxon	1234567890	1234567890	1234567890
Cistecephaloides boonstrai	1002210001	01000n0000	0n0?0???01
Kingoria nowacki	1002210001	01000n0000	1n01001101
Oudenodon spp.	1002210001	01000n0001	1n00001101
Pelanomodon sp.	1002210001	01000n0001	1n01001101
Aulacephalodon spp.	1002210001	00000n000?	1n000?1101
Dicynodon spp.	1002210001	00000n0001	1n01001101
Lystrosaurus spp.	1002210001	00000n0000	1n01001101
Tetragonias njalilus	1002210001	00000n0001	1n01010001
Kannemeyeria spp.	1002210001	00000n0001	1n01001101
Placerias gigas	100221000?	00000n0000	1n01001101
Stahleckeria potens	100221000?	00000n0001	1n0100??01
Aelurosaurus felinus	0001000000	02000n0000	0n01000001
Arctognathus spp.	0001000000	02000n0000	0n00000001
Cyonosaurus spp.	0001000000	02000n0001	0n000?0001
Scylacops spp.	0001000?00	02000n000?	0n00000001
Lycaenops spp.	000100000?	02000n0000	0n01000001
Prorubidgea spp.	0001000000	02000n0000	0n00000001
Dinogorgon spp.	0001?0000?	02000n0000	0n000000?1
Rubidgea spp.	0001000000	02000n0000	0n00000001
Aloposaurus spp.	000100000?	02000n0000	0n01000001
Gorgonops spp.	000100000?	02000n0000	0n00000001
			2
Hofmeyria atavus	0000000000	02100n0010	0n00020001
Moschorhinus kitchingi	0001000000	02000n0000	0n00020001
Olivieria parringtoni	0001000000	02000n0000	0n00020001
Theriognathus spp.	0000000000	02000n0010	0n00020001
Ictidosuchoides spp.	0000000000	02100n0000	0n00020001
Viatkosuchus sumini	0000000000	02000n0000	0n000?0001
Bauria cynops	0000000000	02100n0000	0n00020001
Lycosuchus vandereti	0001000000	02000n0000	0n00000001
Glanosuchus macrops	0001000000	02000n0000	0n00020001
Ptomalestes avidus	0001000000	02000n0000	0n00020001
Dvinia prima	0000000000	0200100100	0n00020001
Procynosuchus delaharpeae	0000100000	0200100100	0n00000001
Cynosaurus suppostus	0001000000	02??110100	0n00020001
SAM-PK-K9954	0000000000	0200110100	0n00020001
Galesaurus planiceps	0000000000	0210110100	0n00020001
Thrinaxodon liorhinus	0001000000	0210110000	0n00020001
Cynognathus spp.	1000000000	0210110100	0n01020001
Diademodon spp.	1000000000	0210110100	0n0102000?
Trirachodon spp.	1000000000	0220111100	0001020001
Massetognathus spp.	1000000000	0221110200	0n01020001
Exaeretodon frenguelli	1000000000	0220112200	00011200?1
Tritylodon longaevus	0000100000	12?0110200	0n00020011
Oligokyphus spp.	0000100000	1220110200	0n000200??
Bienotherium elegans	0000100000	1220111200	0000020011
Kayentatherium wellesi	0000100000	1220111200	000?020001
Bocatherium mexicanum	0000110000	1220111200	00????00??
Bienotheroides wanhsienensis	0000100000	1220112200	000002000?
Lumkuia fuzzi	1000000000	0210110100	0n01020001
Ecteninion lunesis	100??0000?	??2111??00	0?01??00??
Probelesodon lewisi	1000000000	0220111200	0001020001
Probelesodon sanjuanensis	100??00000	0220112?00	00??????0?
Probainognathus jenseni	1000100000	0220110200	0n01020001
Pachygenelus monus	0000000000	0210110200	0n00020001
Sinoconodon spp.	0000000000	0210121200	011n1nnn??
Morganucodon spp.	0000100000	0210111200	011n1nnn01

Appendix 3. Extended.

3333333334	4444444445	5555555556	6666666667	7777777778	88
1234567890	1234567890	1234567890	1234567890	1234567890	12
101100010?	0100??0111	?0311101n1	nnn11002?0	0n0200n0nn	nn
1011000100	0110000111	00311?01n1	nnn0n00200	0n0200n0nn	nn
1011000101	0000010101	00311101n1	nnn1000200	0n0200n0nn	nn
101?000100	00000?0111	00311?01n1	nnn10002?0	0n0200n0nn	nn
101?000101	??????????	00311?01n1	nnn1?002?0	0n0200n0nn	nn
1011000101	00000001?1	00311101n1	nnn11002?0	0n0200n0nn	nn
1011000101	0000010101	00311101n1	nnn11002?0	0n0200n0nn	nn
1010000101	00000?0111	00311?01n1	nnn1000200	0n0200n0nn	nn
1011000101	0100010111	00311001n1	nnn1000200	0n0200n0nn	nn
1010000001	00000001?1	00311101n1	nnn1000200	0n0200n0nn	nn
101?000001	01000?0111	00311?01n1	nnn1?002?0	0n0200n0nn	nn
1021100100	0000??000?	?0100?01n0	0000n00001	1010320000	00
1021100100	00000?0100	10100001n0	0000n00011	1010320000	00
1021100100	0000000??0	?0100?01n?	???0n000??	1010320000	00
1021100100	0000000???	??????0???	???0n000??	101032?000	00
1021100100	00000?0000	?0???1????	0??0n000??	1010320000	00
1021100100	0000000??0	1010000???	???0n000??	???????0??	0?
1021100100	??00??010?	?????0????	???0n000??	???????0??	0?
1021100100	0000000100	?0?00101n0	0000n00011	1010320000	00
1021100100	0000?00???	??????0???	???0n000??	??????????	0?
1021100100	00000001??	1??00?0??0	0000n00011	1010?20000	00
1011001000	00001?0000	01100101n?	0??10000??	1010?20000	0?
1011001000	0000100001	00100101n0	00011000??	10?0???000	0?
1011001000	00001?0000	?0100101n?	0??10000?1	1010320000	00
1011001000	0000100000	00100001n0	0001100001	101022n00n	00
1011001000	000100???	02100001n?	0??10000?2	101032?000	0?
1011001000	00001?0??0	0010010???	???10000??	?????2?000	0?
1011001000	0?0???0???	01?00?0???	0??10000?2	1010220000	00
				3	
1011001???	0000??000?	??????0???	0??0n000?2	1010220000	00
1011001000	0000100000	01100001n0	0000n00002	1010220000	00
1011001000	0000100000	01100001n0	0000n000?2	1010220000	00
1???01100	0000100000	01100101n0	0002100002	1010420000	00
1?11?01100	0000100000	00100001n0	0002100002	1010320000	00
1011001100	00001?0??0	?110??0???	0??0n000??	1010220000	00
1011001?00	00001?0000	01?00?0???	???0n000?2	1010220000	??
1011001100	0000100000	01100101n0	0000n?0002	1010220000	00
1111001100	0000100000	01100101n0	0000n00002	1010220000	00
1111001100	0000020000	01100101n0	0000n01002	1010220000	00
1111001100	00000201?0	01100101n0	0000n01202	1010221001	00
1111001100	0000020100	02100101n0	0000n01002	1010221001	00
			2		
111??01100	0000021100	01200101n0	0000n01202	1110221001	00
111?001100	0000021100	02200101n0	00?0n01202	1120221001	00
1110001100	0100001110	02400101n0	0010n012?1	1120111011	nn
????01?00	0100001110	02400?01n?	???0n012?1	1120211011	nn
111??01100	0100001110	02400?01n0	0010n01201	1120111011	nn
1110001100	0100001110	02400101n0	0010n01201	1120111011	nn
????01?00	??????1???	?2????01n0	0010n?1201	1120111011	nn
111??01100	0100001110	0240?101n0	0010n01201	1120111011	nn
111?001100	0000000001	02?0010???	???0n01001	1010220000	00
????0????0	000002010?	00?00?????	???0n010??	???????0??	0?
1110001100	0000021101	02400101n0	0000n01002	1010220000	00
???001?00	000002011?	02?001????	???0n010??	???????0?0	0?
1110001100	0100021111	01400101n0	0000n01002	1010220000	00
1110001100	01000n1110	02400101n0	0010n11001	1110121000	00
??????1??0	??????????	?2400??1n0	0010n111?1	1010320001	00
1110001100	0000001100	02400101n0	0010n11102	1010320011	00

