

## SIMPLIFICATION AS A TREND IN SYNAPSID CRANIAL EVOLUTION

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**Abstract.**—The prevalence and meaning of morphological trends in the fossil record have undergone renewed scrutiny in recent years. Studies have typically focused on trends in body size evolution, which have yielded conflicting results, and have only rarely addressed the question as to whether other morphological characteristics show persistent directionality over long time scales. I investigated reduction in number of skull and lower jaw bones (through loss or fusion) over approximately 150 million years of premammalian synapsid history. The results of a new skull simplification metric (SSM), which is defined as a function of the number of distinct elements, show that pronounced simplification is evident on both temporal (i.e., stratigraphic) and phylogenetic scales. Postcranial evolution exhibits a similar pattern. Skull size, in contrast, bears little relationship with the number of distinct skull bones present.

Synapsid skulls carried close to their observed maximum number of elements for most of the Late Carboniferous and Early Permian. The SSM decreased in the Late Permian but, coincident with the radiation of early therapsids, the range of observed SSM values widened during this interval. From derived nonmammalian cynodonts in the Early Triassic through the earliest mammals in the Early Jurassic, both the minimum and maximum SSM decreased. Data from three representative modern mammals (platypus, opossum, and human) suggest that this trend continues through the Cenozoic.

In a phylogenetic context, the number of skull elements present in a taxon shows a significant negative relationship with the number of branching events passed from the root of the tree; more deeply embedded taxa have smaller SSM scores. This relationship holds for various synapsid subgroups as well. Although commonly ascribed to the effects of long-term selection, evolutionary trends can alternatively reflect an underlying intrinsic bias in morphological change. In the case of synapsid skull bones (and those of some other tetrapods lineages), the rare production of novel, or neomorphic, elements may have contributed to the observed trend toward skeletal simplification.

**Key words.**—Evolutionary trends, macroevolution, mammal-like reptile, neomorphy, Synapsida, Williston's law.

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The transition from life in an aquatic medium to one on dry land resulted in profound changes that affected all aspects of the vertebrate skull and postcranial skeleton (Ahlberg and Milner 1994). One of the most conspicuous differences between aquatic and terrestrial vertebrates lies in the organization of the skull; fish (i.e., nontetrapod vertebrate) skulls are typically composed of numerous loosely connected elements, whereas those of extant tetrapods (i.e., amphibians, reptiles, birds, and mammals) tend to be more rigidly constructed with fewer elements (de Beer 1937; Romer 1956). Although this is undoubtedly an oversimplification of a much more complicated pattern, an inverse relationship between skull complexity (in terms of the number of distinct elements) and terrestriality has been considered a prominent feature of vertebrate evolution (Gregory et al. 1935). Even among wholly terrestrial lineages far removed from their aquatic ancestry, however, increasing solidification of the skull appears to be common (e.g., Trueb and Cloutier 1991). In this paper, I provide quantitative data to document patterns of cranial element evolution in the synapsid (mammal and mammal-like reptile) fossil record. These data demonstrate that a significant bias in favor of bone loss exists on both temporal and phylogenetic scales.

### *Historical Background and Study Taxa*

Although the loss or fusion of skull elements characterizes other modern amniote lineages (e.g., snakes, birds; Rieppel 1993; Sereno 1997), the synapsid fossil record arguably provides the best sequence of morphological changes en route to a major living vertebrate group, the mammals (Crompton and Jenkins 1973; Kemp 1982). Indeed, fossil synapsids were

a major source of data for Williston (1914) and Gregory's (1927, 1929) classic proposal that the loss or fusion of skull elements, as opposed to their addition or subdivision, was "the normal course of skull evolution in vertebrates" (Gregory 1927, p. 268). Gregory interpreted the loss of skull bones to result in a *more* complex skull because the remaining elements showed a greater degree of differentiation ("anisomerism," in his terminology).

In a series of papers, Gregory (1927, 1929; Gregory et al. 1935) traced the evolution of the human skull through a series of structural grades that he took as exemplifying the stages through which the ancestral line leading to humans must have passed. Since his work, decades of systematic attention on fossil taxa have produced a more precise (and hopefully more accurate) understanding of the synapsid family tree (reviewed by Rubidge and Sidor 2001).

The fossil record of nonmammalian synapsids spans over 100 million years (Hopson 1994). Precladistic taxonomies recognized a series of paraphyletic grades that successively approached the mammalian condition. Because early amniotes were indiscriminately termed "reptiles," regardless of whether they were more closely allied with the mammalian or reptile lineages (e.g., Carroll 1982), the transition from basal synapsids to mammals was termed the "reptile-to-mammal" transition and the fossil synapsid taxa, the "mammal-like reptiles" (e.g., Crompton and Jenkins 1973).

**Study taxa.**—Nontherapsid synapsids (Fig. 1, 2A), or "pelycosaur" of traditional usage, are predominantly known from Pennsylvanian to Lower Permian (~310–270 million years ago) strata of North America, although several species survive into the beginning of the Upper Permian elsewhere (Reisz 1986; Reisz et al. 1998). Beyond the elongate dorsal

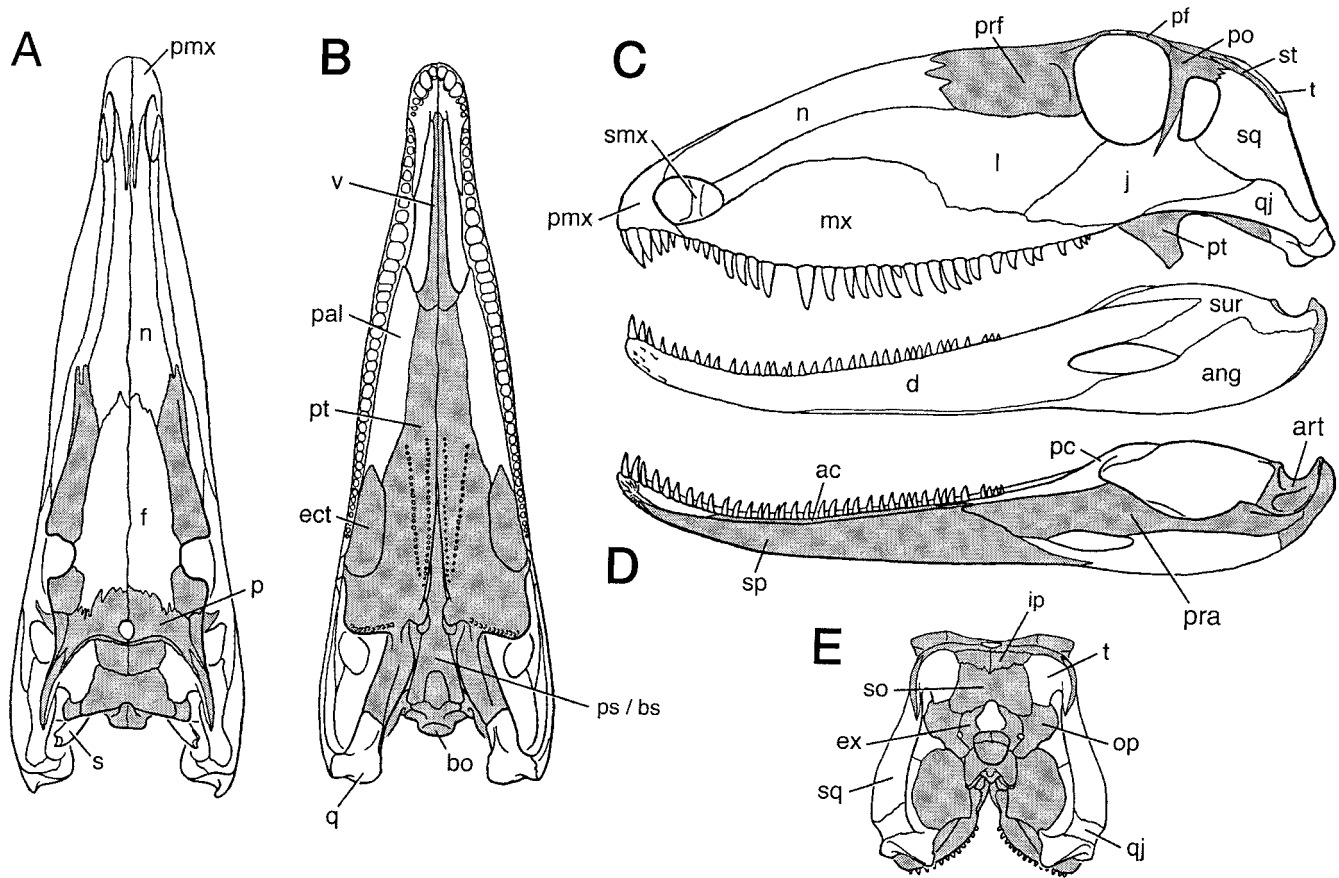


FIG. 1. Skull and lower jaw of a representative early synapsid, *Ophiacodon*, in (A) dorsal; (B) ventral; (C) lateral; (D) medial (lower jaw only); and (E) posterior views. Shaded bones are those that are fused to an adjacent element or are lost in the early mammal, *Morganucodon* (see Table 1; Fig. 2H). Reconstructions are modified from those of Romer and Price (1940). Anatomical abbreviations are given in Table 1.

sails present in some genera (e.g., *Dimetrodon* and *Edaphosaurus*), these earliest synapsids are morphologically conservative and tend to retain the primitive complement of amniote skull bones.

Noncynodont therapsids (e.g., biarmosuchians, dinocephalians, anomodonts, gorgonopsids, and therocephalians; Fig. 2B–F) taxonomically dominated the terrestrial vertebrate fauna of Late Permian times (~270–250 million years ago), although only anomodonts and therocephalians survived the mass extinction at the end of the Permian and persisted until Middle and Late Triassic times, respectively (Kemp 1982; Rubidge 1995). Noncynodont therapsids span a large range of morphologies and presumed ecologies, with several groups independently acquiring mammal-like features such as: (1) a complete secondary palate (Mendrez 1975; King 1988); (2) precise crown-to-crown occlusion between the upper and lower toothrows (Hopson and Barghusen 1986); (3) the mammalian phalangeal formula (Hopson 1995); and (4) the loss of several primitive skull roofing elements (i.e., postfrontal, ectopterygoid; Sidor and Hopson 1998).

Cynodonts (Fig. 2G) first appear in the latest Late Permian and include the mammals as their extant subgroup. Many of the morphological hallmarks of mammals (e.g., differentiated dentition and jaw adductor musculature, enlarged epipterygoid) first appear as apomorphies in the premammalian cy-

nodonts. Although there is still substantial disagreement regarding the phylogenetic relationships among the advanced cynodont clades (cf. Kemp 1982; Hopson and Barghusen 1986; Rowe 1988; Hopson 1991), mammalian monophyly is well supported (Hopson and Crompton 1969). When compared to those of their Paleozoic and Triassic antecedents, the skulls of even the earliest mammals (Mammaliaformes sensu Rowe 1988, 1993; Fig. 1H) are remarkably small and show a marked reduction in the number of distinct skull elements (Kermack et al. 1981; Crompton and Luo 1993).

The rich fossil record of nonmammalian synapsids documents with remarkable detail the gradual acquisition of mammalian features (Sidor and Hopson 1998; Rubidge and Sidor 2001). Major changes that occurred within the mammalian stem-lineage include: (1) sprawling to upright posture and locomotion; (2) transformation from one bony middle ear element (stapes) to three (malleus, incus, stapes); and, perhaps most significantly (3) ectothermic to endothermic physiology. At one time or another, each of the aforementioned evolutionary changes has been considered to be the result of prolonged selective pressure (Olson 1959; Simpson 1959; Hopson 1973). Persistent directed selection posits testable predictions about the distribution of different morphologies through time (i.e., evolutionary trends; Gould 1988; McShea 1994). Here, I examine the loss of cranial bones in this light.

