

EVOLUTIONARY PATTERNS AMONG PERMO-TRIASSIC THERAPSID^{*}

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■ **Abstract** A rich fossil record documents nonmammalian evolution. In recent years, the application of cladistic methodology has shed valuable light on the relationships within the therapsid clades Biarmosuchia, Dinocephalia, Anomodontia, and Cynodontia. Recent discoveries from South Africa suggest that Gondwana, rather than Laurasia, was the center of origin and radiation for many early therapsids. Because of their relative abundance and global distribution, therapsids have enjoyed widespread use in biostratigraphy, basin analysis, and paleo-environmental and -continental reconstructions. Synapsids (including therapsids) form the bulk of tetrapod diversity (in terms of both number of species and abundance) from Early Permian to Middle Triassic times and thus can provide critical information on the nature of the Permo-Triassic extinction in the terrestrial realm. Quantitative techniques have produced headway into understanding the relative importance of homoplasy and convergent evolution in the origin of mammals.

INTRODUCTION

Central to an understanding of mammalian origins has been an assemblage of primarily Permian and Triassic fossils termed “nonmammalian therapsids” or “mammal-like reptiles” (Hopson & Crompton 1969, Crompton & Jenkins 1973, Kemp 1982). Although the curious blend of reptilian and mammalian features preserved in these fossils puzzled the nineteenth century paleontologists who first described them (e.g., Owen 1844), the morphological stages they preserve are now recognized as documenting in exceptional detail the acquisition of mammalian features within an evolving lineage. More generally, nonmammalian therapsids were the dominant terrestrial vertebrates for much of the late Paleozoic and early

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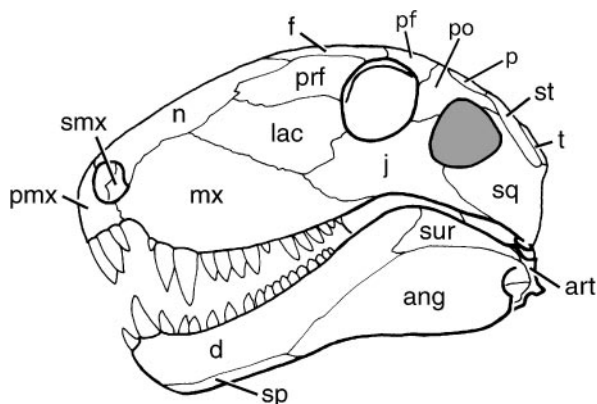


Figure 2 Skull of the pelycosaur-grade synapsid *Dimetrodon* in lateral view. The shaded region represents the lateral temporal fenestra, a diagnostic feature of all synapsids, including modern mammals. Abbreviations: ang, angular; art, articular; d, dentary; f, frontal; j, jugal; lac, lacrimal; mx, maxilla; n, nasal; p, parietal; pf, postfrontal; pmx, premaxilla; po, postorbital; prf, prefrontal; smx, septomaxilla; sp., splenial; sq, squamosal; st, supratemporal; sur, surangular; t, tabular. Reconstruction modified from Sidor & Hopson (1998).

at least 300 Mya (Laurin & Reisz 1995). At the time of their first appearance in the fossil record, however, early synapsids are distinguished from their reptilian contemporaries by only a few features, chief among which is their possession of a lateral temporal fenestra (Figure 2). Although explanations for this feature's origin remain speculative, a temporal opening is retained in all synapsids, including modern mammals.

The early stages of synapsid diversification are primarily recorded in the Upper Pennsylvanian and Lower Permian rocks of North America (Romer & Price 1940). Nontherapsid synapsids, “pelycosaurs” of traditional usage, occupied a wide variety of ecological niches and taxonomically dominated most paleofaunal assemblages in which they are found. Six family-level clades encompassing ~30 genera are currently recognized (Reisz 1986).

Two points are of special ecological note. First, large-bodied sphenacodontids such as the familiar sailback *Dimetrodon* (Figure 2) likely represent the earliest terrestrial carnivores to prey on similar-sized animals. Second, phylogenetic studies have postulated that herbivory originated twice within the early synapsids—once in the edaphosaurid *Edaphosaurus* (Modesto 1995) and once in the Caseidae (Olson 1968). Indeed, the successful diversification of early amniotes in general, and synapsids in particular, has been suggested by at least some workers to be tied to the advent of herbivory in these groups (Modesto 1992, Reisz & Sues 2000).

Pelycosaur-grade synapsids and their descendents, the therapsids, have long been known to have disjunct geographic and temporal distributions. In general,

Early Permian pelycosaurids are recorded from paleoequatorial regions (e.g., Europe and North America), whereas therapsids were, until very recently, predominantly known from the Late Permian of Russia and South Africa (i.e., high latitude regions). The apparent lack of overlap between these two groups has been considered by some to indicate a physiological advance of the latter permitting their geographic dispersal (McNab 1978, Parrish et al. 1986). More recent discoveries, however, have increased the degree of overlap between these two groups. Finds of early therapsids alongside the pelycosaur genera *Elliotsmithia* (Dilkes & Reisz 1996, Reisz et al. 1998, Modesto et al. 2001), *Mesenosaurus* (Reisz & Berman 2001), and *Ennatosaurus* (Ivachnenko 1990) clearly demonstrate the ability of pelycosaur-grade taxa to persist into the Late Permian in presumably more temperate climates.

THE ORIGIN OF THERAPSID

All synapsids phylogenetically more derived than sphenacodontids form the clade Therapsida (Laurin & Reisz 1996). When compared with their pelycosaur-grade precursors, the members of this clade are characterized by a greatly increased number of mammal-like features in both the cranial and postcranial skeleton (Kemp 1982, Sidor & Hopson 1998). For example, the loss of several skull elements [e.g., supratemporal (Figure 2) anterior coronoid] foreshadows the drastically reduced complement of skull bones characteristic of mammals (Sidor 2001), and the acquisition of an inflected femoral head has been thought to signal a more upright hindlimb posture in this group (Kemp 1978; Blob 1998, 2001). In addition, carnivorous adaptations initiated within sphenacodont-grade taxa are carried further within therapsids: The temporal fenestra is increased in size such that jaw adductor muscles have a larger area of origination (contrast Figure 2 with Figures 4 and 5), the upper and lower canines are enlarged such that the maxilla (mx in Figure 4) gains a new contact with the prefrontal (prf in Figure 4) and the dentary is expanded anteriorly, and fusion of the basicranial articulation reinforces the skull against the forces of subduing larger prey.

Therapsid remains are first recovered unequivocally from Upper Permian strata in Russia (Ivachnenko et al. 1997) and South Africa (Rubidge 1990a, 1995). Although the Russian forms have traditionally been thought to represent an earlier and more primitive radiation (e.g., Olson 1962), the discovery of a new paleofauna from the base of the Beaufort Group in South Africa has cast doubt on this theory (Rubidge 1990a). Moreover, recent phylogenetic work has postulated a Gondwanan origin for several therapsid subgroups (e.g., Modesto et al. 1999). A recently discovered therapsid fauna from the Permian of China (Li & Cheng 1995) is of uncertain temporal relationship to those of Russia and South Africa, but based on the primitive cast of its constituent taxa, it might represent the oldest therapsids yet recovered.

THE POSITION OF *TETRACERATOPS* On the basis of several derived features, Laurin & Reisz (1996) recently suggested that *Tetraceratops insignis* represents the most

primitive therapsid known (i.e., the sister taxon to all other therapsids). Because of its relatively late appearance (middle Early Permian), Laurin & Reisz's phylogenetic hypothesis implies that the greater than 30 characters diagnosing more advanced therapsids probably evolved in a remarkably short window of time (~8–10 myr) (Sidor & Hopson 1998). Although not impossible, the damaged and poorly preserved nature of the single *Tetraceratops* specimen makes a confident assessment of its phylogenetic placement difficult. For the remainder of our discussion, the terms “Therapsida” and “therapsid” will be used to denote post-*Tetraceratops* taxa.

HIGHER-LEVEL THERAPSID RELATIONSHIPS

Higher-level therapsid relationships have been the subject of cladistic attention for over 15 years, and although some areas of consensus have emerged, other areas remain contentious. As noted by Hopson (1991b), these differing perspectives on therapsid phylogeny inevitably produce contrasting views on the prevalence of evolutionary phenomena such as convergent evolution. In this section we review recent work on the relationships among the higher groups of therapsids (i.e., biarmosuchians, dinocephalians, anomodonts, gorgonopsians, therocephalians, and cynodonts). The cladogram depicted in Figure 3 and outlined below represents what we consider to be the best-supported hypothesis, although we note differing viewpoints where appropriate.

Therapsida

Romer & Price (1940) recognized that all therapsids arose from a single sphenacodont lineage, but Olson (1959, 1962) later advocated a polyphyletic origin of Therapsida, with anomodonts being independently derived from caseid ancestors. A similar view was held by Boonstra (1972), who argued for three independent originations of the therapsid grade of organization. Cladistic analyses have shown, however, that diverse features unite all therapsids in a clade, and that the features shared between anomodonts and caseids are more easily interpreted as convergent adaptations to an herbivorous diet.