Appendix 4

The following table provides a summary of the results for the measurement-based analyses, the similarity to *Morganucodon* metric used in Figure 7, and the stratigraphic and phylogenetic data used elsewhere. Taxa are arranged as in Figure 4. Average ratios are provided where a taxon is represented by multiple specimens preserving two or more measurements. FA = First Appearance (in age ranks); LA = Last Appearance (in age ranks); CR = Clade Rank; PD = Patristic Distance from the root of the cladogram shown in Figure 4; D/J = ratio of distance to surangular suture to jaw length; V/J = ratio of distance to angular suture to jaw length; C/R = ratio of coronoid height to jaw length; Area = area of dentary relative to entire lower jaw area; DI = cumulative Dentary Index (average of the previous four ratios when each is z-transformed); S_{SM} = Simple matching coefficient for every taxon when the data in Appendix 3 are compared with the early mammal *Morganucodon*. The following geologic formations or biozones correspond to age rank values: 1 = Late Pennsylvanian (Stanton Formation); 2 = Moran, Cutler Abo, and Putnam Formations; 3 = Admiral and Belle Plains Formations; 4 = Clyde, Arroyo, Vale, Hennesey, and Choza Formations; 5 = San Angelo, Flower Pot, and Chickasha Formations; 6 = Mezen Assemblage; 7 = *Eodicynodon* Assemblage Zone, Middle Dinocephalian Complex; 8 = *Tapinocephalus* Assemblage Zone, Upper Dinocephalian Complex; 9 = *Pristerognathus* Assemblage Zone; 10 = *Tropidostoma* Assemblage Zone; 11 = *Cistecephalus* Assemblage Zone and Kotelnich Assemblage; 12 = *Dicynodon* Assemblage Zone and Sokolov Assemblage; 13 = *Lystrosaurus* Assemblage Zone; 14 = *Cynognathus* Subzone A; 15 = *Cynognathus* Subzone B + C, Manda and N'twere formations; 16 = Chañares Formation; 17 = Ischigualasto, Santa Maria, Los Rastros, and Chinle Formations; 18 = Lower Lufeng (dull purplish beds and dark red beds), Kayenta, La Boca, Upper Elliot, and Clarens Formations, and the Shazimiao Series. Electronic copies of this matrix are available upon request.

Taxon	FA	LA	CR	PD	D/J	V/J	C/J	Area	DI	S_{SM}
Eothyris parkeyi	3	3	1	2	0.736	0.418	0.08	0.382	-1.038	0.603
Casea broilii	4	4	1	3	0.618	0.365	0.106	0.544	-1.085	0.629
Casea rutena	4	4	1	4	0.757	0.385	0.199	0.509	-0.485	0.61
Cotylorhynchus romeri	4	5	1	5	0.507	0.359	0.083	0.471	-1.535	0.606
Ennatosaurus tecton	6	7	1	5	0.744	0.319	0.185	0.396	-0.839	0.606
Hamilton Form	1	1	2	3	0.713	0.428	0.054	0.354	-1.198	0.639
Mesenosaurus romeri	6	6	2	5	0.742	0.535	0.067	0.527	-0.65	0.606
Elliotsmithia longiceps	8	8	2	5	———	———	———	———	———	0.592
Aerosaurus wellesi	2	2	2	5	0.724	0.461	0.097	0.284	-1.086	0.569
Varanops brevirostris	4	4	2	6	0.796	0.393	———	0.443	———	0.604
Varanodon agilis	5	5	2	6	0.739	0.413	0.052	0.382	-1.127	0.585
Varanosaurus acutirostris	3	4	3	4	0.659	0.626	0.017	0.578	-0.771	0.585
Ophiacodon spp.	2	4	3	4	0.729	0.452	0.049	0.488	-0.936	0.576
Ianthasaurus hardestii	1	1	4	5	0.648	0.303	0.074	———	———	0.673
Edaphosaurus spp.	2	4	4	5	0.69	0.369	0.186	0.374	-0.911	0.567
Haptodus garnettensis	1	1	5	5	0.785	0.309	0.121	0.396	-0.96	0.657
Sphenacodon spp.	2	2	6	7	0.714	0.31	0.188	0.402	-0.907	0.616
Secodontosaurus obtusidens	3	4	6	8	0.635	0.447	0.085	0.463	-1.09	0.62
Dimetrodon spp.	2	5	6	8	0.701	0.441	0.213	0.446	-0.571	0.616
Tetraceratops insignis	4	4	7	7	0.603	0.411	0.124	0.444	-1.133	0.632
Biarmosuchus tener	6	8	8	9	0.811	0.538	0.132	0.578	-0.204	0.657
Hipposaurus sp.	8	9	8	10	0.849	0.521	0.218	0.492	-0.003	0.621
Rubidgina augusticeps	12	12	8	11	0.767	0.569	0.142	0.526	-0.301	0.611
CGP 1/61	9	9	8	12	———	———	———	———	———	0.606
Proburnetia viatkensis	11	11	8	12	0.779	0.558	0.206	———	———	0.576
Anteosaurus magnificus	8	8	9	13	0.794	0.478	———	———	———	0.608
Titanophoneus potens	8	8	9	12	0.738	0.515	0.193	0.626	-0.153	0.62
Doliosauriscus yanshinovi	8	8	9	13	———	———	———	———	———	0.653
Australosyodon nyaphuli	7	7	9	11	0.744	0.444	0.198	0.543	-0.368	0.641
Syodon efremovi	8	8	9	11	0.858	0.473	0.2	0.683	0.164	0.648

Appendix 4. Continued.