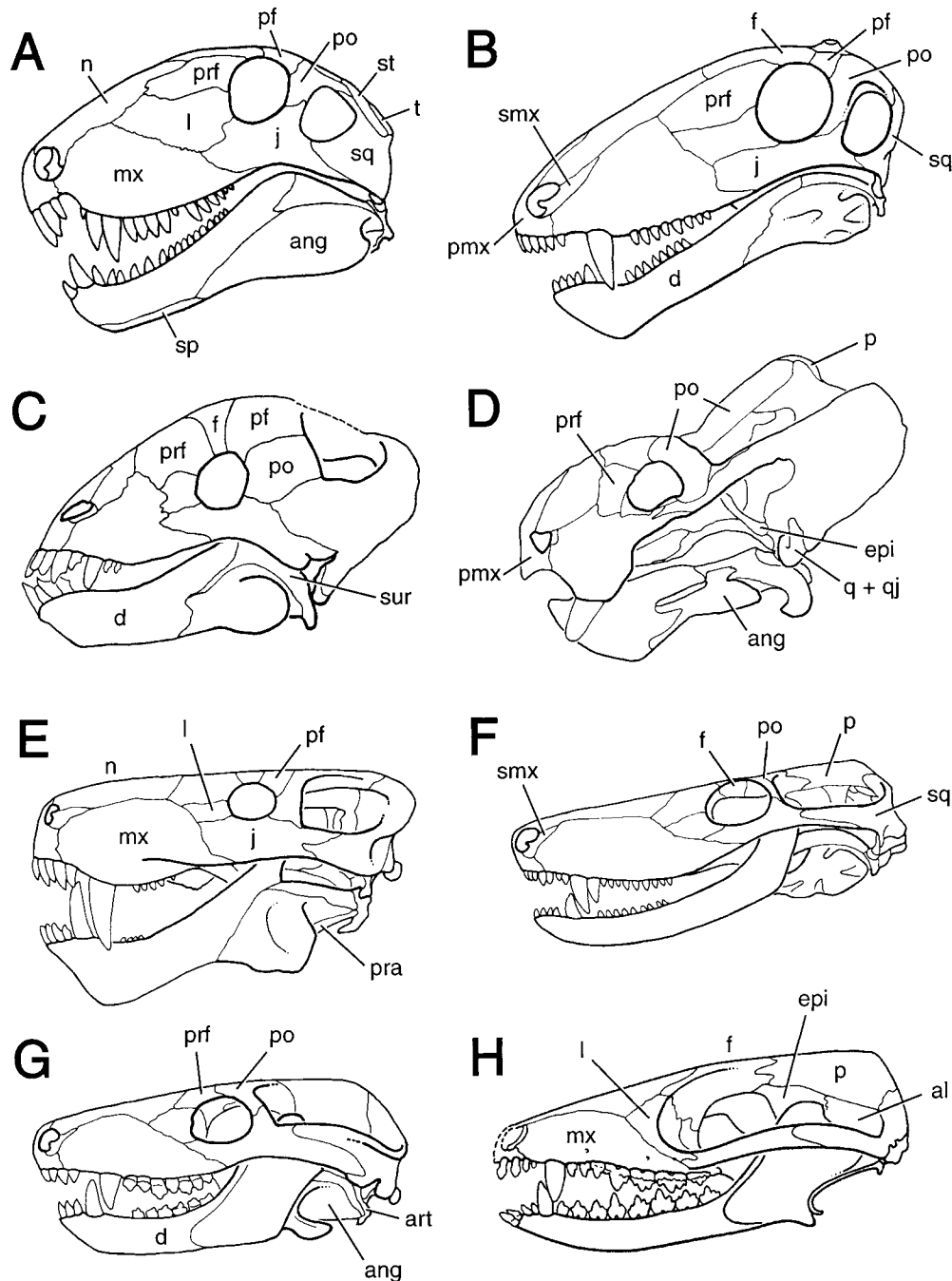


FIG. 2. Skulls of representative synapsids in lateral view: (A) the Early Permian pelycosaur-grade sphenacodontid, *Dimetrodon*; (B) the Late Permian biarmosuchian, *Biarmosuchus*; (C) the Late Permian tapinocephalid dinocephalian, *Tapinocepalus*; (D) the Middle Triassic dinocephalian, *Ictidosuchoidea*; (E) the Late Permian gorgonopsid, *Leontocephalus*; (F) the Late Permian therocephalian, *Ictidosuchoidea*; (G) the Early Triassic basal cynodont, *Thrinaxodon*; (H) the Early Jurassic mammal, *Morganucodon*. Skulls not to scale. Anatomical abbreviations given in Table 1. Reconstructions modified from those of Hopson (1994) and Rubidge and Sidor (2001).

## MATERIALS AND METHODS

### Data Collection

Fossil taxa were selected to maximize both the taxonomic range and stratigraphic sampling density of the study and range from the phylogenetically most primitive synapsids (caseosaurs) to some of the earliest traditionally defined mammals (e.g., *Morganucodon*). In total, this study includes 21

nontherapsid synapsids, six noneutherapsid therapsids, 11 dinocephalians (including four anteosaurians and seven tapinocephalians, *sensu* Hopson and Barghusen 1986), 24 anomodonts, 13 gorgonopsians, 17 therocephalians, eight primitive cynodonts, 13 cynognathians (including six tritylodontids), and 13 probainognathians (including two Early Jurassic and three Recent mammals). For each fossil taxon, I collected data on the stratigraphic range, inferred phylogenetic posi-

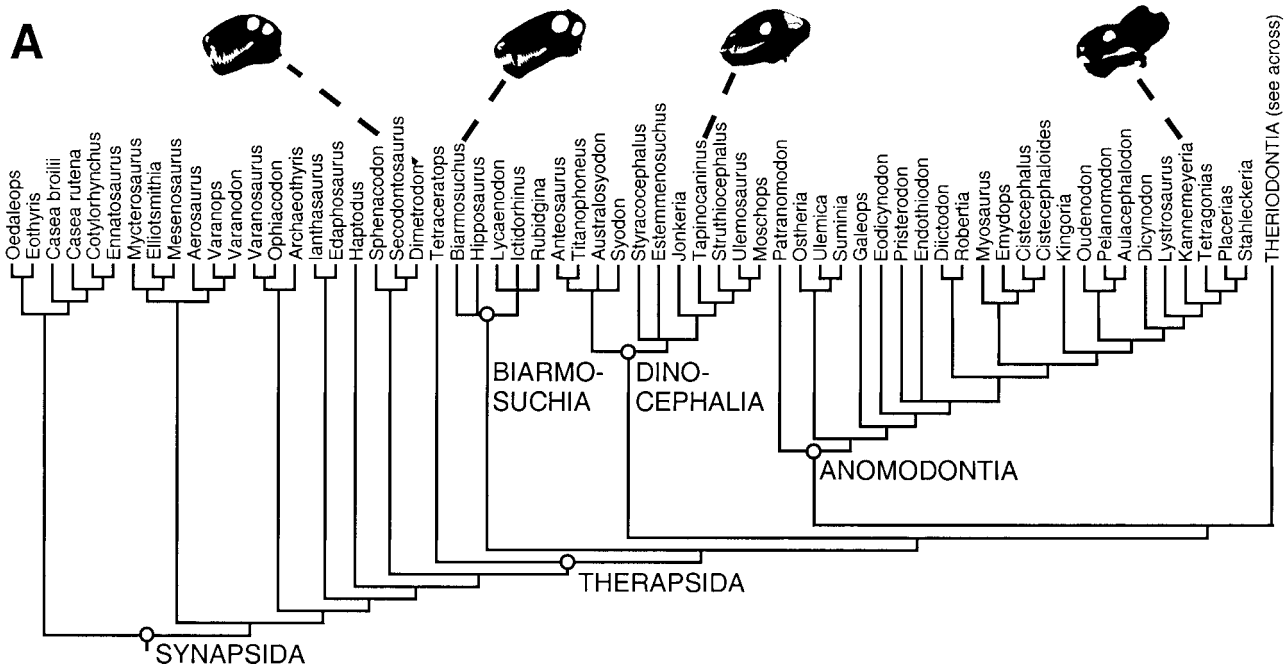


FIG. 3. Cladogram depicting the relationships of the synapsid taxa used in this analysis. Skull icons correspond to the synapsid taxa in Figure 2. In (B), bold numbers indicate the following clades: (1) Cynognathia; (2) Tritylodontidae; (3) Probainognathia; and (4) Mammalia (Mammaliaformes of Rowe 1988). Higher-level topology based on Rubidge and Sidor (2001). Lower-level relationships were taken from the following sources: caseasaurs (Sidor 1996); varanopseids (Reisz et al. 1998; Modesto et al. 2001); ophiacodontids (Berman et al. 1995); edaphosaurids (Modesto 1995); sphenacodonts (Reisz et al. 1992a; Laurin 1993); *Tetraceratops* (Laurin and Reisz 1996); biarmosuchians (Hopson and Barghusen 1986; C. A. Sidor and B. S. Rubidge, unpubl. data); dinocephalians (Hopson and Barghusen 1986; Rubidge 1991, 1994; Rubidge and van den Heever 1997); anomodonts (King 1988; Modesto et al. 1999); gorgonopsids (Sigogneau 1970); therocephalians (Hopson and Barghusen 1986; van den Heever 1994); primitive cynodonts (Hopson 1994); cynognathians (Clark and Hopson 1985; Sues 1985; Hopson 1994); probainognathians (Hopson 1994; Luo 1994); mammals (Luo 1994). "New galesaurid" refers to a new genus housed in collections of the South African Museum, Cape Town (SAM-PK-K9954). "Probelesodon-lew." refers to *Probelesodon lewisi* (Romer 1969) and "Probelesodon-san." refers to *P. sanjuanensis* (Martinez and Forster 1996). BP/1/2669 refers to a new probainognathian (Hopson and Kitching 2001).

tion, average skull size, and number of discrete or fused cranial bones. These data are presented in Appendices 1 and 2. Representatives of the three major groups of modern mammals (i.e., monotremes, marsupials, and placentals) were also studied for comparative purposes.

I studied the majority of fossil taxa included in this investigation at the following institutions: American Museum of Natural History, New York; Field Museum of Natural History, Chicago; Museum of Comparative Zoology, Harvard University, Cambridge, MA; 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; 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. I used descriptions from the literature only when the original fossil material had been lost or was otherwise unavailable for study.

Stratigraphic data consisted of each taxon's first and last

appearance in the fossil record. Initially these endpoints were recorded at the finest scale of temporal resolution available (generally from locality information in museum records) but were subsequently binned into 24 age ranks (AR; Gauthier et al. 1988; Norell and Novacek 1992) for the purpose of analysis. Where gaps in the stratigraphic range of a taxon were present (i.e., the taxon was inferred to be present in a particular interval although not actually recorded in those beds because of its occurrence above and below the interval), these missing intervals were also included in that taxon's stratigraphic duration. Ghost lineages (Norell 1993), however, were not used to extend observed taxon ranges. Although a ghost lineage can imply a taxon's presence before its first observed appearance, it does not provide information concerning the taxon's morphology (without assuming stasis). Contrasting the number of skull bones with stratigraphic position allows the examination of whether there is a geologically persistent trend in synapsid skull simplification.

I gathered cladistic topologies from the literature and combined them to create an ensemble cladogram of synapsid relationships (see Fig. 3 and its legend). Each taxon's phylogenetic position was then quantified as either its clade rank (CR; Gauthier et al. 1988; Norell and Novacek 1992) or as the number of branching points passed from the root of the cladogram (i.e., patristic distance, PD). CR represents the

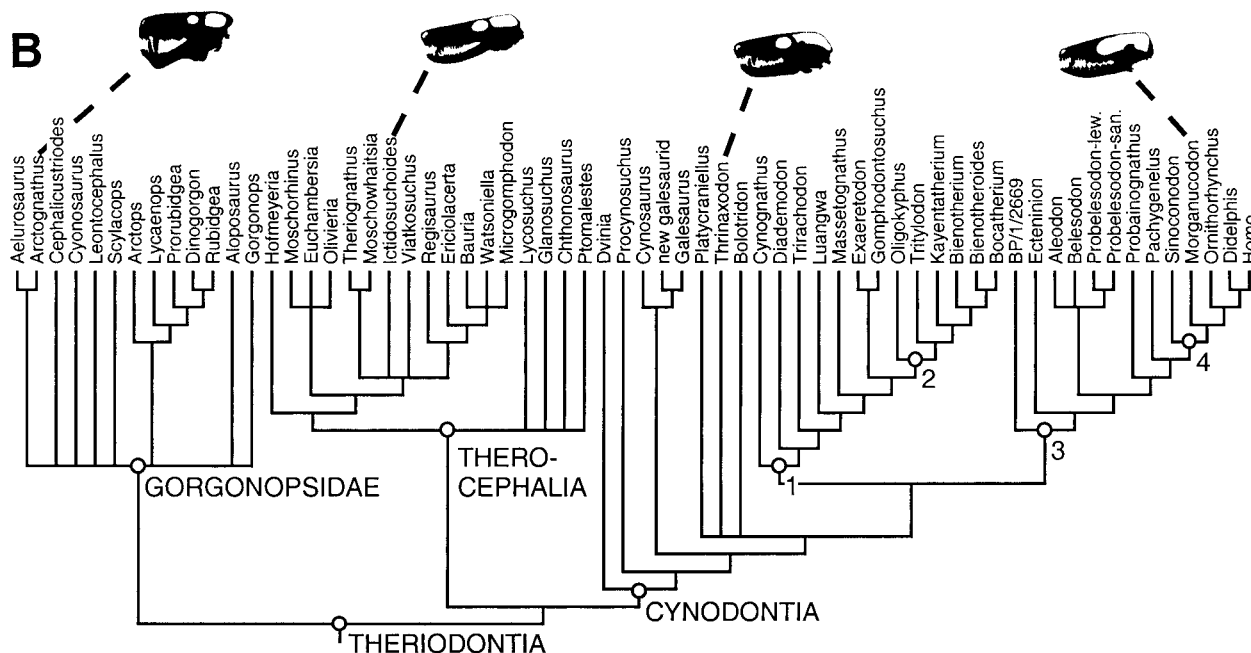


FIG. 3. Continued.

number of branch points passed along the primary spine of the cladogram (here, between Synapsida and Theria), but does not take into account branching events once a clade has diverged from the primary axis. For example, all caseasaur genera (the basalmost clade in Fig. 3) have a CR of one. The values from CR and PD will therefore be identical when a singleton taxon attaches directly to the spine of the cladogram (e.g., *Tetraceratops insignis* has both a CR and PD of seven). Phylogenetic analyses contrasting the number of distinct skull elements with either CR or PD examine the hypothesis that cladogenetic (i.e., speciation) events are positively related with morphological change (cf. Eldredge and Gould 1972). This type of analysis is also predicated on the observation that the synapsid terminal taxa used herein are morphologically static with regard to their complement of skull roofing bones (Sidor 2000).

Using both stratigraphic and phylogenetic approaches has several benefits. First, if speciation rates vary among the different therapsid clades or at different times during the history of the same clade, then stratigraphic sampling might be too coarse to resolve these changes, and a more finely resolved phylogenetic perspective would be preferable. Alternatively, if speciation rates were constant but the majority of phylogenetic relationships were inaccurate, then a stratigraphic proxy might be better. Weaknesses or shortcomings of one method should be compensated by the other, and concordant results are more probably reliable. It is worth adding here a statement regarding the scale of analysis used. Analyses of large-scale trends typically focus on the summary statistics of a large clade at different points in its history: for example, *average* body size, *maximum* skull length (McShea 1998a). Although some of the present analyses use lower taxonomic units, I am *not* principally investigating deviations from stasis within an individual lineage (cf. Bookstein 1987; Gingerich 1993; Roopnarine et al. 1999).

Skull size was estimated in two ways: (1) as a simple measure of maximum skull length; and (2) as the first principal component (PC) derived from a principal components analysis (PCA) of several skull measurements (Bookstein et al. 1985). Although the latter method is probably preferable, fossil incompleteness limited its usefulness to a smaller subsample of the total number of taxa studied. Measurements for the PCA included skull length, longitudinal orbital diameter, interorbital width, preorbital length, and snout width (measured transversely from the lateral margins of the premaxilla-maxilla suture). These data were log-transformed and then subjected to correlation matrix-based PCA. Average skull lengths or PC1 scores were used when a taxon was represented by multiple specimens. Where both techniques could be used, a good linear relationship between PC1 and skull length obtained ( $R^2 = 0.97$ ). Raw measurement data are provided in Sidor (2000). Contrasting the number of skull bones present in a taxon and its skull's size investigates whether the former can be explained solely by changes in the latter. In other words, is skull bone loss simply hitchhiking on the real underlying trend—persistent changes in skull size?