As briefly discussed above, numerous morphological changes distinguish therapsids from their Early Permian pelycosaur forebears. For example, Sidor & Hopson (1998) suggested that between 36 and 48 characters can be used to identify Therapsida, depending on character optimization (see also Rowe 1986, Laurin & Reisz 1996). In addition to those previously discussed, modifications of the therapsid skull include an elongation of the dorsal process of the premaxilla (pmx in Figure 2), the pineal foramen being raised on a prominent boss or chimney (pin b in Figure 4), the posterior coronoid shifting ventrally so that it fails to form the dorsal margin of the lower jaw in medial view, and the reflected lamina adopting a characteristic pattern of ridges on its lateral surface and becoming more deeply

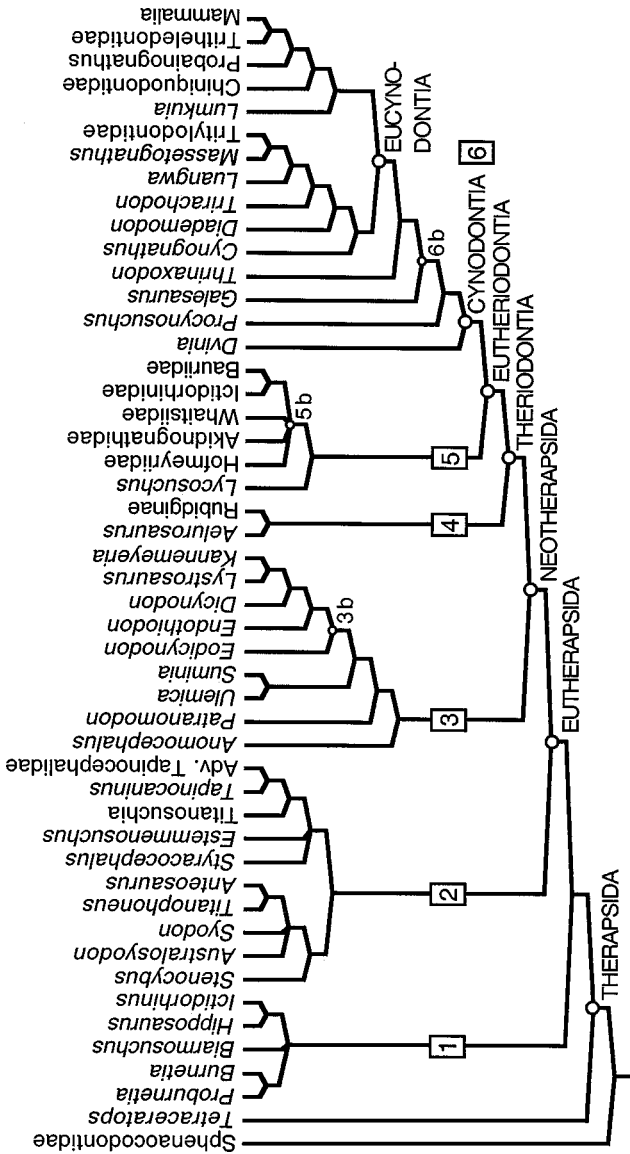


Figure 3 Cladogram of the therapsid groups considered in the text. 1, Biarmosuchia; 2, Dinocephalia; 3, Anomodontia; 3b, Dicyonodontia; 4, Gorgonopsia; 5, Therocephalia; 5b, Eutherocephalia; 6, Cynodontia; 6b, Epicynodontia. This cladogram is by no means exhaustive. For example, only the most derived pelycosaur family is shown here (e.g., Sphenacodontidae). Relationships depicted here are based on those proposed by Hopson (1991, 1994), Rubidge & van den Heever (1997), Sidor & Hopson (1998), Modesto et al. (1999) and B. S. Rubidge & C. A. Sidor (unpublished data). See text for further details.

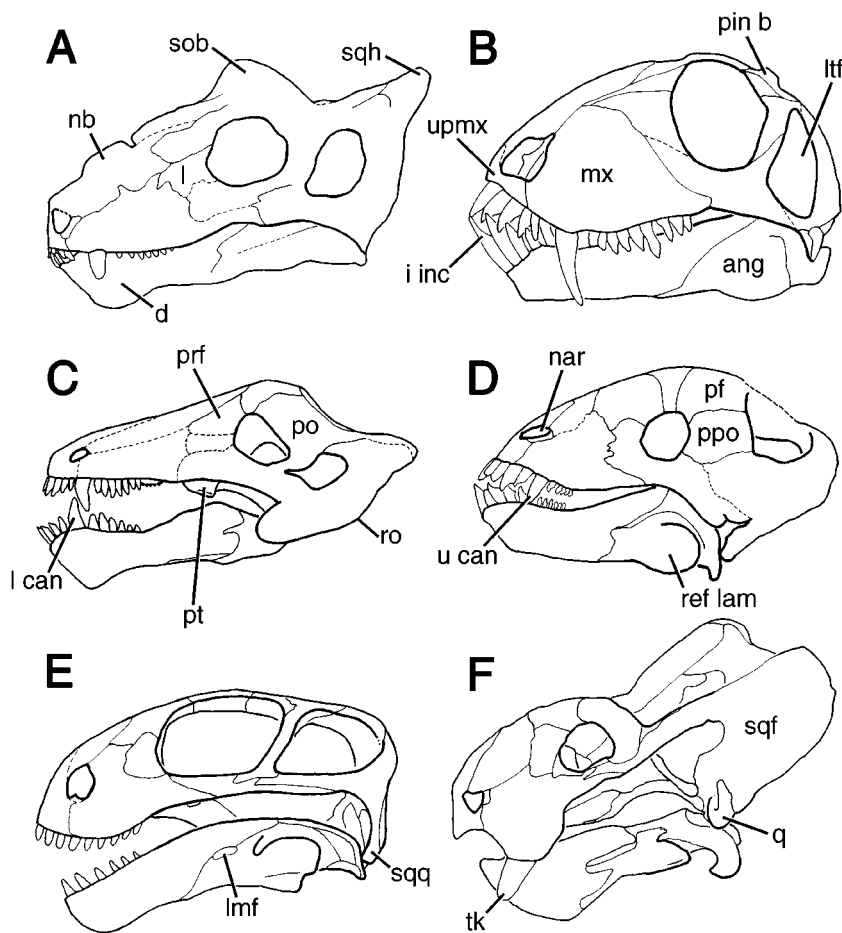


Figure 4 Skulls of selected nontheriodont therapsids in lateral view (not to scale). (A) the burnetiamorph biarmosuchian *Proburnetia*; (B) the anteosaurid dinocephalian *Stenocybus*; (C) the tapinocephalian dinocephalian *Styracocephalus*; (D) the basal tapinocephalid dinocephalian *Tapinocanius*; (E) the basal anomodont *Patranomodon*; (F) the advanced dicynodont *Kannemeyeria*. Anatomical abbreviations: ang, angular; d, dentary; i inc, intermeshing incisors; l, lacrimal; l can, lower canine; lmf, lateral mandibular fenestra; ltf, lateral temporal fenestra; mx, maxilla; nar, external naris; nb, nasal boss; pf, postfrontal; pin b, pineal boss; po, postorbital; ppo, pachyostosed postorbital bar; pt, transverse flange of the pterygoid bone; ref lam, reflected lamina of the angular; ro, anteriorly rotated occiput; sob, supraorbital boss; sqf, squamoal fossa for jaw adductor musculature; sqh, squamosal horn; sqq, quadrate process of squamosal; tk, tusk-like upper canine; u can, upper canine; upmx, upturned premaxilla. Reconstructions modified from the following original sources: (B) Cheng & Li (1997); (C) Rubidge & van den Heever (1997); (D) Rubidge (1991); (E) Hopson (1994); (F) Renault; 2000.

incised dorsally and, thus, more separated from the body of the angular (ang, ref lam in Figures 2, 4). Postcranial synapomorphies are also abundant and are suggestive of improved locomotor ability in therapsids. These include a deepening and rounding of both the pectoral glenoid and pelvic acetabulum, the replacement of the primitively screw-shaped humeral articular head with a rounded surface, the inflection of the femoral head to permit the hindlimbs to adopt a more adducted configuration, a narrowing of the scapular blade, and loss of intercentra in the trunk region.

Eutherapsida

Hopson & Barghusen (1986) and Rowe (1986) initially recognized a clade uniting dinocephalians, anomodonts, and theriodonts, which Hopson (1994) later termed Eutherapsida. However, because of the divergent morphologies of its subgroups, unambiguous synapomorphies uniting this proposed clade have been difficult to identify. Among the best candidates are that (*a*) the zygomatic arches are bowed such that the temporal fenestra is expanded laterally, (*b*) the ulna lacks a distinct, ossified olecranon process, and (*c*) the fifth pedal digit has only three phalanges. Rowe & van den Heever (1988) have suggested that the mammalian phalangeal formula (i.e. 2-3-3-3-3) should be considered a eutherapsid synapomorphy, but therapsid phalangeal evolution is extremely complex and recent workers have rejected the use of the mammalian phalangeal formula as a synapomorphy at this hierarchical level (Hopson 1995, Sidor 2000). Kemp (1982), Battail (1992), and Sidor (2000) have put forward alternatives to the recognition of a eutherapsid clade, but these are also supported by only a few characters.