Taxon	FA	LA	CR	PD	D/J	V/J	C/J	Area	DI	S_{SM}
Styracocephalus platyrhynchus	8	8	9	11	0.809	0.653	—	0.572	—	0.667
Estemmenosuchus uralensis	7	7	9	13	0.81	0.455	0.227	0.534	-0.117	0.609
Estemmenosuchus mirabilis	7	7	9	13	—	—	0.199	0.604	—	0.548
Jonkeria ingens	8	8	9	13	0.752	0.45	0.163	0.608	-0.351	0.603
Tapinocaninus pamelae	7	7	9	14	0.805	0.513	0.222	0.588	0.035	0.652
Criocephalus vanderbyli	8	8	9	15	0.803	0.394	0.248	0.548	-0.151	0.627
Ulemosaurus svijagensis	8	8	9	15	0.749	0.552	0.254	0.597	0.083	0.609
Moschops capensis	8	8	9	15	0.792	0.522	0.307	0.531	0.2	0.648
Anomocephalus africanus	8	8	10	11	—	—	—	—	—	0.595
Patronomodon nyaphulii	7	7	10	12	—	—	—	0.533	—	0.6
Ulemica spp.	8	9	10	14	0.777	0.633	0.285	0.697	0.532	0.472
Suminia getmanovi	11	12	10	14	0.667	0.564	0.216	0.625	-0.166	0.514
Galeops whaitsi	8	8	10	14	0.626	0.532	0.168	0.508	-0.641	0.569
Eodicynodon oosthuizeni	7	7	10	15	0.59	0.389	0.308	0.493	-0.554	0.47
Eodicynodon oelofseni	7	7	10	15	0.548	0.481	0.217	0.558	-0.684	0.456
Pristerodon sp.	8	12	10	16	0.702	0.442	0.186	0.625	-0.386	0.5
Endothiodon uniseries	9	11	10	16	0.717	0.369	0.118	0.706	-0.567	0.415
Diictodon spp.	8	12	10	17	0.665	0.424	0.204	0.632	-0.436	0.444
Robertia broomiana	8	8	10	17	0.646	0.571	0.143	0.534	-0.566	0.429
Myosaurus gracilis	13	13	10	19	0.741	0.41	0.118	0.507	-0.735	0.492
Emydops sp.	10	12	10	20	0.61	0.425	0.181	0.58	-0.713	0.4
Cistecephalus microrhinus	10	11	10	21	0.569	0.429	0.303	0.536	-0.487	0.492
Cistecephaloides boonstrai	12	12	10	21	0.727	0.473	0.259	0.624	-0.048	0.433
Kingoria nowacki	11	12	10	18	0.657	0.399	0.157	0.592	-0.704	0.453
Oudenodon spp.	11	12	10	20	0.632	0.417	0.206	0.607	-0.557	0.446
Pelanomodon sp.	12	12	10	20	0.639	0.399	0.215	0.542	-0.639	0.443
Aulacephalodon spp.	11	12	10	19	0.632	0.491	0.147	0.542	-0.711	0.392
Dicynodon spp.	11	12	10	19	0.66	0.398	0.151	0.595	-0.713	0.444
Lystrosaurus spp.	13	13	10	20	0.676	0.324	0.19	0.575	-0.709	0.453
Tetragonias njalilus	15	15	10	21	0.682	0.514	0.216	0.561	-0.311	0.444
Kannemeyeria spp.	14	15	10	22	0.607	0.347	0.094	0.567	-1.144	0.4
Placerias gigas	17	17	10	23	0.641	0.304	0.125	0.536	-1.086	0.476
Stahleckeria potens	17	17	10	23	0.681	0.452	0.183	0.573	-0.504	0.4
Aelurosaurus felinus	8	8	11	13	0.829	0.596	0.224	0.647	0.326	0.652
Arctognathus spp.	11	11	11	12	0.755	0.511	0.251	0.595	0.015	0.644
Cyonosaurus spp.	10	12	11	12	0.732	0.581	0.222	0.517	-0.126	0.656
Scylacops spp.	11	12	11	12	0.733	0.592	0.233	—	—	0.655
Lycaenops spp.	10	12	11	13	0.778	0.543	0.209	0.646	0.068	0.656
Prorubidgea spp.	11	12	11	14	0.802	0.514	0.333	—	—	0.618
Dinogorgon spp.	11	12	11	15	0.677	0.455	—	0.631	—	0.605
Rubidgea spp.	11	12	11	15	0.769	0.437	0.231	0.637	-0.078	0.681
Aloposaurus spp.	11	12	11	12	0.73	0.425	—	—	—	0.622
Gorgonops spp.	8	11	11	12	0.693	0.578	—	—	—	0.652
Hofmeyria atavus	10	12	12	14	0.781	0.629	0.196	0.617	0.138	0.682
Moschorhinus kitchingi	12	13	12	16	0.847	0.593	—	0.701	—	0.642
Olivieria parringtoni	13	13	12	16	0.852	0.649	0.254	0.639	0.553	0.662
Theriognathus spp.	12	12	12	16	0.792	0.646	0.238	0.701	0.449	0.653
Ictidosuchoides spp.	9	12	12	15	0.789	0.644	0.202	0.605	0.183	0.708
Viatkosuchus sumini	11	11	12	15	0.782	0.608	0.211	0.647	0.196	0.649

Appendix 4. Continued.