#### Character Coding

Outside of a few median elements making up the braincase (e.g., supraoccipital, basioccipital, basisphenoid, parasphenoid), amniote skulls are primitively composed of paired (i.e., bilaterally symmetrical) elements. Each of the skull and lower jaw bones in Table 1 was coded in each taxon (Appendix 2) as one of four discrete character states: (1) present and paired; (2) present but at least partially fused to an adjacent element; (3) absent; or (4) neomorphic. Skull bones were considered neomorphic (e.g., the preparietal, echidna pterygoid, and anterior lamina) if they were not present in pelycosaur-grade

TABLE 1. Synapsid skull elements used in this study, including their primitive position and observed states. Bone numbers refer to the columns in Appendix 2; unnumbered bones were not included. Anatomical abbreviations are used in Figures 1 and 2. The sphenethmoid is considered here to be equivalent to the orbitosphenoid.

Bone #	Name	Abbr.	Position	Observed States	Notes
1	premaxilla	pmx	bilateral	paired, fused to pmx, mx	1
2	septomaxilla	smx	bilateral	paired, fused to pmx, absent	3
3	maxilla	mx	bilateral	paired, fused to pmx, j	
4	nasal	n	bilateral	paired, fused to n	1
5	lacrimial	l	bilateral	paired	
6	jugal	j	bilateral	paired, fused to mx, sq	
7	quadratojugal	qj	bilateral	paired, fused to q	
8	squamosal	sq	bilateral	paired, fused to j, pro, op	
9	prefrontal	prf	bilateral	paired, absent	
10	frontal	f	bilateral	paired, fused to f	1
11	postfrontal	pf	bilateral	paired, absent	
12	preparietal	pp	median	absent, present	4
13	parietal	p	bilateral	paired, fused to p	1
14	interparietal	ip	bilateral	paired, fused to ip	1
15	postorbital	po	bilateral	paired, absent	
16	supratemporal	st	bilateral	paired, absent	
17	tabular	t	bilateral	paired, absent	
18	pterygoid	pt	bilateral	paired, fused to pt	1
19	ectopterygoid	ect	bilateral	paired, absent	
20	palatine	pal	bilateral	paired	2
21	vomer	v	bilateral	paired, fused to v	1
22	quadrate	q	bilateral	paired, fused to qj	5
23	stapes	s	bilateral	paired	
24	epipterygoid	epi	bilateral	paired, fused to al	6
25	dentary	d	bilateral	paired, fused to d	1
26	splénial	sp	bilateral	paired, fused to sp	1
27	angular	ang	bilateral	paired, fused to art, pra, sur	7
28	surangular	sur	bilateral	paired, fused to ang, art, pra, absent	
29	prearticular	pra	bilateral	paired, fused to ang, art, sur	
30	articular	art	bilateral	paired, fused to ang, pra, sur	8
31	anterior coronoid	ac	bilateral	paired, absent	
32	posterior coronoid	pc	bilateral	paired, absent	
33	echidna pterygoid	ech	bilateral	absent, paired	4
34	anterior lamina	al	bilateral	absent, paired	4
35	sclerotic plates	scl	bilateral	paired, absent	
	supraoccipital	so	median	present, fused to op, ip, ex	9
	exoccipital	ex	bilateral	paired, fused to so, bo	9
	basioccipital	bo	median	present, fused to ex, bs	9
	prootic	pro	bilateral	paired, fused to so, op, j	9
	opisthotic	op	bilateral	paired, fused to pro, j	9
	basisphenoid	bs	median	present, fused to ps	9
	parasphenoid	ps	median	present, fused to bs, bo	9
	presphenoid	pre	median	present	9
	orbitosphenoid	orb	median	absent, paired	4, 9

<sup>1</sup> Skull element that contacts the midline.

<sup>2</sup> Midline element in gorgonopsids and some other therapsids (see Hopson and Barghusen 1986).

<sup>3</sup> Following Wible et al. (1990), the monotreme septomaxilla is considered homologous with that in nonmammalian synapsids.

<sup>4</sup> Neomorphic ossification inferred not to be present in the common ancestor of synapsids.

<sup>5</sup> Homologous to the incus in living mammals (Allin and Hopson 1992).

<sup>6</sup> Homologous to the alisphenoid of mammals (Hopson and Rougier 1993).

<sup>7</sup> At least partially homologous to the tympanic ring in living mammals (Allin and Hopson 1992).

<sup>8</sup> Homologous to the malleus in living mammals (Allin and Hopson 1992).

<sup>9</sup> Element not included in this analysis due to lack of adequate material.

synapsids. Therefore this definition of neomorphy may include elements that were presumably present in cartilaginous form (see Generating Neomorphies section below). I made no attempt to code for an element's relative size (e.g., large or small) or shape (e.g., the presence or absence of processes or foramina). Terminal taxa (genera, for the most part) found to display both the primitive and one of the apomorphic character states for a particular character, were coded as possessing the latter (i.e., fused, lost, or neomorphic) condition. This was done because, in general, paired elements are di-

agnostic of smaller, presumably juvenile skulls, whereas fused elements typify larger, presumably adult, individuals of the same species (van Heerden 1972). This coding procedure should therefore help to maintain a degree of ontogenetic equivalence among the fossils used.

Several skull elements, primarily of the braincase, were not included in this analysis because they were exposed on too few specimens to make adequate comparisons (note 9 in Table 1). However, under the protocol adopted below, including these elements would only tend to reinforce the ob-

served pattern because fusions and losses among preexisting bones are much more common than the appearance of neomorphic bones.

#### *The Skull Simplification Metric*

To quantify synapsid cranial bone evolution, I employed a simple tabulation scheme: each paired skull bone or neomorphic element (regardless of whether the latter was paired or median) was given a value of two, bones found to be fused were given a value of one, and bones deemed lost (= absent) were scored as zero. A taxon's skull simplification metric (SSM) then was calculated as the sum of these values for the 35 elements included in this analysis. As the number of distinct skull bones decreases, so does the SSM. For example, a taxon with distinct postorbitals and postfrontals received a score of two for both of these elements (SSM = 4). However, if the latter bones were found to be partially fused to one another, then each would receive a score of one (SSM = 2). Therefore, bones fused across the midline (e.g., parietals, vomers) are the only ones that do not effect a decreased score in another bone. No matter how many bones a specific element was found to be fused to, however, the minimum SSM score that it could be assigned was one. This scheme is conservative in that it minimizes decreases in SSM. Finally, because nearly all taxa suffer some degree of incompleteness, missing entries were conservatively scored as present and paired (i.e., two) for the purpose of analysis unless phylogenetic optimization unambiguously implied otherwise (see Appendix 2).

The SSM is a very simple metric that can only address one aspect of synapsid skull complexity—the number of elements present. This type of complexity measure corresponds to what McShea (1996a,b) has termed nonhierarchical object complexity, or, more simply, the number of parts in a system without relation to their interaction or configuration. Other measures of a skull's complexity, such as the average number of sutural connections between bones or the average number of characters used to describe bones, could also be used. Gregory (1929) implied that among-bone variation is an important measure of complexity. Creating a single metric that effectively captures the various ways to describe complexity is difficult. In all cases, however, one's interpretation of complexity needs to be operationalized before it can be objectively studied. Being discrete to begin with, changes in the number of skull elements are relatively easy to quantify.

## RESULTS

### *Stratigraphic Results*

*General patterns.*—Based on the cladistic relationships proposed by Reisz (1986), the primitive SSM score for Synapsida appears to be 64, although simpler-skulled forms actually appear earlier in the fossil record. Importantly, this value is close to the theoretical maximum (70) for the number of skull bones used in this study. Among fossil taxa, the early mammal *Morganucodon* and the advanced nonmammalian probainognathian *Pachygenelus* score lowest (SSM = 45). When extant taxa are included, *Homo* scores lowest (SSM = 27). Other, less specialized, placental mammals score nearly

as low (e.g., *Canis lupus* = 29; *Rattus norvegicus* = 29; *Echinosorex gymnurus* = 28; *Choloepus hoffmanni* = 28). Figure 4 plots the SSM against the stratigraphic range of each of the 123 fossil and three modern synapsids included in this study. When Synapsida is taken as a whole, a significant negative relationship is found between SSM and stratigraphic position (Kendall's  $\tau = -0.686$ ,  $P < 0.0001$ ). Pelycosaur-grade synapsids uniformly score highest on the SSM (64–62), whereas extinct and extant mammals score lowest (49–27). For this analysis, the Late Permian (ARs = 8–13) shows the widest range of SSM scores (64–49). Taxa with SSM scores higher than 58 are unknown after the Late Permian, and from the Early Triassic onward both the maximum and minimum SSM values steadily decrease.

*Subgroup patterns.*—Table 2 displays the results for correlation analyses between SSM and AR for various synapsid subgroups. The most primitive taxa examined here, the pelycosaur- and biarmosuchian-grade synapsids, show little variation in SSM values (range = 63–61) even though they span a combined 13 ARs (from Late Carboniferous to Late Permian). The latest Late Permian ictidorhinids (*Ictidorhinus*, *Lycacnodon*, and *Rubidgina*) are remarkably static, differing by a maximum of only two in their SSM score from the earliest synapsids.

Dinocephalians are the shortest-lived clade of nontheriodont therapsids, recorded only from a short interval during the Late Permian (two ARs), but show a SSM range of 61–55. This might, however, be an overestimate as the absence of a coronoid in *Ulemosaurus* is disputed (cf. Riabinin 1938; Efremov 1940), and I was unable to study the medial aspect of its lower jaw. Similarly, the lack of a coronoid in *Tapinocaninus* (Rubidge 1991) may be taphonomic, as I have observed a coronoid in the closely related genus, *Deuterosaurus* (not included in this analysis). Grine (1997) studied the distribution of the coronoid bone within dinocephalians and suggested that its supposed absence in several genera may represent prefossilization loss or worker error. Nevertheless, fusions within the taxonomically diverse, thick-skulled tapinocephalids suggest that dinocephalians did dramatically reduce their SSM in a relatively short period of time.

The fossil record of anomodonts extends from the Kazanian (Late Permian) to Carnian (Late Triassic) and has been considered among the richest of any nonmammalian synapsid group (King 1989). Basal anomodonts (e.g., *Patranomodon*, *Ulemica*) possess the typical complement of therapsid skull bones (SSM  $\approx$  60), whereas the skulls of Triassic forms are greatly simplified (SSM  $\approx$  47). Gorgonopsid fossils are known exclusively from Late Permian sediments (comprising five ARs) and show little change in SSM values during this time (60–57). Interestingly, in both groups the neomorphic preparietal bone is lost in stratigraphically late appearing taxa (e.g., the anomodont *Stahleckeria*, and the gorgonopsids *Leontocephalus* and *Rubidgea*). Therocephalians first appear in the early Late Permian (*Eodicynodon* Assemblage Zone; Rubidge et al. 1983) and survive until the early Middle Triassic (Rubidge 1995). Spanning seven ARs, therocephalian SSMs range from 59 to 54.

Nonmammalian cynodonts display pronounced cranial simplification (SSMs reduce from 57 to 45), but this grade

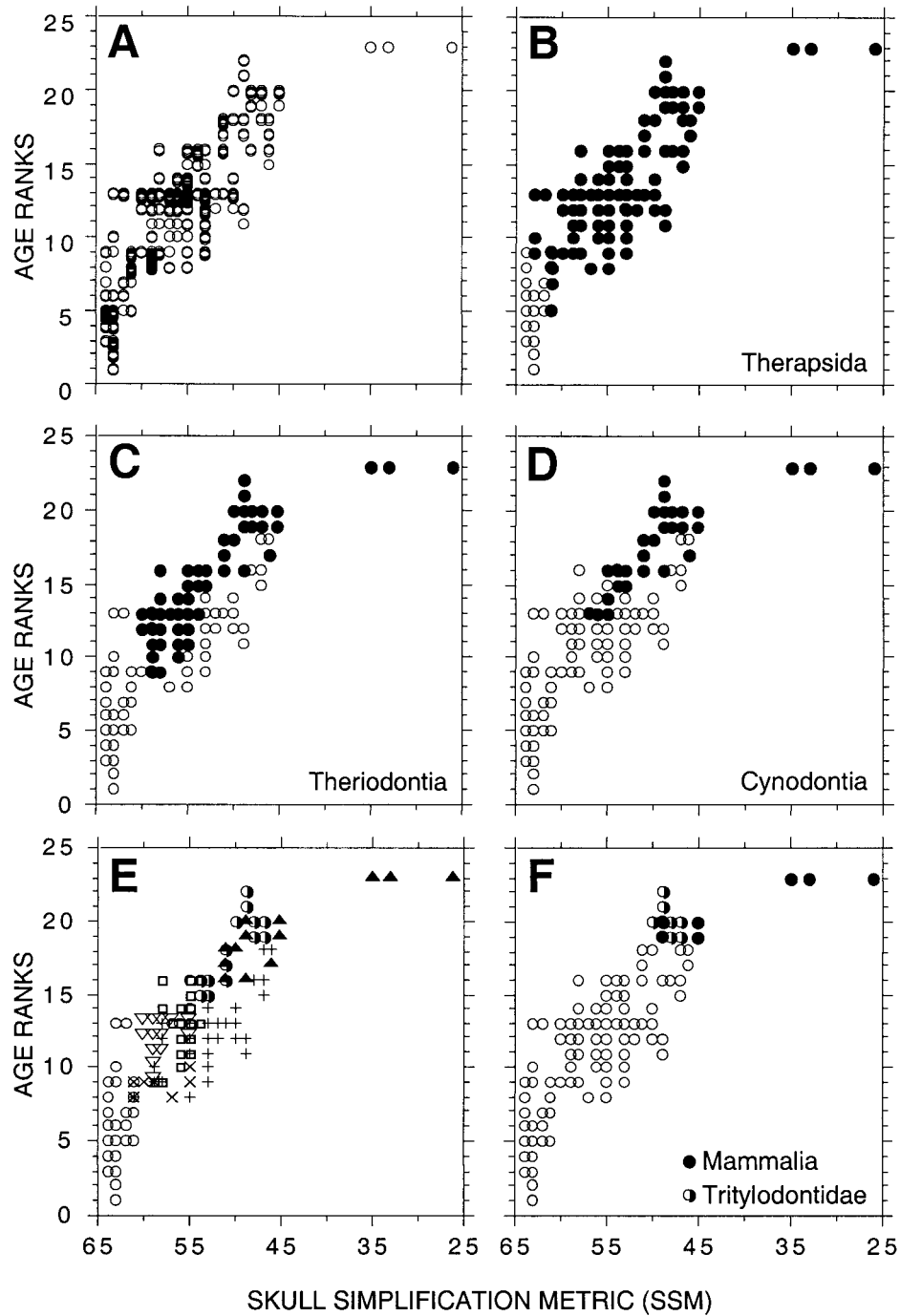


FIG. 4. Plot of the skull simplification metric (SSM) versus the stratigraphic distribution of each taxon in age ranks (AR). Filled circles denote the clades indicated, except for in (E) where:  $\times$ s are dinocephalians; inverted, open triangles are gorgonopsids; squares are therocephalians; +s are anomodonts; half-filled circles are cynognathians; and filled triangles are probainognathians. Overlapping data-points are indicated only in (A), where the superimposed ARs have been smeared downward. Note that AR 13 corresponds to the end of the Permian, where a major mass extinction occurred. See Table 2 for subgroup correlations and Appendix 3 for data.

group also spans 10 long ARs (from the latest Late Permian to Middle Jurassic; see below). Permian and Early Triassic noneucynodont cynodonts (e.g., *Dvinia*, *Galesaurus*, *Thrinaxodon*) range from SSMs of 57–55, but starting in the upper Middle Triassic, more advanced cynognathian and probainognathian cynodonts show a more rapid decrease in SSM values. The advanced cynodont trend reaches its peak in the

terminal members of both of the latter clades, with tritylodontid cynognathians (SSM = 50–47) and early mammal probainognathians (SSM = 48, 45).