Neotherapsida

The clade including all therapsids more advanced than biarmosuchians and dinocephalians (i.e., anomodonts and theriodonts) has recently been termed Neotherapsida by Hopson (1999) (see Figure 3). Cranial synapomorphies for this group include a ventrally expanded squamosal (sq in Figure 4; sq in Figure 5) that hides most of the quadrate (q in Figures 4, 5) and quadratojugal in posterior view and an epipterygoid (epi in Figure 5) that broadly contacts the underside of the parietal (p in Figure 5). Postcranial synapomorphies include the presence of atlantal epiphyses and an enlarged obturator foramen on the puboischial suture. Although most workers accept the monophyly of a clade including anomodonts, gorgonopsians, therocephalians, and cynodonts, the branching sequence among these taxa has been strongly disputed (discussed below).

Theriodontia

Theriodonts are advanced carnivorous therapsids. This clade comprises three main subgroups, Gorgonopsia, Therocephalia, and Cynodontia, that are united by their common possession of a flat, low snout (i.e., the dorsal surface of the nasals is

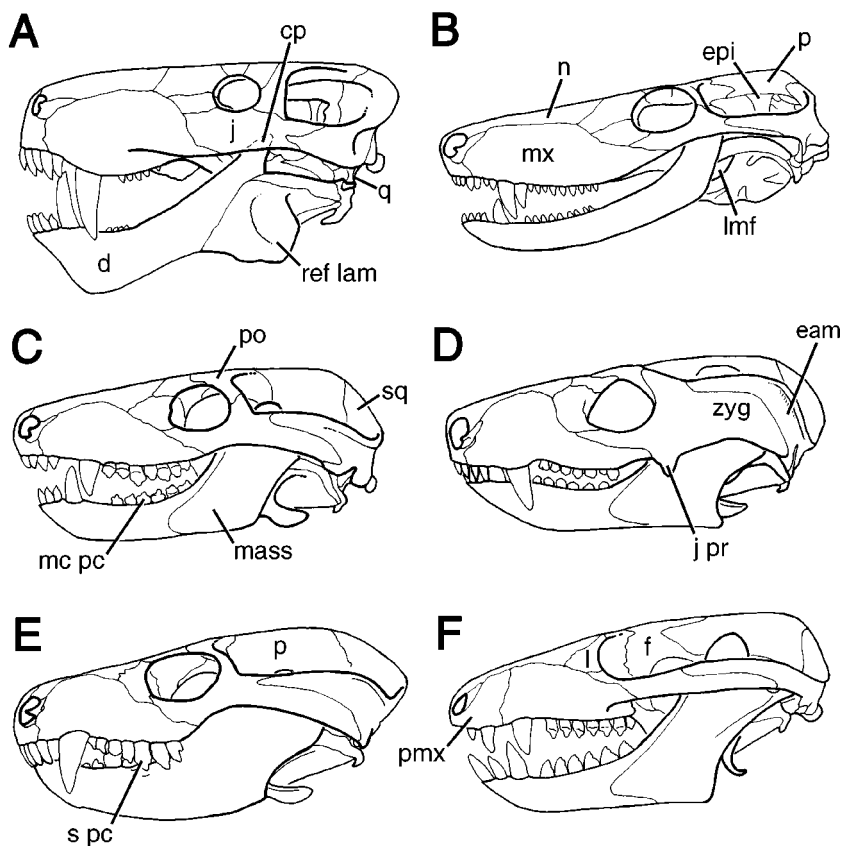


Figure 5 Skulls of selected theriodonts in lateral view (not to scale). (A) the gorgonopsian *Leontocephalus*; (B) the eutheriocephalian *Ictidosuchooides*; (C) the basal cynodont *Thrinaxodon*; (D) the basal cynognathian *Trirachodon*; (E) the basal probainognathian *Lumkuia*; (F) the tritheledontid *Pachygenelus*. Anatomical abbreviations: cp, coronoid process of the dentary; d, dentary; eam, fossa on the squamosal termed the external auditory meatus; epi, epipterygoid; f, frontal; j, jugal; j pr, jugal suborbital process; l, lacrimal; lmf, lateral mandibular fenestra; mass, masseteric fossa; mc pc, multicusped postcanine teeth; mx, maxilla; n, nasal; p, parietal; pmx, premaxilla; po, postorbital; q, quadrate; ref lam, reflected lamina of the angular; s pc, sectorial postcanine teeth; sq, squamosal; zyg, zygomatic arch (composed of the jugal and squamosal bones). Reconstructions modified from the following original sources: (A) Sidor & Hopson (1998); (B) (C) (D) (F) Hopson (1994); (E) Hopson & Kitching (2001).

horizontal), a narrow temporal roof (such that the intertemporal width is equal to or less than the interorbital width), and most importantly, a free-standing coronoid process (for the localized insertion of jaw adductor musculature) (cp in Figure 5).

Kemp (1988) contested the features used by Hopson & Barghusen (1986) to support the grouping of gorgonopsians with therocephalians and cynodonts (to form a monophyletic Theriodontia), but gave little indication of where gorgonopsians should be placed. In contrast, Rowe (1986; see also Gauthier et al. 1988) suggested that anomodonts are more closely related to eutheriodonts (therocephalians + cynodonts) than are gorgonopsians, thereby rendering Theriodontia paraphyletic. After assessing these proposals, Hopson (1991b, p. 659) suggested that “the alternatives to accepting an association of Gorgonopsia with Therocephalia and Cynodontia are not sufficiently convincing to require abandonment of the Theriodontia.” In a final permutation, Modesto et al. (1999) suggested that therocephalians and anomodonts form a clade to the exclusion of dinocephalians and gorgonopsians. The paucity of phylogenetic research on gorgonopsians and therocephalians has led to little progress in understanding theriodont monophyly or its alternatives.

Eutheriodontia

A sister-group relationship between therocephalians and cynodonts is currently accepted by most, if not all, workers (e.g., Kemp 1982, 1988; Hopson & Barghusen 1986, Rowe 1986, Hopson 1991b, 1994; Sidor & Hopson 1998). Eutheriodontia is a well-supported clade with synapomorphies that can be easily traced to their mammalian homologues. For example, eutheriodonts lose palatine teeth, antero-posteriorly expand the epipterygoid (epi in Figure 5), which is the homologue of the alisphenoid in mammals, reduce the temporal roof to a narrow sagittal crest, and shorten the posterior ramus of the postorbital (po in Figure 5) so that it fails to contact the squamosal (sq in Figure 5).

Hillenius (1992, 1994) noted the presence of ridges on the inner surface of the nasal and maxilla bones in the basal therocephalian *Glanosuchus* and several primitive cynodonts and argued that they indicate the presence of respiratory turbinate bones. This type of turbinate is found exclusively in mammals and birds and is thought to be an osteological correlate of endothermy. As such, this apparent synapomorphy may be indicative of increased oxygen consumption rates and an eutheriodont beginning for mammal-like metabolism.

Cynodontia

Cynodonts, in the form of *Procynosuchus* and *Cynosaurus* from southern Africa and *Dvinia* from Russia, first appear near the end of the Late Permian and include mammals as their extant subgroup. Many of the morphological hallmarks of mammals first appear as apomorphies in the premammalian cynodonts, and as noted by Hopson (1991b), most of these can be related to obtaining and orally processing

food. In addition, some of these features have been suggested to be adaptations indicative of some degree of endothermy (McNab 1978, Hillenius 1994). Cynodontia is the best-supported therapsid subclade, with at least 25 characters diagnosing it (Hopson & Barghusen 1986, Rowe 1986, Sidor & Hopson 1998). We restrict our discussion to only a few features of special evolutionary significance.

The appearance of several apomorphic features early in cynodont evolution signal a fundamental reorganization of the jaw closing musculature. In *Dvinia* and *Procynosuchus*, the two earliest cynodonts known, the coronoid process of the dentary bears a shallow fossa on its dorsolateral surface (Tatarinov 1968, Kemp 1979). This fossa, in combination with a flaring of the zygomatic arch that situates the coronoid process near the middle of the temporal fenestra, has been taken as evidence for the differentiation of the primitively unipartite *m. adductor mandibulae* into the mammalian *m. temporalis* and *m. masseter* (Barghusen 1968). The possession of these two muscles is a uniquely mammalian feature that underlies the muscular “sling” that permits the complex jaw movements characteristic of this group (Crompton & Parker 1978). In cynodonts more derived than *Dvinia* and *Procynosuchus* (Epicynodontia sensu Hopson & Kitching 2001) (clade 6b in Figure 3), the masseteric fossa is enlarged such that it approaches the ventral margin of the mandible (mass in Figure 5).

Several other cynodont apomorphies can be interpreted as consequences of a more refined set of jaw-closing muscles. The parietal bone extends ventrally to more extensively contribute to the sidewall of the braincase, and the epipterygoid is expanded to alisphenoid-like proportions and makes a new contact with the frontal (f in Figure 5). In addition, the origination site of the *m. temporalis* on the parietal crest is elongated anteriorly so as to incorporate the pineal foramen.

Two more features have been considered to represent adaptations to the increased oral processing (i.e., chewing) of food. First, the postcanine dentition is elaborated early in cynodont evolution by the addition of mesial and distal accessory cusps (mc pc in Figure 5) and a lingual cingulum (a small shelf on the medial side of the tooth's crown). Second, all cynodonts possess at least a rudimentary secondary palate. In the most basal forms (e.g., *Dvinia*, *Procynosuchus*, *Galesaurus*), the bony plates extending medially from the maxilla and palatine bones fail to contact one another. In *Thrinaxodon* and eucynodonts, however, the plates suturally connect along the midline and thereby create a complete secondary palate (Fourie 1974). As in modern mammals, the secondary palate serves to separate the airway from the food-processing system.