Taxon	FA	LA	CR	PD	D/J	V/J	C/J	Area	DI	S_{SM}
Bauria cynops	14	15	12	16	0.709	0.694	0.22	0.752	0.355	0.7
Lycosuchus vandereti	8	8	12	13	0.838	0.644	—	—	—	0.684
Glanosuchus macrops	8	8	12	13	0.776	0.662	—	0.725	—	0.676
Ptomalestes avidus	8	8	12	13	0.711	0.66	0.265	0.67	0.32	0.671
Dvinia prima	12	12	13	13	0.836	0.673	0.204	0.774	0.6	0.718
Procynosuchus delaharpeae	12	12	14	14	0.8	0.672	0.222	0.685	0.438	0.726
Cynosaurus suppostus	12	12	15	16	0.851	0.648	0.233	0.833	0.771	0.705
SAM-PK-K9954	12	12	15	17	0.779	0.687	0.304	0.759	0.78	0.714
Galesaurus planiceps	13	13	15	17	0.817	0.735	0.285	0.785	0.93	0.757
Thrinaxodon liorhinus	13	13	16	16	0.863	0.736	0.27	0.82	1.045	0.747
Cynognathus spp.	14	15	17	18	0.933	0.806	0.274	0.953	1.539	0.76
Diademodon spp.	14	15	17	19	0.961	0.799	0.327	0.955	1.761	0.767
Trirachodon spp.	14	15	17	20	0.928	0.783	0.293	0.898	1.466	0.776
Massetognathus spp.	16	16	17	21	0.953	0.77	0.325	0.946	1.673	0.767
Exaeretodon frenguelli	17	17	17	22	0.945	0.673	0.352	0.928	1.549	0.795
Tritylodon longaevus	18	18	17	23	0.891	0.782	0.345	—	—	0.789
Oligokyphus spp.	18	18	17	24	—	—	—	—	—	0.746
Bienotherium elegans	18	18	17	25	0.958	0.819	0.317	0.988	1.806	0.775
Kayentatherium wellesi	18	18	17	26	—	—	—	0.973	—	0.797
Bocatherium mexicanum	18	18	17	27	—	—	0.405	—	—	0.776
Bienotheroides wanhsienensis	18	18	17	27	0.972	0.811	0.304	0.971	1.759	0.771
Lumkuia fuzzi	15	15	18	18	0.9	0.699	0.257	0.872	1.106	0.779
Ectenininon lunesis	17	17	19	20	0.945	0.849	—	—	—	0.75
Probelesodon lewisi	16	16	19	21	0.962	0.774	0.274	0.939	1.532	0.816
Probelesodon sanjuanensis	17	17	19	21	0.952	0.797	0.357	0.944	1.814	0.783
Probainognathus jenseni	16	16	20	20	0.961	0.746	0.345	0.938	1.702	0.787
Pachygenelus monus	18	18	21	21	0.987	0.75	0.253	0.953	1.505	0.824
Sinoconodon spp.	18	18	22	22	—	0.814	0.195	—	—	0.923
Morganucodon spp.	18	18	22	22	—	0.768	0.179	0.952	—	1.000

Appendix 5

This table provides the six raw measurements used for this study. Entries are arranged alphabetically by taxon name. The four linear measurements (1–4) and two areas (A_d and A_{pd}) are described in the text. All measurements are in mm and areas in mm². A literature reference under the specimen heading means that the measurements were taken from a reconstruction or specimen drawing in that cited work. The following institutional abbreviations are used: AM, Albany Museum, Grahamstown, South Africa; AMNH, American Museum of Natural History, New York; BMNH, The Natural History Museum, London; BP, Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Johannesburg; BSP, Bayerische Staatssammlung für Paläontologie und Historische Geologie, Munich; CGP, Council for Geosciences, Pretoria (formerly Geological Survey of South Africa); FMNH, Field Museum of Natural History, Chicago; GPIT, Institut und Museum für Geologie und Paläontologie, Tübingen; IGM, Instituto de Geología, Universidad Nacional Autónoma de México, Mexico City; IVPP, Institute for Vertebrate Palaeontology and Palaeoanthropology, Beijing; MB, Humboldt Museum für Naturkunde, Berlin; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; MNHN, Muséum National d'Histoire Naturelle, Paris; NM and NMQR National Museum, Bloemfontein; NMNH, National Museum of Natural History, Washington, D.C.; PIN, Paleontological Institute, Moscow; PVSJ, Museo de Ciencias Naturales, Universidad Nacional de San Juan, San Juan, Argentina; RC, Rubidge Collection, Graaff-Reinet, South Africa; ROZ, Collection of Roy Oosthuizen, now housed at the South African Museum; SAM, South African Museum, Cape Town; SGU, Saratov Geological Institute, Saratov, Russia; TM, Transvaal Museum, Pretoria; TSK, Oxford University Museum, Oxford; UCMP, University of California Museum of Paleontology, Berkeley; and UCMZ, Museum of Zoology, University of Cambridge, Cambridge, United Kingdom.

Taxon	Specimen	1	2	3	4	A_d	A_{ad}
Aelurosaurus felinus	BMNH R339	79.4	65.8	47.3	17.8	710	387
Aerosaurus wellesi	UCMP 40097	149	106.1	58.1	14.5	602	1521
Aerosaurus wellesi	UCMP 40096	84.6	62.3	45			
Aloposaurus ?tenuis	BP/1/709	107.3	78.3	52.7			
Aloposaurus tenuis	BP/1/789	111.2		40			
Anomocephalus africanus	BP/1/5582		10.6			4205	
Anteosaurus magnificus	Unpublished data	560		315			
Anteosaurus magnificus	SAM-PK-9329	561.1	445.4	221.1		38,164	
Arctognathus cf. *curvimola*	MCZ 4357	162.5		86.2	44.9		
Arctognathus sp.	UCMZ FRP91	282	213	138.4	63.4	8392	5713
Aulacephalodon moschops	UCMP 42699	377.5	238.6	165.8	69.1	19,536	14,022
Aulacephalodon sp.	USNM 24621	391		212	43.7	16,805	16,702
Australosyodon nyaphuli	NMQR 3152	261.5			58		
Australosyodon nyaphuli	Rubidge 1994	258.8	192.5	115	45		
Bauria cynops	AMNH 5622	102.8		79	20.3	1527	580
Bauria cynops	BP/1/1180	95.9		65.5	19.5	886	250
Bauria cynops	BP/1/3770	100.4		70.6	20.4		
Bauria cynops	USNM 23331	81.4	57.7	50.6	22.5		
Biarmosuchus tener	PIN 1758/2	143.9	109	77.4	22.2	1386	1014
Biarmosuchus tener	PIN 1758/7	176	138.4				
Biarmosuchus tener	PIN 1758/8	177.7	158		19.5		
Bienotherium yunnanense	Hopson 1965	114.7	109.1	93.6	31.8	3649	45
Bienotherium yunnanense	Unpublished data	112	108	92	40		
Bienotheroides wanhsienensis	Sun 1984	100.7	97.9	81.7	30.6	2832	84
Bocatherium mexicanum	IGM 3492	38			15.4		
Casea rutena	MNHN MCL2	81.9	62	31.5	16.3	688	663
Cistecephaloides boonstrai	SAM-PK-6243	43.3	31.5	20.5	11.2	252	152
Cistecephalus microrhinus	SAM-PK-K7852	28.7	16.3	14.3			
Cistecephalus microrhinus	SAM-PK-K6814	37.6	21.4	12.1	11.4	215	186
Cistecephalus sp.	USNM 22942	46		21.5			
Cotylorhynchus romeri	Unpublished data	151	76.5	54.2	12.5	1626	1827
Criocephalus sp.	SAM-PK-K319	330	265	130	82	12,440	10,256
Cynognathus merenskyi	BP/1/1181	284.2	278	227	76.1		
Cynognathus platyceps	BSP 1934 VIII 1	237	219	198.4	62.6		
Cynognathus platyceps	BSP 1934 VIII 2					12,661	505
Cynognathus sp.	UCMP 42749	318.6	289.5	261	95.6	23,495	1161
Cynognathus sp.	Kermack et al. 1973	330.4	304.6	254.1	87.6	24,312	1395
Cynosaurus suppostus	BP/1/4469	46.7	38.7	29.9		309	62
Cynosaurus kitchingi	TM 279	46	40.2	30.2	10.7		
Cyonosaurus longiceps	FMNH WM1515	134		85			
Cyonosaurus longiceps	BP/1/137	146.2	104.6	78.7			
Cyonosaurus longiceps	BP/1/2598	117.6	87.4	73.9		1067	758
Cyonosaurus rubidgei	BP/1/2867	139	102.6	72.5	30.9	1845	2268
Diademodon polyphagus	BMNH R2578	188.2		153.5		5356	
Diademodon rhodesiensis	BP/1/3639	188.8	185	162.8	62.3		