*Absolute temporal durations.*—Although taxa that span many ARs usually show a wider range of SSM values (Fig. 5A), the ARs themselves are not strictly equivalent because they do not encompass equal amounts of geologic time.

TABLE 2. Results of Kendall's  $\tau$  rank correlation tests for skull simplification metric versus stratigraphic age (in age ranks) tests. Note that the majority of correlations are negative. All taxa except pelycosaurians represent clades. The test statistic ( $\tau$ ) and  $P$ -value are corrected for ties in this and subsequent tables.

Subgroup	$\tau$	$P$
Synapsida	-.686	<.0001
"Pelycosaurians"	.369	.0193
Therapsida	-.592	<.0001
Dinocephalia	-.187	ns
Anomodontia	-.668	<.0001
Theriodontia	-.747	<.0001
Gorgonopsidae	.101	ns
Therocephalia	-.329	.0652
Cynodontia	-.787	<.0001
Cynognathia	-.620	.0032
Tritylodontidae	.385	ns
Probainognathia	-.767	.0005
Mammalia	-.755	.0578

Where fossils are plentiful and the stratigraphic resolution good (e.g., the biozonation of the Beaufort group), strata were partitioned into fine divisions of short duration; where the fossil record is spotty (much of the Late Triassic and Jurassic), large sections of the rock record were combined. Thus, the number of ARs that a particular clade spans is only a relative estimate of its temporal duration compared to other clades. Figure 5B plots the range of SSM values obtained for each consecutive synapsid subclade in Figure 3 against an estimate of the actual temporal duration of each clade in millions of years. The significant correlation found (Spearman's  $\rho = 0.809$ ,  $P = 0.005$ ) indicates that long-lived clades achieved greater degrees of skull simplification than did relatively short-lived clades. In addition, because one might expect variation within long-lived clades to exceed that of short-lived clades due to stochastic processes alone, the observation that only the lower bound of a clade's SSM value decreased is of particular note (see below and Fig. 8).

### Body Size Results

One possible mechanism for the type of temporal pattern documented above is a physical constraint (cf. Fisher 1986). For example, perhaps fewer elements can be maintained on a small-sized tetrapod skull. By this means, a trend in decreasing size could effect a trend in skull bone number. This is conceivable because both early mammals and tritylodontids have remarkably simple skulls and both rank among the smallest of their respective eucynodont lineages. Moreover, a trend toward decreasing body size has been previously implicated as an important factor in mammal origins (Hopson 1973; Kemp 1999, p. 227). Among extant tetrapods, miniaturization in salamanders often leads to the loss of several skull elements (Hanken and Wake 1993). If size were correlated with the number of skull elements present in a taxon, then this observation might lead us to consider different mechanisms for large-scale patterns of cranial evolution than if it were not.

A relationship between skull bone number and skull size is not borne out by the data. Skull length plotted against the SSM for all synapsids for which measurement data are available shows no significant correlation between the two (Fig. 6A; Spearman's  $\rho = 0.084$ ,  $P = 0.312$ ). Although fewer taxa can be included in the analysis, a similar result is obtained when PC1 is substituted for skull length (Fig. 6B).

The lack of an overall trend, however, could be the result of several underlying trends in different directions, and so it is important to determine if individual synapsid lineages show significant associations between the SSM and skull size. Interestingly, anomodonts and theriodonts show the only reasonably significant relationships. In the former group, skull length and SSM are negatively related (Spearman's  $\rho = -0.46$ ,  $P = 0.03$ ), whereas in the latter they are positively related ( $\rho = 0.42$ ,  $P = 0.003$ ; see Table 3). Contrary to expectations, the anomodont skull becomes simpler as it becomes larger. Although theriodonts do show increased simplification with smaller skull size, some theriodont subgroups

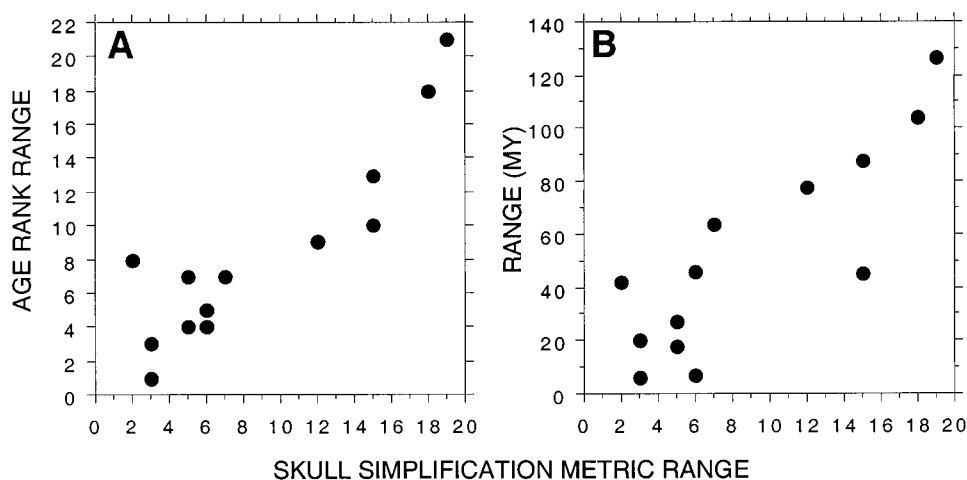


FIG. 5. Plot comparing the range of skull simplification metric (SSM) values versus two measures of the temporal duration of the synapsid subgroups included in Table 2. (A) uses the range of age ranks, whereas (B) uses an estimate of the absolute temporal duration of the subgroup in millions of years (see Appendix 3). In both, a strong positive relationship is evident (A:  $\rho = 0.805$ ,  $P = 0.0053$ ; B:  $\rho = 0.809$ ,  $P = 0.0050$ ), indicating a general correspondence between the life span of a group and its degree of cranial simplification.

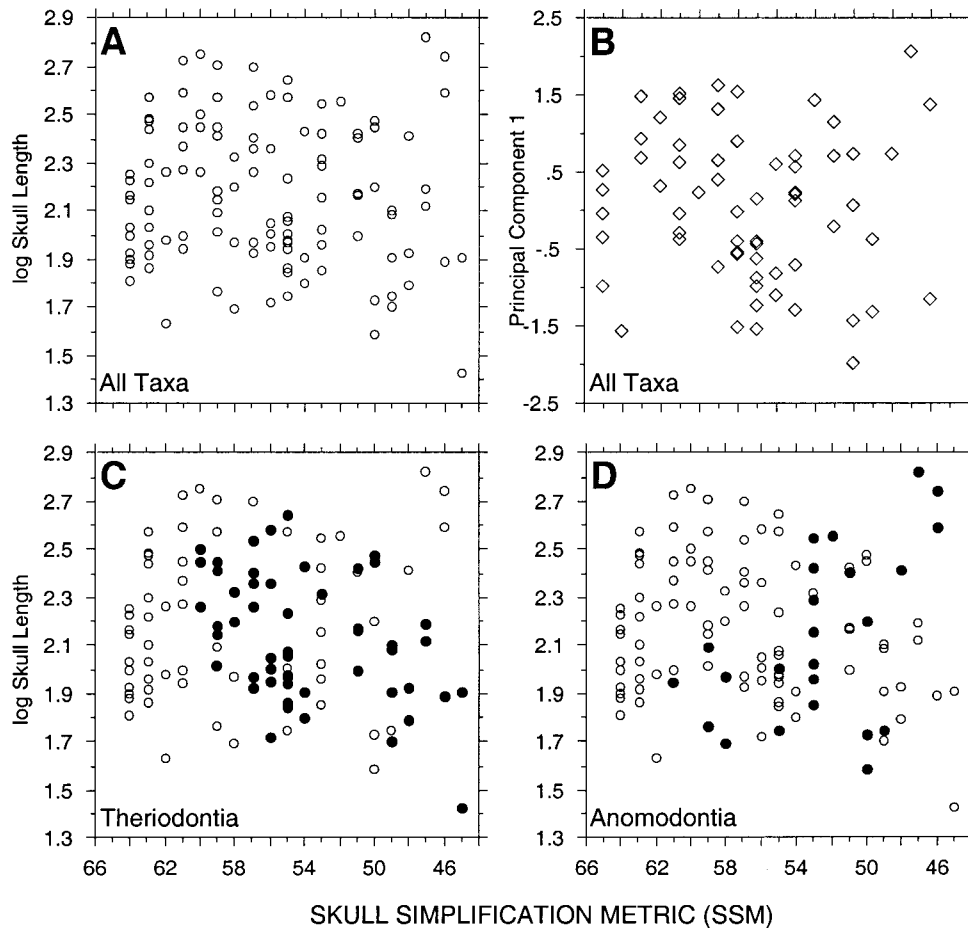


FIG. 6. Plot of the skull simplification metric (SSM) versus two measures of skull size: (A) average skull length, and (B) first principal component (PC) from a principal components analysis of several skull measurements (see text for details). No general relationship between skull size and SSM is present when Synapsida is considered as a whole. Excluding the two or three largest anomodonts (top right corner of A and B) still fails to yield a significant relationship ( $P = 0.08$ ). However, (C) and (D) indicate the conflicting positive and negative relationships for theriodonts and anomodonts, respectively. Again, excluding the three largest anomodonts (top right corner of D) yields no significant relationship between SSM and either skull length or PC1 ( $P = 0.40$  and  $0.78$ , respectively). Recent mammals are not included. See Table 3 for subgroup correlations.

TABLE 3. Results of Spearman rank correlation tests for skull simplification metric versus two measures of skull size. Note approximately equal number of positive and negative correlations. All taxa except pelycosaurs represent clades. Recent mammals were not included in these analyses.

Subgroup	Maximum skull length		Principal component 1	
	$\rho$	$P$	$\rho$	$P$
Synapsida	.084	ns	.133	ns
"Pelycosaurs"	-.187	ns	.775	ns
Therapsida	.225	.0319	.227	.0807
Dinocephalia	-.108	ns	-.772	.0845
Anomodontia	-.456	.0289	-.335	ns
Theriodontia	.417	.0027	.328	.0597
Gorgonopsidae	-.412	ns	-.418	ns
Therocephalia	.546	.0702	.543	ns
Cynodontia	-.093	ns	-.434	ns
Cynognathia	.290	ns	-.154	ns
Tritylodontidae	.000	ns	—	—
Probainognathia	.795	.0354	.500	ns
Fossil Mammalia	1.000	ns	—	—

(e.g., cynodonts, cynognathians) do not continue this relationship and so this may not be a credible result.