Based on phylogenetic evidence, at least two cynodont lineages survived the Permo-Triassic mass extinction. The cynodonts *Galesaurus* and *Thrinaxodon* dominated the Early Triassic, but by the beginning of the Middle Triassic, cynodonts were diversifying and had diverged phylogenetically into two main subgroups: Probainognathia and Cynognathia. The latter group, principally distinguished by their transversely expanded cheek teeth, was much more numerous than the former, but both groups persisted beyond the Triassic. Advanced cynodonts are considered in more detail below.

SYSTEMATIC REVIEW OF THERAPSID DIVERSITY

In this section we review the six major clades of Permo-Triassic therapsids in greater detail. It should be noted that in contrast to the amount of attention that higher-level therapsid relationships have attracted, lower-level systematics have lagged behind. As a result, some of the results we present are based on very recent, or as yet unpublished, research.

Biarmosuchia

The higher-taxon Biarmosuchia (clade 1 in Figure 3) was the most recently recognized higher-level therapsid clade, with Hopson & Barghusen (1986) being the first to determine that taxa such as *Biarmosuchus*, *Hipposaurus*, *Burnetia*, and *Ictidorhinus* were the most primitive of the post-*sphenacodont* synapsids. More recently, Hopson (1991b) produced several characters in support of biarmosuchian monophyly, and Sidor (2000) has provided a preliminary lower-level analysis of the group.

In contrast to those of most other therapsids, biarmosuchian fossil remains are exceedingly rare. Most genera are known from only one or two poorly preserved skulls and, as a consequence, the diagnostic characters common to the group have been difficult to ascertain with confidence.

Biarmosuchians were typically small-to-medium sized carnivores that combine several primitive pelycosaur-grade features (e.g., the configuration of the temporal region), with several unique specializations of their own. The latter include a squamosal with a long ventral quadrate ramus and an elongate zygomatic process that extends under the orbit. In addition, the ventral edge of the occiput is moderately rotated anteriorly, and there is a pronounced difference in the height between the canine and postcanine regions of the dentary. Although few taxa possess postcranial remains, two possible biarmosuchian postcranial synapomorphies are the elongation of the cervical vertebrae (Sidor 2000) and the fusion of distal tarsals IV and V (Hopson 1991b). Although not all taxa have been included in formal cladistic analysis, biarmosuchians can be divided into a (probably) paraphyletic grade including most of the "ictidorhinids" (e.g., *Ictidorhinus*, *Hipposaurus*) and a derived subclade, Burnetiamorpha.

Burnetiamorph skulls are adorned with numerous protuberances and horn-like outgrowths (nb, sob, sqh in Figure 4). For much of this group's history, however, it was known from only two taxa, *Burnetia* and *Proburnetia* (Figure 4A). Two recently discovered taxa are in the process of being described (Sidor 2000, B. S. Rubidge & J. W. Kitching, unpublished data). These new taxa, in addition to the recognition that *Niuksenitia sukhonensis* is a burnetiamorph (Ivachnenko et al. 1997), have prompted the first cladistic appraisals of burnetiamorph relationships (Sidor 2000, B. S. Rubidge & J. W. Kitching, unpublished data). Biogeographically, the phylogenetic conclusions of these workers suggest that burnetiamorphs had a Gondwanan origin and that this clade displays no evidence of Late Permian endemism, as has been suggested for basal anomodonts (e.g., Modesto et al. 1999).

Dinocephalia

Dinocephalians (clade 2 in Figure 3) are a diverse group of basal therapsids primarily known from Upper Permian rocks of South Africa (Boonstra 1963; Rubidge 1991, 1994; Rubidge & van den Heever 1997) and Russia (Ivachnenko 1995, 1996a, 2000), although new finds have been recorded from Zimbabwe (Lepper et al. 2000, Munyikwa 2001), Brazil (Langer 2000), and China (Li & Cheng 1995; Cheng & Li 1996, 1997; Li et al. 1996). Dinocephalia is the earliest group of therapsids for which a significant radiation can be identified, but for all their early success, they became extinct by the middle Late Permian (Boonstra 1971). Important new discoveries have been made since King's (1988) review, and as such, are emphasized here.

Dinocephalians, or the "terrible-headed" therapsids, can be divided into two main groups: the carnivorous anteosaurs and the herbivorous tapinocephalians. Derived characters uniting these two groups have been debated but can be shown to include nonterminal external nares (nar in Figure 4) (Grine 1997), the loss of a vomerine process of the premaxilla so that vomer abuts the body of the premaxilla, a preorbitally positioned transverse flange of the pterygoid (pt in Figure 4), the lack of ridges and fossae on the lateral surface of the reflected lamina (ref lam in Figure 4), and the presence of a foramen on the inner surface of the lower jaw between the prearticular and angular (Sidor 2000). The group's traditional defining feature, intermeshing upper and lower incisors (i inc in Figure 4), has recently been identified in several biarmosuchians (Sigogneau-Russell 1989; CA Sidor & BS Rubidge, unpublished data) and thus requires a more detailed appraisal of its phylogenetic distribution. Postcranially, the fifth metapodial of all dinocephalians in which it is known is more robust and at least as long as the fourth metapodial.

The most basal dinocephalians are thought to be the Russian anteosaurs (Boonstra 1971, Hopson & Barghusen 1986), although some workers consider the estemmenosuchids to be more primitive (Kemp 1982, King 1988). The massive South African genus *Anteosaurus* is considered the most derived anteosaur, prompting the conclusion that dinocephalians originated in Russia and arrived in southern Africa via overland migrations. The description of *Australosyodon* from the *Eodicynodon* Assemblage Zone, however, has shown that primitive anteosaurs are also present in the southern hemisphere (Rubidge 1994). *Sinophoneus* (Cheng & Li 1996) and *Stenocybus* (Figure 4B) (Cheng & Li 1997), from the Gansu Province of China (Li & Cheng 1995, Li et al. 1996), also appear to be basal anteosaurian dinocephalians.

The Tapinocephalia has been defined as all dinocephalians more closely related to *Tapinocephalus* than to *Anteosaurus* (Sidor 2000). Morphological variation related to three main characteristics (viz. adaptations to herbivory, body size, and skull pachyostosis) has formed the basis for most tapinocephalian classifications.

The most primitive members of the Tapinocephalia are *Estemmenosuchus*, from Russia, and *Styracocephalus* (Figure 4C), from South Africa. Both species of *Estemmenosuchus*, *E. uralensis* and *E. mirabilis* (a slightly smaller form), have strange bony protuberances on the skull roof and large temporal fenestrae. As in

other dinocephalians, they have enlarged, intermeshing incisors (but these lack heels), and they also have prominent canines, as are present in anteosaurids and titanosuchians. *Styracocephalus* was previously known only from its very distorted holotype, but several recently discovered specimens have permitted a redescription of the skull (Rubidge & van den Heever 1997). The genus is considered to be characterized by a large posteriorly projected horn made up of the postorbital and squamosal bones. Despite the appearance of a close relationship to *Estemmenosuchus* suggested by the presence of horns in both genera, these structures develop from different bones of the skull roof. In the absence of clear synapomorphies, these two genera are best considered as basal tapinocephalians forming a trichotomy with the remaining members of the clade (Rubidge & van den Heever 1997).

The next most derived taxa in the Tapinocephalia are *Jonkeria* and *Titanosuchus*, the Titanosuchia of Boonstra (1969). Although titanosuchians retain a prominent canine tooth (as is present in anteosaurians and more primitive tapinocephalians), the incisors have a large talon and a prominent crushing heel on their lingual surface. The upper incisors intermesh with the lowers in such a way that when the jaws occlude, the heels meet to form a crushing surface, used to grind plant material. *Estemmenosuchus* and *Jonkeria/Titanosuchus* share several dental features not seen in other dinocephalians (e.g., the lower postcanine teeth are inset from the lateral margin of the dentary, and the upper postcanines are continuous with the incisors medial to the canine).

Tapinocephalians more derived than the titanosuchians form the Tapinocephalidae. A plethora of tapinocephalid genera have been described from the *Tapinocephalus* Assemblage Zone of South Africa (see Boonstra 1969, King 1988). Other tapinocephalids include one species of *Criocephalus* from the Madumabisa mudstones of Zimbabwe (Boonstra 1969) and *Ulemosaurus* from the Eshevo complex of Russia (Efremov 1940).

Tapinocephalids carry even further the specializations toward herbivory initiated in the titanosuchians. In tapinocephalids, however, the postcanines as well as the incisors have a lingual heel, and interdigitation of the entire dentition occurs instead of just the anterior teeth. The basal form *Tapinocaninus* (Figure 4D) (Rubidge 1991) has canine teeth in both the upper and lower jaws (e.g., u can in Figure 4), a feature that is lost in all other tapinocephalids. *Tapinocaninus* also retains a large temporal fenestra compared with other, more derived, tapinocephalids, in which it is impinged upon by the increasingly pachyostotic bones of the skull roof (particularly the postorbital) (ppo in Figure 4). Barghusen (1975) makes convincing arguments that the heavily thickened skulls of tapinocephalids were used for head butting.