Appendix 5. Continued.

Taxon	Specimen	1	2	3	4	A_d	A_{ad}
Diademodon sp.	MB R1004		160			5791	270
Diademodon sp.	MCZ 7843	162.7	151.9	121.7	48.8		
Diademodon tetragonus	RC 112	112	112.4	90.2	41.6		
Diademodon tetragonus	USNM 22937	255.8	237	194.8	78.9		
Dicynodon lacerticeps	USNM 25183	78.9	53.6	31.1	14.2		
Dicynodon leoniceps	BP/1/349	363.4	226.8	161	43.9	19,154	13,019
Dicynodon leoniceps	MB R992	325	230	110	65		
Dicynodon leontops	AMNH 5582	232	152.4	77.4	40.4		
Dicynodon sp.	Cluver and King 1983	104.6	63.4	50.8	9	1400	946
Dicynodon trigonocephalus	TSK 14	147.9	101.4	58.3	21.4	3828	2621
Diictodon feliceps	RC 100	80	49	34.4	6		
Diictodon feliceps	CGP RS97	168	104.4	73	20		
Diictodon grimbeeki	AMNH 1991	70.9		29.4	16.6		
Diictodon grimbeeki	USNM 25157	90.3	54.1	38.6	18.2	1096	640
Diictodon grimbeeki	USNM 452057	86.6	67.4	34.9	25.4		
Diictodon grimbeeki	UCMP 42396	70.4	42.4	22.4	10.2	675	312
Diictodon sollasi	USNM 25217	72.3	45.3	34.2	14.3	432	310
Diictodon sp.	BMNH R11184	74.2	53.3	39.3	18.7		
Diictodon sp.	MB R1000	73	49.6	20.2	18	809	485
Diictodon sp.	UCMP 42837	68	39.8	29.1	10.2		
Diictodon sp.	UCMP 41757	100.6	62.8	35.4			
Diictodon sp.	UCMP 42049	80.8	50	35.9	11.1		
Diictodon sp.	USNM 22915	44.4	30.9	24.1	10.4		
Diictodon sp.	USNM 22939	75.2	50.9	31.9	16.5	876	545
Diictodon sp.	USNM 22949	79.7	56.2	38.1	17.6	836	382
Diictodon sp.	USNM 452060	84.8	65.4	41.2	21.5	1675	897
Diictodon sp.	SAM-PK-K6873	83.1	56.7	38.3	24.1		
Diictodon sp.	SAM-PK-K6929	96.3	64.5	41	25		
Diictodon sp.	SAM-PK-K7084	60.3	37.9	25.9	8.4		
Diictodon testudirostris	USNM 22982	62	42.6	14.4	10.7	505	302
Diictodon testudirostris	SAM-PK-10086	68.2	48.5	33.8	15.8	643	457
Dimetrodon limbatus	MCZ 2779	336.1	269	174	80.9	8887	13,082
Dimetrodon limbatus (m)	AMNH 4081	383.5	230.9	139.5	71.3	13,775	14,448
Dinogorgon quinquemolaris	RC 103	292		144			
Dinogorgon quinquemolaris	GPIT K16	377	255.1	157.3		17,736	10,367
Dvinia prima	Unpublished data	86.3	70.9	57.8	17	823	240
Dvinia prima	PIN 2005/2469	83.3	70.8	56.4	17.5		
Ecteninion lunensis	Martinez et al. 1996	91.3	86.3	77.5			
Edaphosaurus boanerges	Modesto 1995	123	88	47	22	1087	2078
Edaphosaurus pogonias	AMNH 4009	160.6	110	45.8	20.6		
Edaphosaurus pogonias	Romer and Price 1940	164	105.9	56.9	23.4	1699	2955
Edaphosaurus sp.	AMNH 21326	154			20.3		
Edaphosaurus sp.	MCZ 3417	138.7	106.9	64.5	39.8	2233	3085
Edaphosaurus sp.	USNM 299844	140.7	88.9	51.2	34.8	1593	2738
Emydops arctatus	BMNH R1690	40.5		21.3			
Emydops sp.	AMNH 8209	35.9	21.9	11.6	6.5		
Endothiodon uniseries	AMNH 5334	256.2	194.2	93.3	28.2	11,668	4833
Endothiodon uniseries	BMNH R4044	206	141.7			7072	3050
Endothiodon uniseries	AMNH 5612	278	200.7	91.9	34.7	12,250	4979
Endothiodon whaitsi	AMNH 5565	393.8	276.5	162.2	47.3		
Ennatosaurus tecton	PIN 1580/16	146.1	103.7	51.5	35.4		
Ennatosaurus tecton	PIN 1580/14	163.8	135.8	51.3	21	2871	4685
Ennatosaurus tecton	PIN 1580/24	95.2	65.9	38.2		549	781
Ennatosaurus tecton	PIN 1580/17	165.7		34.4			
Eodicynodon oelofseni	NMQR 2913	51.6	28.3	24.8	11.2	373	296
Eodicynodon oostuizeni	NMQR 2991	82	49.5	27.2	20.2	682	717
Eodicynodon oostuizeni	NMQR 2911	64.9	37.4	29	24	631	633
Eothyris parkeyi	MCZ 1161	55.3	40.7	23.1	4.4	145	235
Estemmenosuchus mirabilis	PIN 1758/6	281.6			56	7984	5230
Estemmenosuchus uralensis	PIN 1758/4	460	385	190	115	21,148	18,436
Estemmenosuchus uralensis	PIN 1758/327	415	325	206	85		
Exaeretodon freguelli	Bonaparte 1962	284	240	192			
Exaeretodon freguelli	MCZ 4493	197.4	188	132	49.8		
Exaeretodon freguelli	MCZ 4469	184	163.6	133.1			

Appendix 5. Continued.