Patterns of synapsid cranial evolution, in terms of skull size and degree of simplification, are summarized in Figure 7. Late Carboniferous synapsids, which are especially poorly known, were, in general, relatively smaller animals than their Early Permian descendants. The degree to which this is a taphonomic or preservational effect is unknown. Early Permian synapsids are relatively well known and span a broad range of skull sizes but show little variation in SSM. The first major expansion in the area occupied in this morphospace occurs in the Late Permian, which for the purpose of visualization has been split into two intervals. The first half represents the large-bodied, dinocephalian-dominated biota, whereas in the second dinocephalians were absent and theriodonts and anomodonts were widespread. Synapsid fossils are less commonly recorded from Early and Middle Triassic sediments, but data from these epochs together suggest little change in the range of skull sizes from the Late Permian. The Late Triassic and Early Jurassic data (combined into a

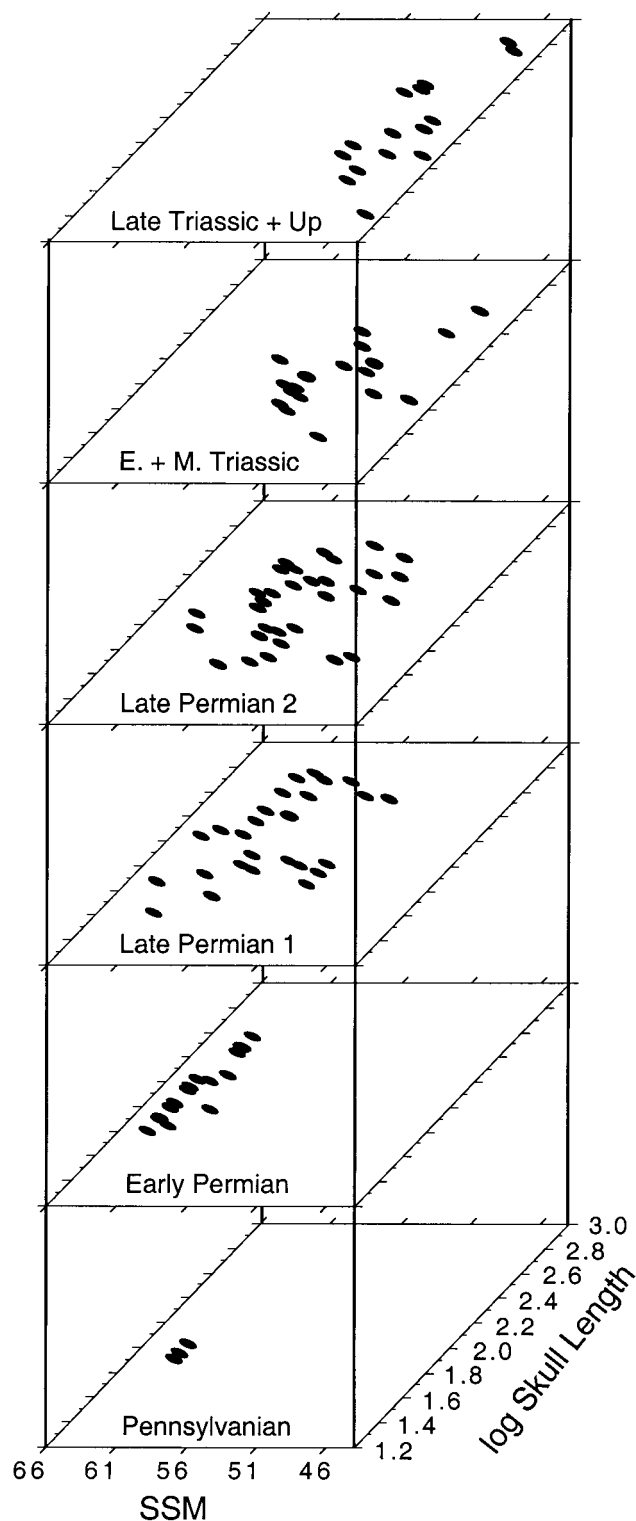


FIG. 7. The evolution of cranial simplification and skull size over pre-mammalian synapsid history. The skull simplification metric (SSM) is plotted against log skull length and binned into six time intervals. Only first appearances were used and Recent mammals were excluded.

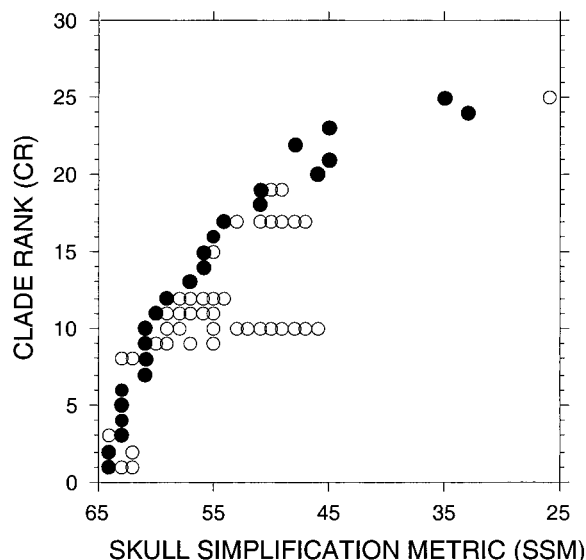


FIG. 8. Plot of the skull simplification metric (SSM) versus the clade rank (CR) for each taxon. Filled points correspond to those taxa considered to represent the primitive condition for their respective clade. These include: *Casea broilii* and *Eothyris* for Caseasauria; *Mycterosaurus* and *Varanops* for Varanopseidae; *Archaeothyris* for Ophiacodontidae; *Ianthasaurus* for Edaphosauridae; *Haptodus* (singleton); *Sphenacodon* for Sphenacodontidae; *Tetraceratops* (singleton); *Biarmosuchus* for Biarmosuchia; *Syodon* and *Estemmenosuchus* for Dinocephalia; *Patranomodon* for Anomodontia; *Scylacops* for Gorgonopsidae; *Lycosuchus* for Therocephalia; *Dvinia* (singleton); *Procyonosuchus* (singleton); *Cynosaurus* for Gallesauridae; *Thrinaxodon* (singleton); *Cynognathus* for Cynognathia; BP/1/2669 for Probainognathia; *Ecteninion* (singleton); *Aleodon* for Chiniquodontidae; *Probainognathus* (singleton); *Pachygenelus* (singleton); *Sinoconodon* for Mammalia; *Morganucodon* (singleton); *Ornithorhynchus* for crown-group mammals; and *Didelphis* for Theria. Overlapping datapoints are not indicated.

single bin) indicate an expansion in the range of recorded skull sizes, with massive dicynodonts (e.g., *Stahleckeria* and *Placerias*) expanding the upper bound and the earliest mammals (e.g., *Morganucodon* and *Sinoconodon*) markedly smaller than most preceding synapsids. As previously noted, mean SSM decreases steadily from Early Permian to Late Triassic (and more recent) times. Extending this analysis further into the Mesozoic, where only mammals and tritylodonts persisted, would undoubtedly show a different pattern. During this time, both of these groups were restricted to a rather narrow range of small body size and low SSM scores.

#### Phylogenetic Results

Fossil synapsids have been the focus of cladistic scrutiny for more than 20 years (Kemp 1972, 1983; Reisz 1980, 1986; Hopson and Barghusen 1986; Rowe 1986, 1988, 1993; Hopson 1991, 1994; Sidor and Hopson 1998). Although there are still points of contention among the various authorities (e.g., the position of anomodonts relative to gorgonopsids, or tritylodontids relative to gomphodonts and mammals), the majority of analyses support the same fundamental topology. Importantly, all of the previous studies have used the loss of skull bones as cladistic synapomorphisms.

*Clade rank.*—In Figure 8, SSM is plotted against CR, a

measure of phylogenetic advance. These two variables show a strong negative slope (Kendall's  $\tau = -0.837$ ,  $P < 0.0001$ ); consecutively more mammal-like clades consistently have simpler skulls. Because the primitive members of each synapsid subclade tend to appear earliest in the fossil record (shaded points in Fig. 8; Sidor and Hopson 1998), the maximum SSM value at each CR approximates the degree of simplification inferred to have occurred at each stage in the phylogenetic progression from basal synapsids to mammals. This makes the more-or-less monotonic decrease in SSM between consecutive CRs additionally noteworthy. This steady decrease is especially prevalent among the well-sampled pelycosaur to early cynodont record (CRs 1–16). When ignoring the Recent mammals, the largest jumps occur between the CRs defined by: (1) the basal cynodonts *Thrinaxodon* and the earliest probainognathian, BP/1/2669 (CRs 17–18); and (2) the chiniquodontids and the *Probainognathus*-clade (CRs 19–20). These discontinuities might indicate gaps in the fossil record if gradual character evolution were a dominant feature of synapsid history (Sidor and Hopson 1998).

Additional cranial simplification occurs within most subclades branching from the phylogenetic trajectory towards mammals (e.g., anomodonts [CR 10] and cynognathians [CR 17]). Because synapsid genera persist only for relatively short durations, (relatively) longer-lived clades are the product of greater numbers of constituent taxa. Thus, as shown in the stratigraphic results, speciose, longer-lived clades tend to accumulate greater amounts of cranial simplification.

*Patristic distance.*—Figure 9 plots the SSM versus the number of branching points (patristic distance, PD) passed from the root of the cladogram, for each of the 126 synapsid taxa in this analysis. A significant negative correlation was found for the entire data set (Kendall's  $\tau = -0.837$ ,  $P < .0001$ ) and for multiple subclades (therapsids, dinocephalians, anomodonts, theriodonts, cynodonts, and cynognathians; Table 4). The latter analyses are particularly interesting because they roughly correspond to two of McShea's (1994) proposed tests for driven trends, the subclade, and ancestor-descendant (A-D) tests. The subclade test asks whether the large-scale trend of the entire clade in question is mirrored within its constituent subclades that are away from any reflecting boundaries in the state space. A strict use of the A-D test (where a random subsample of A-D pairs from the clade in question is tested for a significant departure from equiprobable increases and decreases) or the tests advocated by Alroy (2000) are infeasible for this study. Instead, contrasting SSM and PD within synapsid subclades tests if consecutive sister-groups (which might be A-D pairs) persistently trend in a single direction along the SSM axis.

## DISCUSSION

### *Evolutionary Trends*

Vertebrate paleontologists have typically attributed evolutionary trends, the persistent change in the distribution of morphologies through geologic time, to the long-term effects of natural selection (e.g., Simpson 1944). More recent inquiry into the basis of such trends, however, has led to the distinction between passive and active (or driven) trends (e.g., Fisher 1986; Gould 1988; McShea 1994, 1998a,b; Wagner

1996), with the former type emerging as a natural outcome of nondirectional processes in a bounded space. Empirical studies have yet to reach a consensus on which type of trend, if either, is prevalent in the fossil record. Depending on the clade in question, body size evolution (i.e., Cope's rule) has been shown to be either passive (Cretaceous molluscs, Jablonski 1997), active (Cenozoic mammals, Alroy 1998; dinosaurs, Carrano 1999), or disputed (fossil horses, MacFadden 1986; McShea 1998a). Results are similarly mixed for trends in other types of features. Wagner (1996) found evidence for several active trends in the geometry of early gastropod shells, whereas Valentine et al. (1994) explained increases in metazoan complexity (in terms of numbers of cell types) as diffusion away from a lower bound of one cell.

The distribution of SSMs through synapsid evolutionary history argues strongly for the recognition of a driven trend, in that it passes both McShea's (1994) "behavior of the minimum" (Fig. 3; Table 2) and, in modified form, "ancestor-descendant" (Fig. 8; Table 4) tests. Briefly discussed below are both selective and nonselective mechanisms that can be used to explain this pattern of results.

*Selection for skull strength.*—The pattern of SSM scores conforms to that put forth by McShea (1994) when natural selection provides a driving force. One potential reason for selection to favor skulls with fewer elements could be related to the development of a more rigid, boxy skull in many synapsid groups, especially mammals.

In contrast to the cranial kinesis inferred to be present in pelycosaur-grade synapsids (Reisz 1986), and retained in many modern reptiles (e.g., lizards, snakes), therapsids begin a trend toward limiting intracranial mobility (Russell and Thomason 1993). For example, the fused basicranial articulation consolidates the palate and braincase into one functional unit. Biomechanical studies on modern mammals have shown that loads induced by jaw adductor muscles on their skull roof origination sites can affect bone and suture morphology (Herring 1993). Interestingly, fossil taxa with enlarged temporal fenestrae (indicative of large jaw adductor musculature) and/or characteristics of complex jaw movements or tooth-to-tooth occlusion tend to have low SSM scores (e.g., advanced anomodonts, bauriid therocephalians, gomphodont cynodonts [including tritylodontids], and mammals). Because sutural joints permit some degree of interbone mobility, reducing skull bone number (and therefore suture number) is a way to solidify the skull against the forces induced by mastication. Continued selection pressure for stronger and more rigid skulls could therefore produce the observed pattern.

*Intrinsic bias.*—McShea (1994) and Wagner (1996) both suggest that even if natural selection is sufficient to explain the presence of an active trend, it may not be necessary. Intrinsic bias (or constraint) provides an alternative, nonselective, driving mechanism to explain the distribution of synapsid SSM scores. But why should bone loss be more probable than bone gain?

Skull bones are the adult manifestation of embryonic ossification centers. In many cases single bones are formed by multiple ossification centers, whereas in others there is a one-to-one correspondence between the two. To my knowledge, single ossification centers cannot give rise to more than one

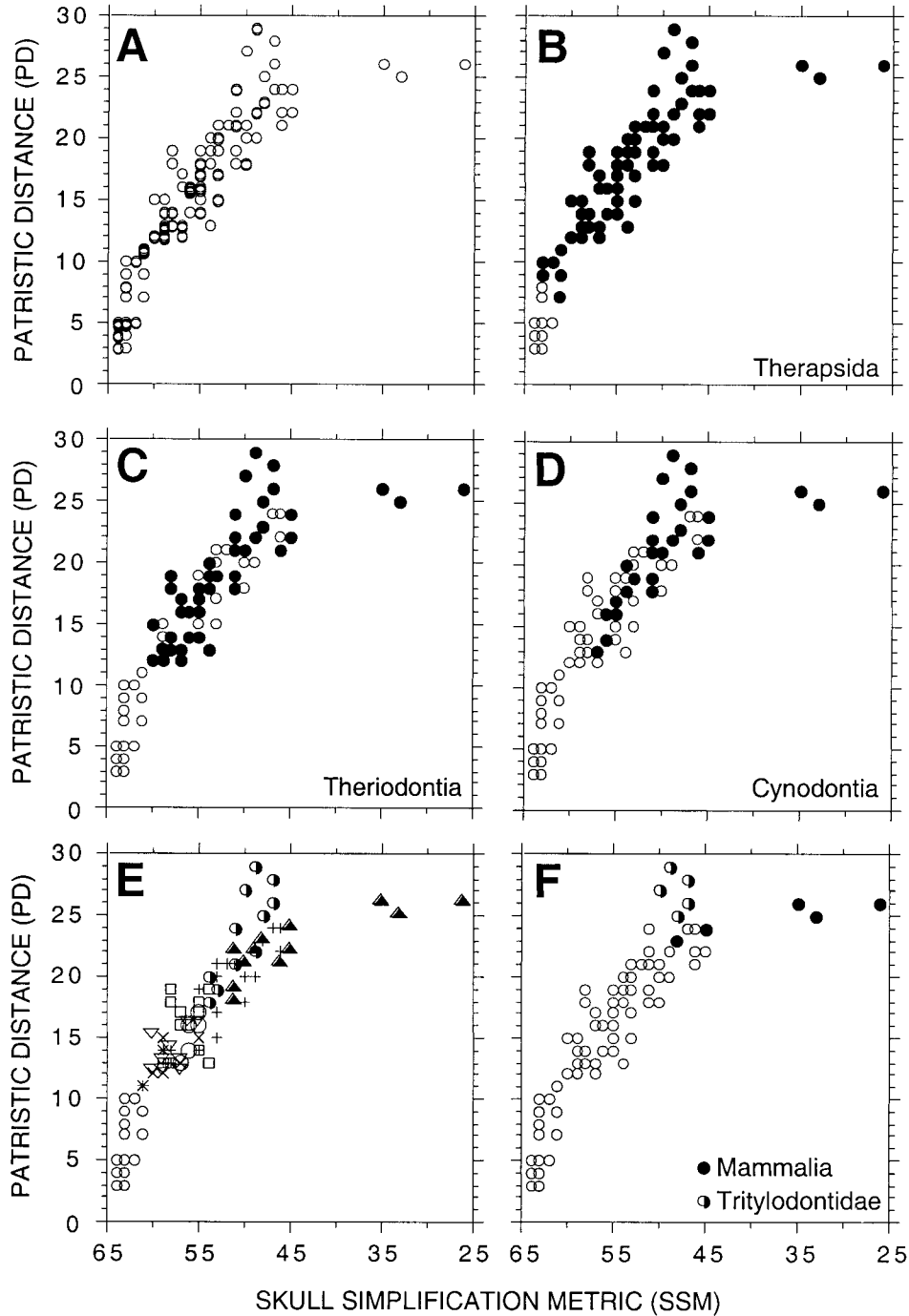


FIG. 9. Plot of the skull simplification metric (SSM) versus the patristic distance (PD; i.e., number of nodes) from the root for each terminal taxon in this analysis. Filled circles denote the clades indicated, except in (E) where:  $\times$ s are dinocephalians; inverted, open triangles are gorgonopsids; squares are therocephalians; +s are anomodonts; half-filled circles are cynognathians, and filled triangles are probainognathians. Overlapping datapoints are indicated only in (A), where the superimposed PDs have been smeared downward. See Table 4 for subgroup correlations.