Anomodontia

Anomodontia (clade 3 in Figure 3) and their highly diverse subclade, Dicynodontia (clade 3b), were arguably the single most successful group of Permian

therapsids (King 1990). Appearing early in the Late Permian and surviving until the Late Triassic, anomodonts are known from all continental landmasses. Only a few genera lie phylogenetically outside the dicynodont clade, but it is within this pre-dicynodont grade that most investigations into the adaptive radiation of dicynodonts have been focused (King et al. 1989, King 1994). Most recent workers restrict the term Anomodontia to dicynodonts and their near relatives, although in the past this name was considered to encompass dinocephalians as well (e.g., Watson & Romer 1956). Recent cladistic propositions of a sister-group relationship between dinocephalians and anomodonts (*sensu stricto*) have been refuted (Hopson 1991b, Grine 1997; *contra* King 1988).

Dimacrodon hottoni, from the San Angelo Formation of Texas, has been suggested to be the oldest anomodont (Olson 1962). Restudy of the material, which includes a partial lower jaw and very fragmentary remains of the skull, by Sidor & Hopson (1995) has shown that this specimen consists of misidentified pelycosaur remains and displays none of the diagnostic features of anomodonts.

The most basal member of the Anomodontia is the newly described *Anomocephalus africanus* from the Beaufort Group of South Africa (Modesto & Rubidge 2000). The position of this genus is supported by the relatively long snout compared with other anomodonts, a vertically aligned and blade-like zygomatic process of the squamosal, and the fact that the squamosal does not contact the ventral tip of the postorbital. Other primitive members of the Anomodontia include *Patranomodon* (Figure 4E), which is known from a well-preserved skull and lower jaw as well as several postcranial elements including a beautifully preserved manus (Rubidge & Hopson 1996). Additional early anomodonts include *Otsheria*, *Ulemica*, and *Suminia*, which have been proposed to form a clade of Russian endemic genera (Rybczynski 2000; *contra* Ivachnenko 1994, 1996b), and the South African taxa *Galepus*, *Galechirus*, and *Galeops* (Brinkman 1981, Rubidge & Hopson 1996).

Dicynodontia

Dicynodonts form the bulk of anomodont taxonomic diversity and dominated terrestrial herbivorous niches for most of the Late Permian. It is estimated that in South Africa's Karoo Basin their remains are 10 times more plentiful than those of contemporaneous carnivores. Indeed, their abundance has been used as ecological evidence that dicynodonts were primary consumers and that modern trophic structure had appeared by this time. Until relatively recently, the vast number of named dicynodont species clouded our understanding of this group's evolutionary history. However, as a result of the efforts of several workers (e.g., Cluver & Hotton 1981, Cluver & King 1983, King 1988, King & Rubidge 1993, Keyser 1993, Keyser & Cruickshank 1979, Renaut 2000), the number of valid taxa has been greatly reduced and it has become possible to resolve relationships within the Dicynodontia (Cox 1998, Angielczyk 2001).

The oldest and most primitive dicynodont is *Eodicynodon*, from the base of the Beaufort Group in South Africa (Rubidge 1990b). As in other dicynodonts, the

premaxilla and anterior portion of the dentary are edentulous in *Eodicynodon*. Both of these areas are pock-marked with numerous foramina that suggest the presence of a horny covering in life. Adding to their unusual appearance, the dicynodont dentition consists of paired, tusk-like upper caniniforms (tk in Figure 4) and a vestigial complement of small postcanine teeth. These features, in addition to their characteristic sliding jaw joint, have been traditionally regarded as underlying the success of dicynodonts (Crompton & Hotton 1967, Barghusen 1976, King 1994).

Until the recent discovery of a new species from India (Ray 2000), the aberrant dicynodont *Endothiodon* had been known only from rather fragmentary material (e.g., Cox 1964). The most striking feature of this genus, which contrasts sharply to the condition present in most dicynodonts, is its numerous obliquely arranged rows of teeth in both the upper and lower jaws. New work by Latimer et al. (1995) has demonstrated that these tooth rows correspond to the concept of Zahnreihen, as in several other Paleozoic genera with multiple tooth rows.

The end of the Permian brought a catastrophic drop in dicynodont numbers so that by the beginning of the Triassic (~251 Ma), only *Lystrosaurus* was common. This genus was extremely widespread, however, as its remains have been found in Western Europe, Russia, India, China, Africa, Antarctica, and possibly Australia (King 1988). *Lystrosaurus* was traditionally considered to have first appeared in the Early Triassic, but the recent discovery of an overlap in the stratigraphic ranges of *Dicynodon* and *Lystrosaurus* has demonstrated that the latter also occurs in the Late Permian and thus it was the only dicynodont known to cross the Permo-Triassic boundary (Cheng 1993, Smith 1995, King & Jenkins 1997).

Dicynodonts underwent a second, relatively minor, radiation during the Middle Triassic, with taxa such as *Kannemeyeria* (Figure 4F) becoming common. Using only cranial characters, King (1988) provided the first cladistic analysis of the Triassic dicynodonts. More recently, Surkov (2000) provided a cladogram based on postcranial features and has reiterated the traditional viewpoint (e.g., Cluver 1971) that Triassic dicynodonts probably originated from an advanced Late Permian form similar to *Dicynodon*. The latest surviving dicynodonts are preserved in the Middle and Upper Triassic sediments of North and South America and tend to be massively built, with genera such as *Stahleckeria*, *Ischigualastia*, and *Placerias* being the largest dicynodonts on record. Compared with their Permian antecedents, Triassic dicynodonts were scarce and faced competition with a host of newly evolved herbivores, including bauriid therocephalians, gomphodont cynodonts, and rhynchosaurs.

Postcranial studies have suggested that dicynodonts were powerful animals and that the forelimb retained a sprawling posture, whereas the hindlimb could adopt both sprawling and upright positions (King 1988, 1990). Histological studies on eight dicynodont genera spanning all stratigraphic levels of the Beaufort Group have established the presence of fibro-lamellar alternating with lamellated bone tissue in all taxa except *Diictodon*, which had only the former type of tissue (Chinsamy & Rubidge 1993). This suggests that in most dicynodonts, bone was deposited rapidly, but with intermittent periods of slow growth. The absence of

annuli in *Diictodon* suggests that it was capable of sustained rapid growth, as are extant endotherms.

Gorgonopsia

Gorgonopsians (clade 4 in Figure 3; Figure 5A) were the dominant large-bodied carnivores for much of the Late Permian. In the rocks of South Africa's Lower Beaufort Group, from where they are most abundantly known, hundreds of specimens have been collected and over 25 genera are currently recognized (Sigogneau-Russell 1989). All gorgonopsians possess a distinctive palatal morphology. The unpaired vomer is broad anteriorly but tapers rapidly posteriorly and, when well-preserved, can be seen to possess a system of three ridges on its ventral surface: a weak median ridge and two lateral ridges that parallel the choanal margin. In addition, the palatines form an extensive sutural contact on the ventral midline of the palate, thereby separating the vomer from the pterygoids. On the skull roof the preparietal (when discernible) is diamond-shaped and positioned between the parietals and frontal (i.e., it does not contact the pineal foramen as in some biarmosuchians and anomodonts), and the jugal (j in Figure 5) lacks a distinct postorbital process. The lower jaw of gorgonopsians is also highly diagnostic; the reflected lamina of the angular (ref lam in Figure 5) has an attached dorsal margin and bears a unique system of lateral ridges including a near-vertical, anterior ridge in front of a deep, pocket-like depression.

Studies of gorgonopsian functional morphology have principally focused on the jaw opening and closing mechanism. Although there remains room for dispute, two features are clear: (a) Gorgonopsians possessed a quadrate (q in Figure 5) that was only loosely attached to the skull (i.e., they lacked a sutural connection between the quadrate and squamosal), and (b) when the jaw was fully opened, the shape of the jaw joint forced the articular to be translated relative to the quadrate (i.e., as the articular rotated to open the jaw, it was compelled to slide laterally as well) (Parrington 1955). Kemp (1969) and Tatarinov (2000) have proposed alternative interpretations of quadrate movement, whereas Laurin (1998) argued against any type of motion because of the quadrate's firm connection with the epipterygoid and stapes.

Gorgonopsians flourished during the Late Permian despite a rather unsophisticated masticatory apparatus. Although both the canines and large incisors of gorgonopsians were armed with serrations, a lack of regular wear facets and the reduced postcanine dentition in some forms indicate that little processing of food was done. Instead, it appears that gorgonopsians simply tore hunks of flesh out of their prey. Despite their common preservation in Upper Permian sediments, gorgonopsians were victims of the end-Permian extinction.

The unsatisfactory state of gorgonopsian taxonomy has been the single largest impediment to a broader understanding of this group's evolution. Indeed, gorgonopsians possess such a stereotyped cranial morphology that ontogenetic changes appear to have been used to identify species and even genera. Since the

precladistic work of Sigogneau (1970; see also Sigogneau-Russell 1989), little progress has been made in determining the interrelationships within Gorgonopsia. However, one group recognized by Sigogneau (1970) that does appear to represent a valid clade is the subfamily Rubidgeinae. This group includes most of the latest appearing, large gorgonopsians that possess a thickened postorbital bar and a very deep zygomatic arch whose ventral margin descends to a level lower than that of the quadrate.

Terocephalia

In contrast to the morphological conservatism seen in gorgonopsians, therocephalians (clade 5 in Figure 3) evolved a wide range of morphologies and presumed ecologies in the course of their evolutionary history. The earliest therocephalians occur as low in the Permian sediments of South Africa as any of the other major therapsid groups (Rubidge et al. 1983), and they survived until early Middle Triassic times (Rubidge 1995). Geographically, therocephalians are known not only from southern and eastern Africa (Keyser 1973, Kitching 1977, Gay & Cruickshank 1999), but from China (Li & Cheng 1995), Russia (Ivachnenko et al. 1997), and Antarctica (Colbert & Kitching 1981) as well.