Taxon	Specimen	1	2	3	4	A_d	A_{ad}
Galeops whaitsi	Brinkman 1981	42.3	26.5	22.5	7.1	283	274
Galesaurus planiceps	BP/1/4714	65.2		46.4	17.4		
Galesaurus planiceps	BP/1/5064	89.8	70.3	65.5	21.2	1015	313
Galesaurus planiceps	CGP 1/74	88.6			29		
Galesaurus planiceps	NMQR 860	99.1	81.6	68.8	24.9		
Galesaurus planiceps	NMQR 1451	74		56.2			
Galesaurus planiceps	NMQR 3340	86.8	73.1	63.2	31.3	1490	333
Galesaurus planiceps	SAM-PK-K9956	60.2	49.4	42.6	16.2	435	127
Galesaurus planiceps	TM 83	86.7		70.6			
Glanosuchus macrops	van den Heever 1994	221.1	171.6	146.3		4867	1849
Gorgonops torvus	BP/1/4089	155.8	107.9	85.3			
Gorgonops whaitsi	BP/1/1426	285.7		173.9			
Gorgonopsid indet sp.	SAM-PK-6417	113.1	93.9	75.7	18	1691	541
Hamilton form	KUVP 12483	31.5	22.5	15	1.6		
Hamilton form	KUVP 12483	33.4	23.8	12.7	1.9	28	51
Haptodus garnettensis	ROM 43602	94.6	71.1	26.4	10.2		
Haptodus garnettensis	ROM 30099	100.9	81	31.4			
Haptodus garnettensis	Laurin 1993	102.1	81.6	34.4	13.7	566	865
Hipposaurus boonstrai	SAM-PK-8950	137	119.1	73.4	38.5	1974	1623
Hipposaurus boonstrai	SAM-PK-9081	193.7	168.2	87.8	39.6	3602	3743
Hipposaurus sp.	CGP 1/66	173.3	140.3	99.6	29	2215	2867
Hofmeyeria avatus	TM 254	79.3	61.4	47.4	17.2		
Hofmeyeria avatus	BP/1/4404	52.8	41.6	34.9	9.2	387	240
Ianthasaurus hardestii	Unpublished data	61.1	39.6	18.5	4.5		
Ictidosuchoides intermedius	BP/1/218	89.8	75	60.6	21.3		
Ictidosuchoides longiceps	USNM 336444	79.9	65	60	16.9		
Ictidosuchoides longiceps	RC 646	70.5	54.5	42	10		
Ictidosuchoides sp.	GPIT K70	115.7	92	74.5	27.3		
Ictidosuchoides sp.	SAM-PK-K6731	84.5	57	45.5		546	524
Ictidosuchoides sp.	SAM-PK-K8659	92.5	77.8	60.1	15.3	608	262
Ictidosuchoides sp.	SAM-PK-K6886	130.1	102.5	84.7	28.5		
Jonkeria augusticeps	AMNH 5633	545.3	396.3	265.7	57.4	30,810	21,186
Jonkeria sp.	SAM-PK-12030	508	395	210	112.6	34,377	20,792
Kannemeyeria simocephalus	UCMP 38371	301.7	181.4	112.1	23.3	9912	9204
Kannemeyeria simocephalus	Renaut 2000	374.7	220.5	130.5	35.6	18,328	14,393
Kannemeyeria sp.	BMNH R3602	303.9	193.1	95.6	43.6	10,912	8609
Kannemeyeria vanhoepeni	UCMP 42916	299.4	181	106	17.6	12,029	7106
Kayentatherium wellesi	MCZ 8812		208	168.9	82.1	13,067	367
Kingoria nowacki	UCMZ T747	99.4	63.2	40.6	18	1237	943
Kingoria nowacki	Cluver and King 1983	102.6	67.5	43.6	11.4	1154	751
Kingoria nowacki	UCMZ T748	95.4	68.8	37.2	17.3		
Kingoria nowacki	UCMZ T746	100.6	61.6	37.5	15.6	1272	836
Lumkuia fuzzi	BP/1/2669	33.9	30.5	23.7	8.7	197	29
Lycaenops angusticeps	RC 60	247.2		126.9			
Lycaenops angusticeps	AMNH 5537	250.8	193.1	143.2	49.6	7590	3010
Lycaenops minor	BP/1/209	135.3	113.7	74.9			
Lycaenops ornatus	BP/1/881	201	158.3	107.1	44.2	4984	3327
Lycaenops ornatus	BP/1/2470	151	107.8	81.9		2235	1356
Lycosuchid sp.	van den Heever 1994	185.6	155.6	119.6		5004	
Lystrosaurus latirostris	AMNH 5600	127.8	90.3	63.5	24.7	2941	2000
Lystrosaurus declivis	NM C403	87.9	52.5	43.7	14.2	1113	969
Lystrosaurus murrayi	MB R2880	81.7	55.5	30.1	14.2		
Lystrosaurus murrayi	BP/1/269	83.9	56	15.2	16.7		
Lystrosaurus murrayi	BP/1/3908	73	51.1	22.3	12		
Lystrosaurus murrayi	BP/1/4798	75.4	53.8	24.7	10.3		
Lystrosaurus murrayi	MB R2881	80.7	51.9	17	20.7		
Lystrosaurus murrayi	NM C150	82.4	52.1	19.8	16.9		
Lystrosaurus murrayi	NM C6457	89.8	63.4	25.3	22.1	1251	821
Lystrosaurus murrayi	NMQR 3300	65.8	52.6	25.4	14.8		
Lystrosaurus murrayi	NMQR 3239	97	62.9	27.8	21.5	1059	695
Lystrosaurus sp.	UCMP 31359	118.3	82.3	48.2	21.7		
Lystrosaurus sp.	UCMP 42870	87	52.3	19.9	8.8	948	808
Massetognathus sp.	BP/1/4245	77.2	76.9	61.4	25.6		

Appendix 5. Continued.