bone. Although relatively little is known about the genetics controlling ossification centers, it seems reasonable to assume that their genetic underpinning could be disrupted by any number of standard means (e.g., mutations, insertions, deletions). Therefore given enough time, mutations might eventually disrupt ossification center formation. As long as a single bone still had at least one functional ossification center,

however, it would be recognized as present. (As one reviewer aptly mentioned, what we might really be looking at is the loss of ossification centers in synapsid history, rather than the loss of skull bones per se.) If gaining a novel bone requires at least one novel ossification center and assembling the new gene(s) for this ossification center is less probable than is a gene's loss, then we would expect the observed pattern at

TABLE 4. Results of Kendall's  $\tau$  rank correlation tests for skull simplification metric versus patristic distance (PD) from the root of the cladogram tests. Note that nearly all correlations are negative. All taxa except pelycosaurs represent clades. Recent mammals were not included in this analysis.

Subgroup	$\tau$	<i>P</i>
Synapsida	-.837	<.0001
"Pelycosaurs"	-.345	.0287
Therapsida	-.783	<.0001
Dinocephalia	-.818	.0005
Anomodontia	-.730	<.0001
Theriodontia	-.731	<.0001
Gorgonopsidae	-.337	ns
Therocephalia	-.215	ns
Cynodontia	-.683	<.0001
Cynognathia	-.631	.0027
Tritylodontidae	.222	ns
Probainognathia	-.562	.0348
Fossil Mammalia	-1.000	ns

the hierarchical level of the bone. Similar arguments have been made in the hypothetical case by McShea (1996a) and for the acquisition versus loss of features associated with viviparity (live birth) among lizards and snakes (Blackburn 1992; see also Lee and Shine 1998). This model also suggests that whereas stochastic processes could account for bone loss, it is the rarity of neomorphic bones that deserves further attention.

*Generating neomorphies.*—What are the possible ways of producing new ossification centers? As new skull elements are a rare phenomenon, understanding likely mechanisms for their appearance can be difficult. Subdividing a previously existing element is one intuitive possibility. Frazzetta (1970) describes the evolution and functional significance of a jointed, double, maxilla in bolyerine snakes. In amphisbaenids, the three embryological ossification centers of the parasphenoid sometimes fail to coalesce in the adult, yielding three "bones" instead of one (Romer 1956, p. 51). A similar mechanism might underlie the variable number of palpebral elements in modern crocodiles (H. Larsson, pers. comm.), or the neomorphic "echidna pterygoid" in monotremes (de Beer 1937, p. 435).

Gene duplication provides a second method for increasing the number of distinct skull bones, by doubling an element. Mechanistically, gene duplication could rapidly provide the raw material for a new ossification center and bypass a period of gradual gene assembly. Studies from body segmentation and limb development suggest that this method of generating neomorphies is relatively common and has played an important role in some aspects of both vertebrate and invertebrate evolution (Patel 1994; Shubin et al. 1997). Within vertebrate cranial evolution, however, this possibility has not been discussed.

A third alternative mechanism for generating novel skull bones is epigenetic. That is, a new ossification center is not created through a direct genetic pathway of its own, but rather through some other heritable feature which, in turn, produces the ossification. For example, there is evidence that ossification site number is positively related to growth rate. In an elegant experiment on the formation of the sclerotic ring, Coulombre et al. (1962) were able to reduce the final number

of individual sclerotic ossicles by draining the developing eye of its vitreous humor at different points in its development. Cranial volume growth can also effect supernumerary ossification centers in humans. Supernumerary, or Wormian, bones are occasionally found interposed between the normal skull roofing bones (Gray 1977). De Beer (1937, p. 486; see also Herring 1993) notes that Wormian bone number appears related to cranial volume and that in hydrocephalic individuals (where the meninges surrounding the brain swell) large numbers of Wormian bones are formed. In addition, Ossenberg's (1970) studies positively associating swaddling and cranial deformation with increased numbers of Wormian bones in Native Americans suggests that they may be, to some degree, epigenetic.

Perhaps the most difficult neomorphies to understand are those that appear underivable from subdividing or duplicating a previously unipartite element. Examples include the pre-auricular bone within therapsids, the preauricular bone of ornithischian and rostral bone of ceratopsian dinosaurs (Serenio 1997), and the preglossale of some passeriform birds (*Passer*, *Petronia*, *Montifringilla*; Bock and Morony 1978).

*Confounding factors.*—The window on morphology provided by the fossil record can make understanding neomorphies even more difficult. Because (noncalcified) cartilage is only rarely preserved in the fossil record, the ossification of a previously cartilaginous element would likely be interpreted as a neomorphic element. Among synapsids, the complicated distribution of the orbitosphenoid and anterior lamina (see Hopson and Rougier 1993) supports this hypothesis, and appears to be related to the need for increased rigidity in those taxa typically considered to use powerful jaw movements (i.e., dicynodonts, tritylodontids, and mammals). Fortunately, the majority of skull bones in tetrapods are dermatocranial in origin (i.e., they are not preformed in cartilage), and therefore not subject to this possible difficulty. A second error could stem from mistaking taphonomic loss for true absence. The sporadic appearance of loosely attached elements (e.g., sclerotic plates) could make their occasional preservation of appear neomorphic.

#### *Postcranial Simplification in Synapsids*

McShea (1991, 1996b) has argued that many classic examples of increasing complexity through evolutionary time rely more on intuition than on objective study, and that most of these have yet to be examined in a rigorous manner. The results presented here suggest that at least one, admittedly simple, measure of complexity decreases through time within synapsids. However, because this analysis focused solely on the skull, the question remains if this is trend is indicative of synapsid evolution as a whole. Preliminary data from the postcranial skeleton appear to corroborate the cranial pattern.

*Postcranial simplification.*—In terms of the number of distinct postcranial elements, the transition from the earliest synapsids to the first mammals was marked by an excess of simplification over novelty. In a detailed analysis, Hopson (1995) has argued for the repeated loss of individual phalanges, and loss or fusion of mesopodial (carpal and tarsal) elements among Permo-Triassic synapsids. Similarly, although the pelvic girdle retains its primitive tripartite con-

figuration, elements of the pectoral girdle (e.g., interclavicle, anterior coracoid, and clethrium) are lost (Romer 1922).

Plesiomorphic bony elements are also lost within the synapsid axial skeleton. The primitively multipartite atlas-axis complex (consisting of paired proatlantes and atlantal neural arches, and a median atlantal intercentrum, atlantal pleurocentrum, axial intercentrum, axial pleurocentrum, and axial neural arch) is reduced to varying degrees among nonmammalian synapsids (e.g., Romer and Price 1940; Jenkins 1971; Sumida 1989; Reisz et al. 1992b) and reaches an extreme of simplification in modern mammals, where the proatlantes are absent, the atlantal neural arches are fused to one another and to the atlantal intercentrum, and the axial neural arch is fused to its inter- and pleurocentrum and well as to the atlantal pleurocentrum. In contrast to the condition observed in pelycosaur-grade synapsids (Romer and Price 1940), discrete intercentra are lost between the trunk vertebrae among early therapsids (e.g., Orlov 1958) and throughout the entire vertebral column (except as fused within the atlas-axis complex and as haemal arches in the tail) by the appearance of early mammals (Jenkins 1971). In addition, the previously freely articulating ribs in the cervical and lumbar regions become fused to their respective vertebrae starting in cynodont therapsids (Jenkins 1971). Gastralria (belly ribs) were also lost at some point in synapsid history (Romer 1956), although the rare preservation of these elements precludes a confident assessment of when. The latest occurrence of gastralria in the Late Permian primitive anomodont *Galechirus* are misinterpreted rib fragments (J. Hopson, pers. comm.).

*Postcranial novelty.*—Counted among the neomorphic elements originating within the nonmammalian synapsid fossil record are an ossified sternum or sternbrae in gorgonopsids, dicynodonts, tritylodontids, and early mammals. Patellae and other sesamoid ossifications occur in crown-group mammals, but remain unknown in earlier synapsids. Similarly, the acquisition of epipubic (i.e., marsupial) bones appears to have occurred somewhere within the mammal stem-lineage, but these were subsequently lost early within the placental history (Novacek et al. 1997). In sum, postcranial neomorphies are few compared to the loss or fusion of plesiomorphic elements.

#### *Williston's Law*

Williston (1914, p. 21) stated that, "a law in evolution [is] that the parts in an organism tend toward reduction in number, with the fewer parts greatly specialized in function." This principle has been inferred to be prevalent feature of invertebrate evolution, for example, within arthropod limbs and body segments (Cisne 1974; Patel 1994). In a series of articles, Gregory (1927, 1929, 1933; see also Gregory et al. 1935) related similar observations to the evolution of the vertebrate skull and titled this axiom "Williston's Law."

Williston (1914, pp. 24–25), however, also suggested that, "new bones have not appeared in the skulls of reptiles, birds or mammals; and that no bone which has once disappeared has ever been functionally regained by the descendants of those that lost it." Although the mechanisms by which bones such as the preparietal and anterior lamina have appeared in synapsid evolution are disputable, it is clear that they represent neomorphic elements not present ancestrally. Willis-

ton's second assertion is more difficult to test. Hopson (1995) has argued that parallel reductions are, in his view, a better explanation than multiple losses and reacquisitions of autopodial elements. Similar arguments have been made for squamate reproduction by Lee and Shine (1998); oviparity has given rise to viviparity at least 35 times, but the five possible reversals are all based on weak phylogenetic support. Among synapsids, the apparent reacquisition of a distinct supratemporal in the dinocephalian *Titanophoneus* by Orlov (1958) has been suggested to be in error (R. Reisz, pers. comm.).

#### *Systematic Implications of Evolutionary Trends*

Treating all characters as equivalent, both in terms of using unordered multistate characters instead of ordered ones and assuming forward and reverse transitions to be equally probable, is widespread among cladistic analyses of fossil taxa. Typically this procedure is used to "avoid a priori assumptions regarding character evolution" (Motani 1999, p. 474). Sober (1988), however, points out that both ordering and nonordering of characters represent models of evolution. Moreover, Felsenstein (1981) shows that character equivalency schemes imply uniform evolutionary rates for all characters and that changes in all character states are equally probable along each phylogenetic branch. However, given the strong trends for simplification documented above (Figs. 4, 5, 8, 9), is it reasonable to consider that bone gains and losses were equally probable to occur in the course of synapsid evolution?

Evolutionary trends in morphological characters pose a problem similar to that of transition and/or transversion substitution probabilities in molecular systematics; not all character state changes are equally likely to occur (Swofford and Olsen 1990; Broughton et al. 2000). The difference resides in the fact that whereas there are biophysical explanations for transition and/or transversion bias (Moritz et al. 1987), the mechanisms underlying morphological biases are far less clear. In addition, not only can active evolutionary trends make some types of characters more probable to change than others (i.e., presence/absence characters), but they set up a systematic bias in the direction of character state change (i.e., changes from presence to absence). Perhaps because of the intractability of assigning an objective differential weighting scheme to these types of characters, paleontologists have, on the whole, been content to consider all transitions to be equally likely (e.g., Patterson 1982). Recognizing instances of biased morphological change is imperative for appropriately modeling character evolution in phylogeny reconstruction.

#### *Synapsids as a Test Case*

How widespread is loss of skull bones in tetrapod evolution? Is the synapsid case furnished here representative or potentially misleading? My use of the synapsid fossil record obviously does not constitute a random, unbiased sample from the vertebrate tree. Instead, it was deliberately chosen for several reasons: it is the group with which I am most familiar; synapsids have a long, rich, and phylogenetically well-understood fossil record amenable to the type of analyses employed here; and this group's use has a long pedigree in this field of inquiry. Nonetheless, McShea (1991) has right-

ly pointed out that empirical examples demonstrate little if they were chosen because of their peculiarity.

There are reasons to believe, however, that the loss of skull bones is a general phenomenon among tetrapods. The first line of evidence involves comparing other modern tetrapods to their fossil relatives. Although the degree to which skull bones are fused or lost may not be as pronounced as in the basal synapsid-to-mammal transition studied here, extant tetrapods uniformly possess fewer distinct skull elements than do their extinct forebears: for example, frogs, caecilians, or salamanders to Paleozoic temnospondyls; modern turtles to the Triassic turtle *Proganochelys*; lizards, snakes, and *Sphenodon* to Permian lepidosauromorphs; extant crocodiles and alligators to Triassic protosuchids or sphenosuchids; and birds to nonavian theropod dinosaurs. Of course, without more detailed study it is impossible to say if bone loss in these clades corresponds to the driven trend pattern exhibited by synapsids.