By their first appearance in the fossil record, early taxa such as *Lycosuchus* and *Scylacosaurus* share several synapomorphies with all other therocephalians that indicate the monophyly of this group. Most notably, bilateral fenestrae (termed suborbital vacuities) are developed in the palate between the pterygoid, ectopterygoid, and palatine bones. In addition, the stapes is rod-like, lacking a stapedia foramen. Postcranially, the ilium of all therocephalians possesses a distinct, finger-like process that emanates from the bone's anterior margin.

Terocephalians more advanced than lycosuchids and scylacosaurids have been termed eutherocephalians (clade 5b in Figure 3; Figure 5B) (Hopson & Barghusen 1986, van den Heever 1994). Although this clade has strong character support, the interrelationships of its subordinate taxa (viz. Hofmeyriidae, Akidnognathidae, Whaitsiidae, and Baurioidea) remain poorly understood (Hopson 1991b).

Terocephalians increased in taxonomic diversity throughout the Late Permian and are inferred to have been exclusively carnivores during this time. Of particular note in this regard is *Euchambersia*, a short-snouted form possessing specializations that are suggestive of a snake-like venomous bite (e.g., a deep fossa on its cheek communicates with a groove on the upper canine) (Hotton 1991). Beginning in the Early Triassic, however, bauriid therocephalians adopted a herbivorous lifestyle. In this clade the postcanine teeth were transversely expanded and became tightly packed into a curved tooth row. In addition, regular wear facets indicate that bauriids gained precise postcanine occlusion similar to that of advanced cynodonts. Although therocephalians parallel the development of several other cynodont features (e.g., the acquisition of a secondary palate and loss of the postfrontal bone, among others), they retained many other primitive characters and became extinct in the early Middle Triassic.

Cynodontia

Among therapsids, cynodonts (clade 6 in Figure 3) have garnered the greatest amount of attention because of their intimate relationship with the origin of mammals (Kemp 1983, Rowe 1988, Hopson 1994). The early evolution of cynodonts was discussed in a previous section; here we focus on the derived, post-Early Triassic forms.

Cynodonts more derived than *Thrinaxodon* (Figure 5C) have been termed the Eucynodontia (Kemp 1982, 1988) and are characterized by a number of features that produce an increasingly mammal-like skull and postcranial skeleton. Important modifications include: (a) an enlarged dentary and reduced, more rod-like, postdentary bones, (b) the fusion of the dentaries at the mandibular symphysis, (c) a supplementary contact between the surangular and squamosal lateral to the quadrate-articular jaw joint, (d) the formation of an acromion process on the leading edge of the scapula, and (e) the acquisition of the mammalian phalangeal formula.

Advanced nonmammalian cynodont systematics still lack consensus, but most phylogenetic hypotheses fall into one of three camps (Figure 6). 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 (i.e., blade-like) dentition (Crompton & Ellenberger 1957; Crompton 1972; Hopson & Kitching 1972, 2001; Sues 1985; Hopson 1991b; Luo 1994). The second camp 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 dissolves the tooth-type dichotomy completely, and intersperses gomphodont with sectorial taxa as successive mammal outgroups (Gauthier et al. 1988; Rowe 1988, 1993). Battail (1991) groups gomphodonts and tritylodontids but suggests that mammals evolved from a *Thrinaxodon*-grade ancestor, a hypothesis unlike that of any of the previous workers.

Hopson & Kitching (2001) have provided the most recent investigation of the higher cynodont problem. Their results support the traditional hypothesis (i.e., Figure 6A) and also have the benefit of the most extensive taxon sampling—an important factor in accurately reconstructing phylogenies (Wagner 2000). For the purposes of the following discussion, we follow Hopson (e.g., Hopson & Barghusen 1986, Hopson 1991b, 1994, Sidor & Hopson 1998) in dividing eucynodonts into two major clades, Cynognathia and Probainognathia.

Cynognathia

A rich fossil record of early cynognathians is known from the Triassic sediments of South Africa and South America. Early in this sequence the most primitive and only carnivorous member of this group, *Cynognathus*, is found alongside its herbivorous relatives, *Diademodon* and *Trirachodon* (Figure 5D). The latter genus is

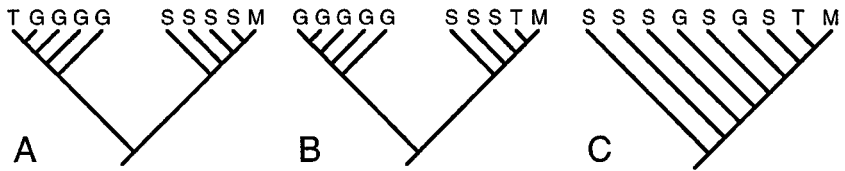


Figure 6 Diagrammatic representation of three hypotheses of advanced cynodont phylogeny. (A) The traditional hypothesis (cf. Crompton & Ellenberger 1957, Hopson & Kitching 1972, Hopson 1991); (B) that of Kemp (1982, 1983); (C) that of Rowe (1988, 1993; see also Gauthier et al. 1988). G, herbivorous, gomphodont cynodonts; T, tritylodontids (the teeth of which are morphologically gomphodont); S, cynodonts with sectorial postcanine teeth; M, early mammals (which have sectorial teeth). The following taxa are characterized by transversely-expanded (gomphodont) postcanine teeth in Figure 3: *Diademodon*, *Trirachodon*, *Luangwa*, *Massetognathus*, and *Tritylodontidae*; all other cynodonts have sectorial (slicing) postcanine teeth. Although we favor the hypothesis depicted in (A), advanced cynodont systematics lacks consensus, and further work is required.

of special interest in that it is one of the only therapsid genera in which qualitative morphologic change can be demonstrated within a taxon's stratigraphic range. The earliest-occurring form, known only from recently collected material, maintains sectorial teeth along much of its tooth row (Neveling 1998). The succeeding morphospecies, *Trirachodon kannemeyeri*, has transversely widened (gomphodont) teeth anteriorly in its tooth row but retains sectorial teeth more posteriorly. The final species, *Trirachodon berryi*, by contrast, has a full complement of gomphodont teeth. The stratigraphic and ontogenetic sequences preserved by fossils of this genus may shed light on the origin and evolution of the gomphodont type of dentition.

Cynognathians can be diagnosed by several synapomorphies including a very deep zygomatic arch that extends above the middle of the orbit (zyg in Figure 5), a suborbital process on the jugal (j pr in Figure 5) for the origination of the masseter jaw closing muscle, and a very deep groove on the lateral surface of the squamosal that connected the middle ear with the outside world (i.e., the "external auditory meatus") (Allin & Hopson 1992) (eam in Figure 5). Gomphodont cynodonts more derived than *Diademodon* and *Trirachodon* typically lack sectorial teeth and have traditionally been termed traversodontids. Members of this group include *Exaeretodon* (Bonaparte 1962), *Luangwa* (Kemp 1980), *Massetognathus* (Abdala & Giannini 2000), and *Pascualgnathus* (Bonaparte 1966), all of which share lower postcanines with two anterior, transversely aligned cusps in front of a posterior basin. Recent fossil finds in Madagascar have prompted Flynn et al. (1999, 2000) to phylogenetically define Traversodontidae as a stem-based group. This type of definition is unfortunate in this case because it ignores the traditional division between pre-traversodontid genera (viz. *Diademodon*, *Trirachodon*, and

even *Cynognathus*) and the more advanced forms. In addition, under most workers' relationships, this definition would be supplanted by Cynognathia (Hopson 1991b, 1994).

According to the phylogenetic hypothesis followed here, tritylodontids represent the most highly derived members of the cynognathian lineage. This group's name is derived from its members' highly modified postcanine dentition, in which the lower molariforms possess three longitudinal rows of cusps. These three rows occlude against two rows in the upper dentition and produce wear facets interpreted as the result of strong, bilateral, backwards jaw movement (Clark & Hopson 1985, Sues 1986). The lower incisors of tritylodontids are enlarged and fit between the uppers to yield a rodent-like appearance. The postcranial skeleton of tritylodontids is mammal-like. For example, the greater trochanter is separated from the femoral head by a notch and, in the pelvis the reduced pubis is positioned posteroventral to the acetabulum and the ilium is rod-like. Hopson (1991a, 1995), however, has suggested that homoplasy is relatively common in the therapsid postcranial skeleton. Tritylodontids are the latest-occurring cynognathians, known primarily from the Jurassic, though recent discoveries have now extended their range to the Early Cretaceous (Tatarinov & Matchenko 1999).

Probainognathia

Compared with the diversity and abundance of basal cynognathians, the fossil record of early probainognathians is relatively poor. Indeed, the earliest-appearing member of this group has only very recently been described (Hopson & Kitching 2001). This taxon, *Lumkuia fuzzi* (Figure 5E), shares with other probainognathians the lack of a pineal foramen and expanded ribs, as well as a posteriorly elongated secondary palate. Prior to their description, probainognathians were known exclusively from younger sediments, principally the upper Middle and Upper Triassic of Argentina (Romer 1969b, 1970; Martinez & Forster 1996; Martinez et al. 1996) and Brazil (Romer 1969a, Hopson 1985).