Taxon	Specimen	1	2	3	4	A_d	A_{ad}
Massetognathus pascuali	BMNH R8430	121.8	119.8	94.9	42.3		
Massetognathus pascuali	MCZ 3800	111.6	102.2	85.9	43.7	2566	100
Massetognathus pascuali	MCZ 4258	70.5	68	55	16.5	792	62
Massetognathus pascuali	MCZ 4214	65.5	60.6	53.8	18.6	837	
Massetognathus pascuali	MCZ 3999	116.1	110.1	83.7	36.3		
Massetognathus teruggii	MCZ 3807	103.9	98.6	79.2	30.1	1893	101
Massetognathus teruggii	MCZ 3812	129.8	122.5	97.7	47.9		
Massetognathus teruggii	MCZ 4047	117.6		88	42.8		
Massetognathus sp.	PVL 3671		116.3	101.7	47.9	3262	
Mesenosaurus romeri	PIN 158/1		37.6	27.8		139	101
Mesenosaurus romeri	PIN 4541/22	51.4		27.5			
Mesenosaurus romeri	SGU 104v/1558		47.9	28		154	171
Morganucodon sp.	Kermack 1973	19		14.6	3.4	40	2
Moschops capensis	AMNH 5550	243.1	189.1	113.1	59.3	7567	8400
Moschops capensis	AMNH 5553	250.7	192.1	133.8	94	9528	9466
Moschops whaitsi	AMNH 5602	268	217.4	146	81.6	11,234	6958
Moschorhinus sp.	NMQR 3351	215.9	182.9	128		7685	3283
New galesaurid sp.	SAM-PK-K9954	76.9	59.9	52.8	23.4	724	230
Olivieria parringtoni	NMQR 62	78.4	70.6	48.2	20.3	613	331
Olivieria sp.	BP/1/3849	85.5	72.7	54	28.8	631	359
Olivieria sp.	Unpublished data	84.2	67.9	59	14	515	303
Ophiacodon retroversus	MCZ 1203	475.9	328.2	153.3	30	11,300	13,694
Ophiacodon sp.	USNM 487096					3394	3778
Ophiacodon sp.	USNM 487098	282.1	229.9	217.2	10		
Ophiacodon uniformis	Romer and Price 1940	272	185.6	72.1	13.3	3709	3190
Oudenodon halli	BMNH R4067	166.1	109.1	60	48.5		
Oudenodon sp.	SAM-PK-3414	98.9	69.5	58.8	31.2		
Oudenodon sp.	SAM 6045	86.2	51.4	29.7	11.9	765	648
Oudenodon sp.	TSK 67	102.8	66.7	38.7	19.2	1420	892
Oudenodon sp.	TSK 104	106.8	65.7	40.2	22.7		
Oudenodon sp.	USNM 22814	250.6	143.7	96.8	42.9		
Oudenodon sp.	USNM 24626	213	130.6	89.1	36.5	6072	3584
Oudenodon sp.	USNM 24922	271	173	99.3	62.9	10,408	6119
Oudenodon sp.	USNM 335338	82	52.6	31.9	13.4	1062	645
Oudenodon sp.	USNM 452032	110.6	69.9	62.1	19.8		
Pachygenelus monus	Unpublished data	63.9	63.1	47.5	11.3	605	30
Pachygenelus sp.	BP/1/4761	36.2		27.4	11.9		
Patranomodon nyaphulii	NMQR 3000				9.6	217	190
Pelanomodon sp.	UCMZ T981	118.4	80.8	43.9	31.3	1918	1639
Pelanomodon sp.	GPIT K114	191	113.9	81.7	31.6		
Pelanomodon sp.	GPIT K14					4545	3797
Placerias gigas	UCMP 32405	302	193.5	91.8	37.6	11,822	10,242
Pristerodon raniceps	BMNH R1650	69.9	50.7	31.1	9.2	614	347
Pristerodon sp.	MB R985	61.4	46.2	24	10.8	361	205
Pristerodon sp.	SAM-PK-10153	49.7	33.2	20.3	8	402	271
Pristerodon sp.	SAM-PK-10161	64.3	42.6	31.6	13.5		
Pristerodon sp.	SAM-PK-10322	41.2	31	15.2			
Pristerodon sp.	SAM-PK-K1658	48.3	34.3	28.6	10.2		
Pristerodon sp.	USNM 23580	39	25.2	15.6	8.9		
Probainognathus jenseni	MCZ 4069	62.6	60.2	47.5			
Probainognathus jenseni	MCZ 4096					747	71
Probainognathus jenseni	MCZ 4274	61.5	58	45.4	25.3	938	65
Probainognathus jenseni	MCZ 4276	61	60	45.1	19.6	708	42
Probainognathus jenseni	MCZ 4293	60.5	57.3	43.3	17.9	746	50
Probainognathus jenseni	Romer 1970	72.7	70.4	56.5	25.5	1148	48
Probelesodon lewisi	BMNH R8429	126.8	120.3	103.9	37.6	3125	157
Probelesodon lewisi	Romer 1969	98	95.5	71.4	24.6	1694	137
Probelesodon sanjuanensis	PVSJ 411	67	63.8	53.4	23.9	1014	60
Proburnetia viatkensis	PIN 2416/1	150.9	117.6	84.2	31.1		
Procynosuchus cf. *delaharpeae*	MCZ 8967	76.1	59.6	50.4			
Procynosuchus delaharpeae	BP/1/226	76.2	59.9	52.5	20.5		
Procynosuchus delaharpeae	BP/1/591	72.2	59.4	48.1	15.8	485	255
Procynosuchus delaharpeae	BP/1/2600	76.7		53.9	15.3		
Procynosuchus delaharpeae	BP/1/3748	121.4		85.5			

Appendix 5. Continued.