Second, our ability to identify bones as homologous over long periods of geologic time suggests that the tetrapod skull pattern is fairly conservative. That is, there is no evidence that skull bones freely come and go. Problems in homologizing the bones of different taxa typically stem from the absence of fossil intermediates that document exactly which elements have been lost. This type of problem can be particularly acute when living forms are highly modified from their ancestral condition but have a scant fossil record.

A third observation, closely related to the second, is that neomorphic skull bones are rarely encountered. Some examples were previously mentioned under the Generating Neomorphies section above. Additional neomorphic skull bones are scarce among tetrapods but include the incorporation of palpebral elements into the skull roof of thyrophan dinosaurs (e.g., ankylosaurs, stegosaurs; Sereno 1986); the addition of osteoderms onto the snout of some heavily armored ankylosaurs (Sereno 1986); the dumbbell-shaped bone of the platypus (although this is considered to be derived embryonically from part of the premaxilla; Presley and Steele 1978); and an additional braincase ossification (termed the pseudomesethmoid) in some advanced pterosaurs (Kellner 1996). The septomaxilla of some xenarthrans is probably homologous with that of earlier synapsids, and not a neomorph as previously considered (Zeller et al. 1993). Thus, if, as has been proposed for synapsids, instances of bone gain are extremely infrequent, then we might expect a trend toward simplification to emerge in other tetrapod lineages as the natural outcome of unequal probability of gain versus loss.

#### SUMMARY

The premammalian synapsid fossil record exhibits a persistent trend of simplification; reductions, fusions, and losses of bony elements are more frequent than is neomorphic origin. Taxa with reduced complements of skull bones are consistently found to be among the most phylogenetically derived members of their respective clades, the stratigraphically highest appearing taxa, or both. Although skull growth has been shown to have an effect on skull bone number in some developmental studies (e.g., Coulombre et al. 1962; Ossen-

berg 1970), adult skull size in fossil synapsids has little relationship with skull bone number.

The distribution of synapsid SSM values corresponds to the pattern predicted by McShea's (1994) driven trend. Two possible mechanisms underlying this morphological trend include continued selective sorting or an intrinsic constraint that biased the direction of morphological change. The former corresponds to the traditional hypothesis that limited intracranial mobility was selectively advantageous among non-mammalian synapsids. The latter could reflect an intrinsic proclivity for the loss (opposed to acquisition) of the developmental regulation of heritable ossification centers. Distinguishing between these two hypotheses probably requires a level of precision unavailable from the paleontological realm. Regardless of its ultimate basis, however, biased morphological change does not conform to an evolutionary model of all character changes being equally likely, a common presupposition of many phylogenetic investigations. Understanding the characters potentially affected by active trends is an important step in establishing the appropriate evolutionary model for phylogeny reconstruction.

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## APPENDIX 1

Temporal, skull size, and phylogenetic data for the synapsid taxa used in this study. Electronic versions of this matrix are available upon request.

Taxon	SSM	AR <sub>F</sub>	AR <sub>L</sub>	CR	PD	L (Skull)	PC1
<i>Oedaleops campi</i>	63	3	3	1	3	1.856	-1.009
<i>Eothyris parkeyi</i>	64	4	4	1	3	1.803	●
<i>Casea broilii</i>	64	5	5	1	3	1.898	●
<i>Casea rutena</i>	64	5	5	1	4	2.032	●
<i>Cotylorhynchus romeri</i>	62	5	6	1	5	2.258	●
<i>Ennatosaurus tecton</i>	64	7	8	1	5	2.249	●
<i>Mycterosaurus longiceps</i>	64	5	5	2	4	1.920	●
<i>Mesenosaurus romeri</i>	62	7	7	2	5	1.626	-1.572
<i>Elliotsmithia longiceps</i>	64	9	9	2	5	1.880	●
<i>Aerosaurus wellesi</i>	64	3	3	2	4	1.993	●
<i>Varanops brevirostris</i>	64	5	5	2	5	2.146	●
<i>Varanodon agilis</i>	64	6	6	2	5	2.224	●
<i>Varanosaurus acutirostris</i>	64	4	5	3	5	2.161	●
<i>Ophiacodon</i> spp.	63	3	5	3	5	2.568	●
<i>Archaeothyris florensis</i>	63	1	1	3	4	1.960	●
<i>Ianthasaurus hardestii</i>	63	2	2	4	5	1.910	●
<i>Edaphosaurus</i> spp.	63	3	5	4	5	2.212	●
<i>Haptodus garnettensis</i>	63	2	2	5	5	2.029	-0.348
<i>Sphenacodon</i> spp.	63	3	3	6	7	2.473	●
<i>Secodontosaurus obtusidens</i>	63	4	5	6	8	2.440	0.490
<i>Dimetrodon</i> spp.	63	3	6	6	8	2.485	●
<i>Tetraceratops insignis</i>	61	5	5	7	7	1.990	●
<i>Biamosuchus tener</i>	61	7	9	8	9	2.266	●
<i>Hipposaurus</i> spp.	63	9	10	8	9	2.293	0.246
<i>Ictidorhinus martinsi</i>	62	13	13	8	10	1.980	●
<i>Lycanodon longiceps</i>	62	13	13	8	10	●	●
<i>Rubidgina angusticeps</i>	63	13	13	8	10	2.099	-0.059
<i>Anteosaurus magnificus</i>	60	9	9	9	12	2.751	●
<i>Titanophoneus potens</i>	59	9	9	9	12	2.701	●
<i>Australosyodon nyaphuli</i>	61	8	8	9	11	2.447	0.904
<i>Syodon efremovi</i>	61	9	9	9	11	2.364	0.658
<i>Styracocephalus platyrhynchus</i>	61	9	9	9	11	2.591	●
<i>Estemmenosuchus</i> spp.	61	8	8	9	11	2.718	1.483
<i>Jonkeria ingens</i>	59	9	9	9	12	●	●
<i>Tapinocaninus pamela</i>	57	8	8	9	13	2.692	1.611
<i>Struthiocephalus</i> spp.	59	9	9	9	14	2.707	1.496
<i>Ulemosaurus svijagensis</i>	55	9	9	9	15	2.574	●
<i>Moschops capensis</i>	59	9	9	9	15	2.574	1.438
<i>Patronomodon nyaphulii</i>	61	8	8	10	11	1.937	●
<i>Ostheria netzvetajevi</i>	58	9	9	10	13	1.969	●
<i>Ulemica invisa</i>	59	9	10	10	14	2.094	-0.302
<i>Suminia getmanovi</i>	58	12	13	10	14	1.691	●
<i>Galeops whaitsi</i>	59	9	9	10	13	1.760	●
<i>Eodicynodon oosthuizeni</i>	55	8	8	10	14	2.006	-0.633
<i>Pristerodon</i> spp.	53	9	13	10	15	1.850	-1.294
<i>Endothiodon uniseriis</i>	53	10	12	10	15	2.545	0.701
<i>Diictodon</i> spp.	53	9	13	10	17	2.018	-0.723
<i>Robertia broomiana</i>	53	9	9	10	17	1.956	●
<i>Myosaurus gracilis</i>	50	14	14	10	18	1.580	-1.995
<i>Emydops</i> sp.	55	11	13	10	19	1.744	-1.567
<i>Cistecephalus microrhinus</i>	49	11	12	10	20	1.745	-1.338
<i>Cistecephaloides boonstrai</i>	50	13	13	10	20	1.730	-1.450
<i>Kingoria nowacki</i>	50	12	13	10	18	2.201	0.069
<i>Oudenodon baini</i>	53	12	13	10	20	2.287	0.103
<i>Pelanomodon</i> sp.	51	13	13	10	21	2.398	0.694
<i>Aulacephalodon baini</i>	52	12	13	10	21	2.552	1.424
<i>Dicynodon</i> spp.	53	12	13	10	20	2.419	0.550
<i>Lystrosaurus murrayi</i>	53	14	14	10	21	2.151	0.184
<i>Kannemeyeria simocephalus</i>	46	15	16	10	22	2.589	1.375
<i>Tetragonias njalilus</i>	48	16	16	10	23	2.415	0.735
<i>Placerias gigas</i>	47	18	18	10	24	2.819	2.068
<i>Stahleckeria potens</i>	46	18	18	10	24	2.744	●
<i>Aelurosaurus felinus</i>	59	9	9	11	13	2.010	●
<i>Arctognathus</i> spp.	57	12	12	11	13	2.257	0.383
<i>Cephalicustriodus kingoriensis</i>	60	13	13	11	12	2.500	1.184
<i>Cyonosaurus</i> spp.	59	11	13	11	12	2.184	-0.387
<i>Leontocephalus</i> spp.	57	13	13	11	12	2.539	1.313
<i>Scylacops</i> spp.	60	12	13	11	12	2.257	0.308

## APPENDIX 1. Continued.

Taxon	SSM	AR <sub>F</sub>	AR <sub>L</sub>	CR	PD	L (Skull)	PC1
<i>Arctops watsoni</i>	59	12	13	11	13	2.447	0.840
<i>Lycaenops</i> spp.	58	11	13	11	14	2.323	0.212
<i>Prorubidgea alticeps</i>	60	12	13	11	15	2.450	●
<i>Dinogorgon</i> spp.	56	12	13	11	16	2.577	1.523
<i>Rubidgea</i> spp.	55	12	13	11	16	2.645	●
<i>Aloposaurus</i> spp.	59	12	13	11	12	2.141	-0.045
<i>Gorgonops</i> spp.	57	9	12	11	12	2.400	0.651
<i>Hofmeyria atavus</i>	55	11	13	12	14	1.861	-0.988
<i>Moschorhinus kitchingi</i>	56	13	14	12	16	2.359	0.886
<i>Euchambersia mirabilis</i>	57	13	13	12	16	1.918	●
<i>Olivieria parringtoni</i>	56	14	14	12	16	2.000	-0.559
<i>Theriognathus</i> sp.	55	13	13	12	17	2.234	0.139
<i>Moschowitsia vjuschkovi</i>	57	13	13	12	17	2.360	●
<i>Ictidosuchoides</i> spp.	56	10	13	12	16	2.050	-0.583
<i>Viatkosuchus sumini</i>	56	12	12	12	16	●	-0.022
<i>Regisaurus jacobi</i>	55	14	14	12	18	2.074	-0.454
<i>Erciolacerta parva</i>	58	14	14	12	18	●	●
<i>Bauria cynops</i>	55	15	16	12	18	2.060	-0.425
<i>Watsoniella breviceps</i>	58	16	16	12	19	2.202	●
<i>Microgomphodon oligocynus</i>	54	16	16	12	19	1.799	-1.111
<i>Lycosuchus vandereti</i>	59	9	9	12	13	●	●
<i>Glanosuchus macrops</i>	58	9	9	12	13	●	●
<i>Chthonosaurus velocidens</i>	54	13	13	12	13	●	●
<i>Ptomalestes avidus</i>	59	9	9	12	13	2.412	0.613
<i>Dvinia prima</i>	57	13	13	13	13	1.969	-0.752
<i>Procynosuchus delaharpeae</i>	56	13	13	14	14	1.947	-0.410
<i>Cynosaurus suppostus</i>	56	13	13	15	16	1.717	-1.529
<i>Galesaurid</i> n. sp.	55	13	13	15	17	1.969	●
<i>Galesaurus planiceps</i>	55	14	14	15	17	1.974	-0.883
<i>Platycraniellus elegans</i>	55	14	14	16	16	1.943	-0.997
<i>Thrinaxodon liorhinus</i>	55	14	14	16	16	1.838	-1.245
<i>Bolotridon frerensis</i>	55	16	16	16	16	1.944	●
<i>Cynognathus</i> sp.	54	15	16	17	18	2.430	0.586
<i>Diademodon mastacus</i>	53	15	16	17	19	2.314	0.236
<i>Trirachodon</i> spp.	54	15	16	17	20	1.905	-0.837
<i>Luangwa drysdalli</i>	51	16	16	17	21	2.161	●
<i>Massetognathus pascuali</i>	49	17	17	17	22	2.104	-0.380
<i>Exaeretodon frenguelli</i>	51	18	18	17	24	2.417	1.146
<i>Gomphodontosuchus brasiliensis</i>	51	18	18	17	24	●	●
<i>Tritylodon longaevus</i>	48	19	20	17	25	1.920	●
<i>Oligokyphus</i> spp.	47	19	20	17	26	2.187	●
<i>Bienotherium elegans</i>	47	20	20	17	28	2.114	●
<i>Kayentatherium wellsi</i>	50	20	20	17	27	2.445	●
<i>Bocatherium mexicanum</i>	49	22	22	17	29	2.086	●
<i>Bienotheroides wanhsienensis</i>	49	21	21	17	29	1.698	●
BP/1/2669	51	16	16	18	18	●	●
<i>Ecteninion lunesis</i>	51	18	18	19	19	1.992	●
<i>Probelesodon lewisi</i>	51	16	16	19	21	1.929	●
<i>Probelesodon sanjuanensis</i>	49	18	18	19	21	2.476	0.716
<i>Aleodon brachyrhamphus</i>	49	17	17	19	22	2.173	-0.227
<i>Belesodon magnificus</i>	50	18	18	19	22	1.904	●
<i>Probainognathus jenseni</i>	46	17	17	20	21	1.885	-1.166
<i>Pachygenelus monus</i>	45	20	20	21	22	1.903	●
<i>Sinoconodon</i> sp.	48	19	20	22	23	1.788	●
<i>Morganucodon oehleri</i>	45	19	20	23	24	1.421	●
<i>Ornithorhynchus anatinus</i>	33	23	23	24	25	2.020	●
<i>Didelphis virginiana</i>	35	23	23	25	26	2.050	●
<i>Homo sapiens</i>	26	23	23	25	26	2.284	●

## APPENDIX 2

Data matrix of the taxa and skull and lower jaw elements used in this study. Characters 1–35 correspond to the elements listed in Table 1. Character state definitions: 2, the bone was observed to be present and paired; 1, the bone was present but fused to an adjacent bone; 0, the bone was considered to be absent; ?, missing data scored as the primitive present and paired value for calculation purposes; X, missing data but phylogenetic optimization implies that a bone is present but fused; and Y, missing data but phylogenetic optimization implies that a bone is absent. Electronic versions of this matrix are available upon request.