Advanced probainognathians can be divided into two subgroups, the chiniquodontids and a lineage including *Probainognathus*, tritheledontids, and mammals. The former subgroup includes taxa such as *Probelesodon*, *Aleodon*, and *Chiniquodon* that uniformly possess a characteristic right-angle bend at the rear of the maxilla, but span a wide range of dental morphologies. For example, *Probelesodon* has mitten-shaped postcanine teeth that completely lack cingula (i.e., the sides of the teeth are smooth), whereas *Aleodon* possesses transversely expanded, multicusped postcanines that led to its early classification as a gomphodont (Crompton 1955). *Probainognathus* coexisted with *Probelesodon*, but is advanced in a mammalian direction in aspects of its postcanine dentition.

Tritheledontids (Figure 5F) are poorly understood as a group, although they have played an important role in understanding the origin of mammals (Crompton 1963, Luo 1994). Although its homology with that of mammals remains controversial, the dentary of the derived tritheledontid, *Pachygenelus*, appears to have made

a contact with the squamosal, although an articular fossa is not present (Hopson 1994). This contact foreshadows the condition in early mammals such as *Morganucodon* and *Sinoconodon*, in which a well-developed dentary-squamosal jaw joint functions beside the primitive quadrate-articular jaw joint (Crompton & Luo 1993).

GEOLOGIC UTILITY OF THERAPSID

The therapsid fossil record enjoys a long pedigree of use in the geological sciences. The rocks of the Beaufort Group, in which there are a paucity of basin-wide lithostratigraphic markers, are divided into eight therapsid-defined “assemblage zones” (Rubidge 1995). Based on their well-known faunal content and the global distribution of some therapsid genera, these zones are now the international standard for global correlation of Permian-Jurassic nonmarine deposits (e.g., Ochev & Shishkin 1989, Lucas 1998).

Therapsid fossils have also been used to interpret paleoenvironments (e.g., Kitching 1977), and more recent high-resolution taphonomic studies have played an important role in delineating the spatial aspects of floodplain subenvironments within the Lower Beaufort Group (Smith 1993, 1995; Smith et al. 1993), and regional base level changes in the Upper Triassic/Lower Jurassic Elliot Formation (Smith & Kitching 1997). Therapsid fossils have also been utilized in defining formational contacts, such as the long disputed Ecca-Beaufort contact, which can now be defined using both lithological and paleontological criteria (Hancox & Rubidge 1997; Rubidge et al. 1999, 2000). Similarly, subdivision of the *Cynognathus* Assemblage Zone has permitted the diachronous (i.e., time-transgressive) nature of the Beaufort-“Stormberg” boundary to be recognized (Hancox et al. 1995, Hancox 2000).

Biodiversity patterns in the Lower Beaufort Group point to major faunal turnovers between the *Tapinocephalus* and *Pristerognathus* Assemblage Zones and between the *Dicynodon* and *Lystrosaurus* Assemblage Zones. The latter turnover traditionally has been considered to coincide with the Permo-Triassic boundary (Smith 1995), a time of global mass extinction (Erwin 1993). Correlating marine and nonmarine strata has been a recalcitrant problem when assessing the various mechanisms proposed to underlie the end-Permian event (Olson 1989). Further research into the Permo-Triassic boundary in the Karoo Basin (i.e., radiometric dating, paleomagnetism, therapsid diversity patterns) will allow for better correlation with the international marine sequence and may help unravel extinction mechanisms (MacLeod et al. 2000, Ward et al. 2000).

MAJOR PATTERNS OF THERAPSID EVOLUTION

Documenting the Acquisition of Mammalian Features

The synapsid fossil record has been considered of special importance because it chronicles the origin of mammals in exceptional detail. Indeed, Kemp (1982,

1985) has stressed the importance of dense fossil sampling in interpreting the macroevolutionary process by which higher taxa emerge. Although the evolution of mammals represents only one branch on the larger synapsid evolutionary tree, a major research goal has been to understand the evolutionary questions of when, how, and why the features we recognize as mammalian first appeared. The numerous cladistic studies published to date have afforded a rigorous basis to answering the first of these questions. The phylogenetic first appearance of many features is now well known. By contrast, our understanding of how and why these features appeared is, and will doubtless continue to be, much more difficult to pin down.

Progress has been made on the evolutionary origins of mammalian limb posture. Experimental approaches using extant reptiles and mammals have helped to identify plausible and implausible loading regimes for hindlimb elements (Blob 1998, 2001), and recent anatomical work has detailed postcranial evolution within therocephalians (Fourie 2001). In addition, preliminary data suggest that discriminating between sprawling and nonsprawling locomotion may be possible on a quantitative basis (Beck et al. 2000).

The evolution of endothermy in the mammalian stem-lineage has also attracted recent work. The formation of a bony secondary palate (Maier et al. 1996), possession of nasal turbinates (Hillenius 1992, 1994), specific bone histologies (de Ricqlès 1974, Chinsamy & Rubidge 1993, Botha & Chinsamy 2001), loss of a pineal foramen, and modern predator/prey ratios (Bakker 1975) have all been suggested as correlates of mammal-like endothermy in therapsids. Although the acquisition of endothermy was probably piecemeal (Ruben 1995), and none of the aforementioned characters alone provides conclusive evidence, taken together they strongly suggest that increased metabolic activity probably characterized eutheriodonts, and that some form of endothermy was present in advanced cynodonts.

The acquisition of mammalian features has also been studied in a temporal framework. Sidor & Hopson (1998) have shown a good correlation between the duration of gaps in the synapsid fossil record and the number of mammalian features inferred to have been gained during those gaps. They argued that this relationship supports the hypothesis of a gradual appearance of mammalian features within the synapsid lineage.

Evolutionary Trends

The synapsid fossil record has also been used to provide insight into broad-scale patterns of evolution. Olson (1959) advocated a polyphyletic origin of mammals, with multiple therapsid lineages independently attaining the mammalian grade of organization. Although this view has now fallen into disfavor among paleontologists, establishing the prevalence of morphological parallelism in nonmammalian therapsids remains an important avenue of research.

Based on phylogenetic arguments, Hopson (1995) has shown that the mammalian phalangeal formula appeared multiple times within therapsid evolution. Hopson argued that this feature, along with fusions in the distal carpals and tarsals and increasing symmetry among the metapodials, is related to an increasingly

forward-facing hand and foot, brought about by the requirements of a less-sprawling posture.

Sidor (2000, 2001) addressed evolutionary parallelism in the synapsid skull. When skull complexity was defined in terms of the number of distinct elements, Sidor was able to show that simplification (in terms of bone loss or fusion) was a widespread feature of synapsid evolution. This pattern was prevalent not only at the broadest scale possible (i.e., all synapsids), but it typified nearly all synapsid subgroups as well. Stratigraphic and phylogenetic tests indicate that skull bone loss in synapsids corresponds to what McShea (1994) termed a driven trend.

SUMMARY AND FUTURE DIRECTIONS

The past decade has produced fundamental advances in synapsid research. Fossil discoveries have offered new taxa with surprising combinations of primitive and derived features and have prompted a new wave of detailed phylogenetic research. The availability of large numbers of finely prepared specimens has helped to refine the taxonomy of many therapsid groups and permits the use of quantitative approaches to understanding their evolutionary history.

The therapsid fossil record also makes valuable contributions to the geological sciences. Therapsid fossils are increasingly utilized as paleoenvironmental indicators and are also routinely employed for both inter- and intracontinental correlation of stratigraphic sequences. Although many of these advances are at an early stage of development, the use of therapsids as age indicators has led to the establishment of global biochrons.

Enhanced paleocontinental reconstructions, together with phylogenetic analyses, have improved our understanding of therapsid biogeography. Whereas therapsids were previously thought to have originated in North America or Russia, it now appears that southern Africa was home to many therapsid groups. Africa has many Permo-Triassic basins that have received only cursory geological and paleontological attention. We predict that these areas are likely to produce important new therapsid faunas in the future.

Systematic research has progressed for anomodonts, biarmosuchians, dinocephalians, basal therocephalians, and higher cynodonts, but almost nothing has appeared on gorgonopsians or derived therocephalians. These and tapinocephalid dinocephalians are obvious targets for future studies. Similarly, although a steady stream of therapsid cranial descriptions have appeared in the past decade, comparable postcranial descriptions are sorely needed. This disparity has resulted in cladistic studies being overly reliant on cranial features, which might lead to biased phylogenetic results if the cranial and postcranial skeletons preserve different qualities of phylogenetic information. An accurate assessment of Permo-Triassic therapsid biodiversity is an important long-term goal. Meeting this goal will require a combination of research on older, previously described taxa, and the continuing discovery of new therapsid faunas.