Taxon	Specimen	1	2	3	4	A_d	A_{ad}
Procynosuchus delaharpeae	RC 87	56	43.5	34	16		
Procynosuchus delaharpeae	RC 92	65	49	36			
Procynosuchus delaharpeae	SAM-PK-K338	72.2	58	51.8	14.1		
Procynosuchus delaharpeae	TSK 34	82.4	69.1	58.4	15.4	734	293
Procynosuchus sp.	MCZ 8968	76.7	63.8	54.7	15.3		
Prorubidgea sp.	BMNH R9750	260		155			
Prorubidgea alticeps	BP/1/813	193.6		93.4			
Prorubidgea alticeps	BP/1/1566	225	181	109	74.9		
Prorubidgea robusta	BP/1/2190	139.4	111.4	78.5			
Prorubidgea maccabei	RC 34	262.2		116.9			
Ptomalestes avidus	SAM-PK-11942	240.6	171.1	158.9	63.7	6608	3255
Robertia broomiana	SAM-PK-11885	41.3	25.7	23.6	5.4		
Robertia sp.	USNM 410241	52.4	35.1		8.1		
Rubidgea atrox	RC 13	392.5		181.6			
Rubidgea platyrhina	BP/1/803	360	277	148	83	19,310	11,021
Rubidgina sp.	BP/1/3924	102.9	83.2	58.6	13.9	828	570
Rubidgina sp.	CGP 1/67	121	87.8	68.8	18.1	1035	1216
Scylacops capensis	UCMZ T356	118.5	86.9	70.1	27.6		
Secodontosaurus obtusidens	MCZ 1124	268.2	170.4	120	22.8	2934	3404
Sinoconodon sp.	IVPP 4727	44		34.4	8.1	268	
Sinoconodon sp.	IVPP 8688	46		38.9	9.5	341	
Sphenacodon ferox	UCMP 83459	238.4		69.3	39.5	4119	5925
Sphenacodon ferox	UCMP 34219	238.3	171	85.9		5136	6715
Sphenacodon ferox	UCMP 34226	200.7	142.7	56.2	42.1	2711	4738
Stahleckeria potens	GPIT 1	380	245	180	65	24,638	18,852
Stahleckeria potens	GPIT 2	206.8	148.3	88.8	40.3	6250	4567
Styracocephalus platyrhynchus	SAM-PK-8936	262.3	212.1	171.2			
Suminia getmanovi	Rybczynski 2000	46	30	26.6	10.5	255	153
Suminia getmanovi	PIN 2212/10	40.2	27.4	22.1	8.2		
Syodon efremovi	PIN 157/2	213	182.7	100.8	42.6	5004	2325
Tapinocaninus pamelae	ROZ K95	353.4	299.9	185.6	71.4		
Tapinocaninus pamelae	NMQR 2986	353.1	278.1	184.4	75.6		
Tapinocaninus pamelae	NMQR 2987	346.8	270	170.1	86.7		
Tetraceratops insignis	AMNH 4526	90.1	54.3	37	11.2	656	822
Tetragonias njalilus	UCMZ T753	169.6	118.2	93.5	34.6	4912	3915
Tetragonias njalilus	GPIT 292	136.4	91.1	64.9	31	2462	1887
Theriognathus sp.	AMNH 8226	140.8	110.8	90.5	23.2		
Theriognathus sp.	BP/1/512	111.9	83	79.1	32.7		
Theriognathus sp.	BP/1/747	116.8	95.7	70.2			
Theriognathus sp.	BP/1/844	135.4	110.3	89.2	36.8	2810	1026
Theriognathus sp.	BP/1/182	55.5	44.9	33	12.6		
Theriognathus sp.	NMQR 3375	112.3	87.8	75.2	26.3	1542	762
Thrinaxodon liorhinus	BMNH R511	68.7	59.6	48.6	19.6	726	129
Thrinaxodon liorhinus	BMNH R511a	67.9	61.2	52.2			
Thrinaxodon liorhinus	BMNH R3731	59.5	51.7	45.9	11.9		
Thrinaxodon liorhinus	BMNH R5480	65.5	53.6	46.7	16.9	575	134
Thrinaxodon liorhinus	BP/1/4263	62.2	55.9	45.9	16.5		
Thrinaxodon liorhinus	BP/1/4280	53.8	44.4	36.5	14.3		
Thrinaxodon liorhinus	BSP 1934 VIII 506	51.8	43.3	38.7	16.3		
Thrinaxodon liorhinus	FMNH UR156	56.3	51.5	45			
Thrinaxodon liorhinus	MCZ 4282	60.8	53.6	43.6	16.3		
Thrinaxodon liorhinus	MCZ K377	67.5	58.9	49.5	21.9		
Thrinaxodon liorhinus	MCZ 2179	51.1		35.5			
Thrinaxodon liorhinus	MCZ 2184	66.1		52.9			
Thrinaxodon liorhinus	MCZ 2226	61.5	51.8	46.3			
Thrinaxodon liorhinus	MCZ uncat.	75.1	63.2	52.7	18.9		
Thrinaxodon liorhinus	SAM-PK-K1461	70.9	63.8	55.2	24.2	904	118
Thrinaxodon liorhinus	TM 80a	60.5	50.5	42.9	15	523	116
Thrinaxodon liorhinus	TM 80b	45	39.5	32.5	13.3		
Thrinaxodon liorhinus	UCMP 40466	123.3	108.4	91.2	25	499	129
Thrinaxodon liorhinus	UCMP 42866	57.8	48.3	39.9	14.1	441	123
Thrinaxodon liorhinus	UCMZ T815	58.1	48.2	43.4	16.2	401	98
Titanophoneus potens	PIN 157/1	374.9	276.6	193	72.5	13,398	8016

Appendix 5. Continued.

Taxon	Specimen	1	2	3	4	A_d	A_{ad}
Trirachodon berryi	BP/1/4658	85	82.1	66	24.6	1519	152
Trirachodon berryi	MCZ 8896	80.7	74.3	61.8	27.2		
Trirachodon sp.	unpublished data	54.5	49.9	42.2	15.9	513	57
Trirachodon sp.	NMQR 3256	71.2	65	59.4	24.9		
Trirachodon sp.	AM 461	76.7	74.9	60.2	21		
Trirachodon sp.	BP/1/4535	40.9	36.6	30	7.3		
Trirachodon sp.	BP/1/5362	97.4		79.4	35.8	1845	155
Trirachodon sp.	BP uncat.	69.8		53.9	19		
Trirachodon sp.	SAM-PK-11481	59.2	53.9	46.9	16.2	575	92
Tritylodon longaevus	BP/1/4778	110	98	86	38		
Tritylodon longaevus	BP/1/5288		116.6	94.4	37	3650	
Tritylodon longaevus	SAM-PK-K1411		84.3	70.5	28	2067	
Ulemica invisa	PIN 157/5	127.5	97.1	74.9	41	2992	1187
Ulemica prima	PIN 157/1112	145.3	115.2	98.7	36.2	3949	1883
Ulemosaurus svijagensis	Efremov 1940	298.8	202.5	164.8	58.1	12,757	9003
Ulemosaurus svijagensis	PIN 2207/2	335	275		105	18,749	12,111
Varanodon agilis	FMNH UR986	163.7	120.9	67.6	8.5	618	1000
Varanops brevirostris	Romer and Price 1940	134.2	106.8	52.8		675	847
Varanosaurus acutirostris	Berman et al. 1995	156.2	110.3	94.9	6.4	1241	905
Varanosaurus acutirostris	BSP 1901 XV 20	150	103.8				
Varanosaurus acutirostris	FMNH PR1760	123	78	81	2.2		
Viatkosuchus sumini	PIN 2213/13	140.5	109.9	85.4	29.6	1912	1042