Taxon	1	1111111112	222222223	3333
	1234567890	1234567890	1234567890	12345
<i>Oedaleops campi</i>	2?2222?222	2021222???	??????????	??YY?
<i>Eothyris parkeyi</i>	2?22222222	20222222??	?2?2222222	?20Y?
<i>Casea broilii</i>	2222222222	20222222?2	?2222222??	??00?
<i>Casea rutena</i>	2222222222	202?222???	?2?2222222	220Y?
<i>Cotylorhynchus romeri</i>	2222222222	2022222222	?222222222	0200?
<i>Ennatosaurus tecton</i>	2222222222	2022222222	?222222222	?200?
<i>Mycterosaurus longiceps</i>	2?22222222	20222?2?2?	?2222?22??	??YY2
<i>Mesenosaurus romeri</i>	2?22222222	2022222222	2222222222	02002
<i>Elliotsmithia longiceps</i>	?2?2222222	2022222222	?2?2?222??	?2Y02
<i>Aerosaurus wellesi</i>	2?2222?222	202?2222??	?2?2222222	22Y02
<i>Varanops brevisrostris</i>	2222222222	2022222222	?222222???	??002
<i>Varanodon agilis</i>	2222222222	2022222???	?2?2222222	?200?
<i>Varanosaurus acutirostris</i>	2222222222	2022222222	2222222222	?2002
<i>Ophiacodon</i> spp.	2?22222222	20212222??	2222222222	22002
<i>Archaeothyris florensis</i>	?2?2?22?2?	2021?2?2??	?2?222???	??YY?
<i>Ianthesaurus hardestii</i>	?222222222	20212?2?2?	?2?2?22222	22Y??
<i>Edaphosaurus</i> spp.	2222222222	2021222222	2222222222	2200?
<i>Haptodus garnettensis</i>	2222222222	202X22?222	2222222222	2200?
<i>Sphenacodon</i> spp.	2222222222	202X2222?2	2222222222	22Y0?
<i>Secodontosaurus obtusidens</i>	2222222222	2021222222	2222222222	2200?
<i>Dimetrodon</i> spp.	2222222222	2021222222	2222222222	2200?
<i>Tetraceratops insignis</i>	222?22??2?	2Y?X2?2222	22?22222??	??00?
<i>Biarmosuchus tener</i>	2222222222	2021202222	?22?2222??	?200?
<i>Hipposaurus</i> spp.	2222222222	23212022??	222?2222??	??0Y?
<i>Ictidorhinus martinsi</i>	222222?222	?2?212Y2?2?	122?2?2?2?	??002
<i>Lycaenodon longiceps</i>	222222?222	23?X2Y?222	1?2?2?2?2?	??0Y?
<i>Rubidgina angusticeps</i>	2222222222	2321202222	22?2222222	?200?
<i>Anteosaurus magnificus</i>	222222?222	2011202222	22?22222??	??00?
<i>Titanophoneus potens</i>	2222222222	2021222222	222?222222	00002
<i>Australosyodon nyaphuli</i>	22222?22?2	202X2Y22?2	22?2222222	?200?
<i>Syodon efremovi</i>	2222222222	2021202222	2222222222	?200?
<i>Styracocephalus platyrhynchus</i>	?2?2?2?2?2	2021?Y2222	222?2222??	?20Y?
<i>Estemmenosuchus</i> spp.	22?2?2?2?2	20?X202222	?2?222?2??	?20Y?
<i>Jonkeria ingens</i>	2222222222	2021202222	22?2222222	020Y?
<i>Tapinocaninus pamela</i>	2222222222	2021202222	222?222222	000Y?
<i>Struthiocephalus</i> spp.	2222222222	202120222?	222?2?2?2?	Y?0Y?
<i>Ulemosaurus svijagensis</i>	2222222222	1021102222	2222222222	0000?
<i>Moschops capensis</i>	2222222222	202120222?	222?2222??	0200?
<i>Patronomodon nyaphulii</i>	2?22222222	23212022?2	222?2?2?22	0200?
<i>Ostheria netzvetajevi</i>	222222?222	202120?222	1?2?2?2?2?	Y?0Y?
<i>Ulemica invis</i>	222222?222	202120?222	2?2?222222	0200?
<i>Suminia getmanovi</i>	2222222222	2021202222	1222222222	0200?
<i>Galeops whaiti</i>	2222222222	2?212Y?222	22?2222222	00Y?2
<i>Eodicynodon oosthuizeni</i>	2222222222	2321202222	2222112211	0000?
<i>Pristerodon</i> spp.	1?22222222	232120?222	1222112211	0000?
<i>Endothiodon uniseries</i>	122222?222	?32120?222	1222112211	0000?
<i>Diictodon</i> spp.	1222222222	232120?222	12221122XX	00002
<i>Robertia broomiana</i>	1?22?2?222	232120?222	122211?2XX	YY0Y?
<i>Myosaurus gracilis</i>	1?22222222	0321202222	12221X22XX	0000?
<i>Emydops</i> sp.	1?22222222	232120?222	122?11?2??	YY00?
<i>Cistecephalus microrhinus</i>	1222222222	002120?222	122211?2XX	0000?
<i>Cistecephaloides boonstrai</i>	1222222222	002120?222	12221?21?1	0000?
<i>Kingoria nowacki</i>	1222222222	032X202222	1222112111	0000?
<i>Oudenodon baini</i>	1222222222	2321202222	12221X2211	0000?
<i>Pelanomodon</i> sp.	122222?222	032120?222	122?112211	0000?
<i>Aulacephalodon baini</i>	122222?222	032120?222	12?2122?XX	0000?
<i>Dicynodon</i> spp.	1222222222	2321202222	12221122XX	00002
<i>Lystrosaurus murrayi</i>	1222222222	2321202202	1222112211	00002
<i>Kannemeyeria simocephalus</i>	1221222221	03?1202202	1222112211	0000?
<i>Tetragonias njalilus</i>	1?22222222	0321202102	12?2?112111	0000?
<i>Placerias gigas</i>	1222221222	Y3212022Y?	1122112211	000Y?
<i>Stahleckeria potens</i>	1?22222222	002120?2Y2	12?2?112111	0000?

## APPENDIX 2. Continued.

<i>Aelurosaurus felinus</i>	2?2222??22	23?X?Y?222	1????21222?	0200?
<i>Arctognathus</i> spp.	222??222??	2??1202122	1222222211	0200?
<i>Cephalicustriodus kingoriensis</i>	222222?222	2321202222	1??????????	Y?0Y?
<i>Cyonosaurus</i> spp.	222222222	2321202122	12222222??	Y?00?
<i>Leontocephalus</i> spp.	222222?222	2021202122	1??????????	Y?00?
<i>Scylacops</i> spp.	222222?222	2321202222	122?2222??	Y?00?
<i>Arctops watsoni</i>	222222?222	2321202122	1??2???????	Y?00?
<i>Lycaenops</i> spp.	222222222	2321202122	12??212222	Y?00?
<i>Prorubidgea alticeps</i>	222222222	2?21202222	122?2222??	Y?0Y?
<i>Dinogorgon</i> spp.	2222?22222	2021202???	X22222??11	Y?YY?
<i>Rubidgea</i> spp.	2222?2?22?	?0?1?Y2122	122?222211	020Y?
<i>Aloposaurus</i> spp.	222222?222	232120??22	1????2122??	Y?00?
<i>Gorgonops</i> spp.	222222222	2321202122	1222222211	Y?00?
<i>Hofmeyria atavus</i>	222222222	0011202222	1222222222	Y?00?
<i>Moschorhinus kitchingi</i>	222222222	0011202222	2222222222	0200?
<i>Euchambersia mirabilis</i>	22222??222	00?1202222	2??2???????	Y?00?
<i>Olivieria parringtoni</i>	222222222	0021202222	1222222222	Y?00?
<i>Theriongnathus</i> sp.	222222222	0011202222	1222222222	0200?
<i>Moschowhatsia vjuschkovi</i>	222222?222	00??2Y?222	1??????????	Y?00?
<i>Ictidosuchoides</i> spp.	222222222	0021202222	12222222??	Y?00?
<i>Viatkosuchus sumini</i>	222222?222	0021202222	12222222??	Y?00?
<i>Regisaurus jacobi</i>	222222?222	0011202222	1??2???????	Y?00?
<i>Eriaciolacerta parva</i>	222222?222	0022202222	2?2????????	Y?0Y?
<i>Bauria cynops</i>	222222222	0011202222	1222222???	Y?00?
<i>Watsoniella breviceps</i>	222222??22	0??X2Y???	X???22???	Y?YY?
<i>Microgomphodon oligocynus</i>	2222?2?2?2	002X2Y?2??	X???11???	Y?00?
<i>Lycosuchus vandereti</i>	2?2222??22	2Y2X2Y2222	2??222222?	Y?00?
<i>Glanosuchus macrops</i>	222222?222	2011202222	2222222222	0200?
<i>Chthonosaurus velocidens</i>	??2222?222	001X2Y?122	1??????????	Y?00?
<i>Ptomalestes avidus</i>	2?2222??22	20?12Y?222	22?2222222	0200?
<i>Dvinia prima</i>	222222?222	002120222?	?2?2222222	0200?
<i>Procynosuchus delaharpeae</i>	222222222	0021202222	1222222222	0200?
<i>Cynosaurus suppostus</i>	222222222	00212022?2	12222222??	Y?00?
<i>Galesaurid</i> n. sp.	222222222	0011202???	X2222222??	Y?0Y?
<i>Galesaurus planiceps</i>	222222222	00112022?2	12222222??	Y?00?
<i>Platycraniellus elegans</i>	2?2222?222	0011202???	X2?2???????	Y?00?
<i>Thrinaxodon liorhinus</i>	222222222	0011202222	1222222222	0200?
<i>Bolotridon frerensis</i>	2?2222??22	0YXX2Y???	X???22???	Y?YY?
<i>Cynognathus</i> sp.	222222222	0011202222	12221?2222	0200?
<i>Diademodon mastacus</i>	222222222	00112022?2	12221122??	0200?
<i>Trirachodon</i> spp.	222222222	0021202222	12221122??	Y?00?
<i>Luangwa drysdalli</i>	??2222??22	YYXX?Y??Y?	X???1X???	Y?0Y?
<i>Massetognathus pascuali</i>	222222222	0011202202	1222112211	0200?
<i>Exaeretodon frenguelli</i>	?22222?222	0011202?02	12?211???	Y?00?
<i>Gomphodontosuchus brasiliensis</i>	222222??2?	YYXX?Y?202	1???1X???	Y?YY?
<i>Tritylodon longaevus</i>	222222?202	001100?2Y?	X222221111	0203?
<i>Oligokyphus</i> spp.	2?2222?202	001X002?02	X2?22??111	Y?Y??
<i>Bienotherium elegans</i>	2222??2202	0011002202	X2?22?1111	0203?
<i>Kayentatherium wellsi</i>	2222222202	002X002202	12?22?2121	0203?
<i>Bocatherium mexicanum</i>	222222?202	0YXX0Y?202	1??22??XX	0203?
<i>Bienotheroides wanhsienensis</i>	2?22222202	0021002?02	X2?2222111	0203?
BP/1/2669	??22222222	0011202202	1222112222	Y?00?
<i>Ecteninion lunensis</i>	?222222222	0011202?22	12221X?211	Y?0Y?
<i>Probelesodon lewisi</i>	222222222	00112022?2	1222112211	0?00?
<i>Probelesodon sanjuanensis</i>	??22222222	00112Y???2	X2?21X1111	Y?YY?
<i>Aleodon brachyrhamphus</i>	222222????	YXX2Y?2?2	1???1X??XX	Y?YY?
<i>Belesodon magnificus</i>	222222?222	00112Y???2	1???21X111?	Y?0Y?
<i>Probainognathus jenseni</i>	2222221222	0011202202	1122112211	0200?
<i>Pachygenelus monus</i>	2222222202	0010002202	1222222111	02Y0?
<i>Sinoconodon</i> sp.	2222222202	002000?102	12222??XX	Y?03?
<i>Morganucodon oehleri</i>	2?22222202	001000?1Y2	X222202211	0203?
<i>Ornithorhynchus anatinus</i>	1112210101	0010000222	1221202011	00330
<i>Didelphis virginiana</i>	2022220201	0021000222	1222202011	00000
<i>Homo sapiens</i>	1012210101	0020000202	1222101011	00000

## APPENDIX 3

Data for Figure 4. Each subgroup's range of skull simplification metric values ( $R_{SSM}$ ), range of age ranks ( $R_{AR}$ ), first and last stratigraphic appearance, and an estimate of its absolute temporal duration in millions of years ( $R_{MY}$ ) is given. Recent mammals were excluded when making these clade duration estimates. The last appearance of Synapsida, Therapsida, Theriodontia, Cynodontia, Cynognathia, and Tritylodontidae is based on the Middle Jurassic tritylodontid genus *Bienotheroides*, because it is the latest appearing fossil taxon included in this analysis. Absolute age estimates were based on the time scales of Gradstein et al. (1995), Opdyke (1995), and Yugan et al. (1997). L, Late; M, Middle; E, Early.

Taxon	$R_{SSM}$	$R_{AR}$	First appearance	Last appearance	$R_{MY}$
Synapsida	18	21	L Moscovian	M Jurassic	127
"Pelycosaurs"	2	8	L Moscovian	M Guadalupian	42
Therapsida	17	18	M Sakmarian	M Jurassic	104
Dinocephalia	6	5	E Guadalupian	L Guadalupian	7
Anomodontia	15	10	E Guadalupian	L Carnian	45
Theriodontia	14	13	E Guadalupian	M Jurassic	88
Gorgonopsidae	5	4	E Guadalupian	L Tatarian	18
Therocephalia	5	7	E Guadalupian	E Anisian	27
Cynodontia	11	9	L Tatarian	M Jurassic	78
Cynognathia	7	7	E Olenekian	M Jurassic	64
Tritylodontidae	3	3	E Sinemurian	M Jurassic	20
Probainognathia	5	4	E Olenekian	M Sinemurian	46
Mammalia	3	1	E Hettangian	M Sinemurian	6