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LITERATURE CITED

- Abdala F, Giannini NP. 2000. Gomphodont cynodonts of the Chañares Formation: the analysis of an ontogenetic sequence. *J. Vertebr. Paleontol.* 20:501–6
- Allin EF, Hopson JA. 1992. Evolution of the auditory system in Synapsida (“mammal-like reptiles” and primitive mammals) as seen in the fossil record. In *The Evolutionary Biology of Hearing*, ed. DB Webster, RR Fay, AN Popper, pp. 587–614. New York: Springer-Verlag
- Angielczyk KD. 2001. Preliminary phylogenetic analysis and stratigraphic congruence of the dicynodont anomodonts (Synapsida: Therapsida). *Palaeontol. Afr.* 37:In press
- Bakker RT. 1975. Experimental and fossil evidence for the evolution of tetrapod bioenergetics. In *Perspectives of Biophysical Ecology*, ed. DM Gates, RB Schmerl, pp. 365–99. New York: Springer-Verlag
- Barghusen HR. 1968. The lower jaw of cynodonts (Reptilia, Therapsida) and the evolutionary origin of mammal-like adductor jaw musculature. *Postilla* 116:1–49
- Barghusen HR. 1975. A review of fighting adaptation in dinocephalians (Reptilia, Therapsida). *Paleobiology* 12:95–311
- Barghusen HR. 1976. Notes on the adductor jaw musculature of *Venjukovia*, a primitive anomodont therapsid from the Permian of the U.S.S.R.. *Ann. S. Afr. Mus.* 69:249–60
- Battail B. 1991. Les Cynodontes (Reptilia, Therapsida): une phylogénie. *Bull. Mus. Natl. Hist. Nat.* 13:17–105
- Battail B. 1992. Sur la phylogénie des thérapside (Reptilia, Therapsida). *Ann. Paléontol.* 78:83–42
- Beck AL, Blob RW, Hopson JA. 2000. Interpreting limb posture in fossil tetrapods: morphological indicators of sprawling and non-sprawling locomotion. *J. Vertebr. Paleontol.* 20:29A
- Blob RW. 1998. *Mechanics of non-parasagittal locomotion in alligator and iguana: functional implications for the evolution of non-sprawling posture in the Therapsida*. PhD thesis, Univ. Chicago. 324 pp.
- Blob RW. 2001. Evolution of hindlimb posture in non-mammalian therapsids: biomechanical tests of paleontological hypotheses. *Paleobiology* 27:14–38
- Bonaparte JF. 1962. Descripción del cráneo y mandíbula de *Exaeretodon frenguelli*, Cabrera, y su comparación con Diademodontidae, Tritylodontidae y los cinodontes sudamericanos. *Publ. Mus. Munic. Nat. Tradic, Mar Plata* 1:135–202
- Bonaparte JF. 1966. Una nueva “fauna” Triásica de Argentina (Therapsida: Cynodontia; Dicynodontia); consideraciones filogenéticas y paleobiogeográficas. *Ameghiniana* 4:243–96
- Boonstra LD. 1963. Diversity within the South African Dinocephalia. *S. Afr. J. Sci.* 59:196–206

- Boonstra LD. 1969. The fauna of the *Tapirocephalus* Zone (Beaufort beds of the Karoo). *Ann. S. Afr. Mus.* 56:1–73
- Boonstra LD. 1971. The early therapsids. *Ann. S. Afr. Mus.* 59:17–46
- Boonstra LD. 1972. Discard the names Theriodontia and Anomodontia: a new classification of the Therapsida. *Ann. S. Afr. Mus.* 59:315–38
- Botha J, Chinsamy A. 2001. Growth patterns deduced from the bone histology of the cynodonts *Diademodon* and *Cynognathus*. *J. Vertebr. Paleontol.* 20:705–11
- Brinkman D. 1981. The structure and relationships of the dromosaurs (Reptilia: Therapsida). *Breviora* 465:1–34
- Cheng Z, Li J. 1996. First record of a primitive anteosaurid dinocephalian from the Upper Permian of Gansu, China. *Vertebr. Pal. Asiat.* 34:123–34
- Cheng Z, Li J. 1997. A new genus of primitive dinocephalian: the third report on Late Permian Dashankou lower tetrapod fauna. *Vertebr. PalAsiat.* 35:35–43
- Cheng Z-W. 1993. On the discovery and significance of the nonmarine Permo-Triassic transition zone at Dalongkou in Jimusar, Xinjiang, China. In *The Nonmarine Triassic*, ed. SG Lucas, M Morales, pp. 65–67. Albuquerque: New Mexico Mus. Nat. Hist. Sci. Bull. No. 3
- Chinsamy A, Rubidge BS. 1993. Dicynodont (Therapsida) bone histology: phylogenetic and physiological implications. *Palaeontol. Afr.* 30:97–102
- Clark JM, Hopson JA. 1985. Distinctive mammal-like reptile from Mexico and its bearing on the phylogeny of the Tritylodontidae. *Nature* 315:398–400
- Cluver MA. 1971. The cranial morphology of the dicynodont genus *Lystrosaurus*. *Ann. S. Afr. Mus.* 56:155–274
- Cluver MA, Hotton N III. 1981. The genera *Dicynodon* and *Diictodon* and their bearing on the classification of the Dicynodontia (Reptilia, Therapsida). *Ann. S. Afr. Mus.* 83:99–146
- Cluver MA, King GM. 1983. A reassessment of the relationships of the Permian Dicynodontia (Reptilia, Therapsida) and a new classification of dicynodonts. *Ann. S. Afr. Mus.* 91:195–273
- Colbert EH, Kitching JW. 1981. Scalopsaurian reptiles from the Triassic of Antarctica. *Am. Mus. Novit.* 1–22
- Cox CB. 1964. On the palate, dentition, and classification of the fossil reptile *Endothiodon* and related genera. *Am. Mus. Novit.* 2171:1–25
- Cox CB. 1998. The jaw function and adaptive radiation of the dicynodont mammal-like reptiles of the Karoo Basin of South Africa. *Zool. J. Linn. Soc.* 122:349–84
- Crompton AW. 1955. On some Triassic cynodonts from Tanganyika. *Proc. Zool. Soc. Lond.* 125:617–69
- Crompton AW. 1963. The evolution of the mammalian jaw. *Evolution* 17:431–39
- Crompton AW. 1972. Postcanine occlusion in cynodonts and tritylodontids. *Bull. Br. Mus. (Nat. Hist.) Geol.* 21:30–71
- Crompton AW, Ellenberger F. 1957. On a new cynodont from the Molteno Beds and the origin of the tritylodontids. *Ann. S. Afr. Mus.* 44:1–14
- Crompton AW, Hotton N. 1967. Functional morphology of the masticatory apparatus of two dicynodonts (Reptilia, Therapsida). *Postilla* 109:1–51
- Crompton AW, Jenkins FA Jr. 1973. Mammals from reptiles: a review of mammalian origins. *Annu. Rev. Earth Planet. Sci.* 1:131–55
- Crompton AW, Luo Z. 1993. Relationship of the Liassic mammals *Sinoconodon*, *Morganucodon oehleri*, and *Dinnetherium*. See Szalay et al. 1993, pp. 30–44
- Crompton AW, Parker P. 1978. Evolution of the mammalian masticatory apparatus. *Am. Sci.* 66:192–201
- de Ricqlès A. 1974. Evolution of endothermy. *Evol. Theory* 1:51–80
- Dilkes DW, Reisz RR. 1996. First record of a basal synapsid ('mammal-like reptile') in Gondwana. *Proc. R. Soc. London Ser. B* 263:1165–70
- Efremov IA. 1940. *Ulemosaurus svijagensis*

- Riab.—ein Dincephale aus den Ablagerungen des Perm der UdSSR. *Nove Acta Leopoldina* 9:155–205
- Erwin DH. 1993. *The Great Paleozoic Crisis: Life and Death in the Permian*. New York: Columbia Univ. Press
- Flynn JJ, Parrish JM, Rakotosamimanana B, Ranivoharimanana L, Simpson WF, Wyss AR. 2000. New traversodontids (Synapsida: Eucynodontia) from the Triassic of Madagascar. *J. Vertebr. Paleontol.* 20:422–27
- Flynn JJ, Parrish JM, Rakotosamimanana B, Simpson WF, Whatley RL, Wyss AR. 1999. A Triassic fauna from Madagascar, including early dinosaurs. *Science* 286:763–65
- Fourie H. 2001. *Morphology and function of the postcrania of selected genera of Theropcephalia (Amniota: Therapsida)*. PhD thesis, Univ. Witwatersrand, Johannesburg, S. Afr. 185 pp.
- Fourie S. 1974. The cranial morphology of *Thrinaxodon liorhinus* Seeley. *Ann. S. Afr. Mus.* 65:337–400
- Gauthier J, Kluge A, Rowe T. 1988. Amniote phylogeny and the importance of fossils. *Cladistics* 4:105–209
- Gay SA, Cruickshank ARI. 1999. Biostratigraphy of the Permian tetrapod faunas from the Ruhuhu Valley, Tanzania. *J. Afr. Earth Sci.* 29:195–210
- Grine FE. 1997. Dinocephalians are not anomodonts. *J. Vert. Paleontol.* 17:177–83
- Hancox PJ. 2000. The continental Triassic of South Africa. *Z. Geol. Paläontol.* 1998: 1285–324
- Hancox PJ, Rubidge BS. 1997. The role of fossils in interpreting the development of the Karoo Basin. *Palaeontol. Afr.* 33:41–54
- Hancox PJ, Shishkin MA, Rubidge BS, Kitching JW. 1995. A threefold subdivision of the *Cynognathus* Assemblage Zone (Beaufort Group, South Africa) and its palaeogeographical implications. *S. Afr. J. Sci.* 91:143–44
- Hillenius WJ. 1992. The evolution of nasal turbinates and mammalian endothermy. *Palaeobiology* 18:17–29
- Hillenius WJ. 1994. Turbinates in therapsids: evidence for Late Permian origins of mammalian endothermy. *Evolution* 48:207–29
- Hopson JA. 1985. Morphology and relationships of *Gomphodontosuchus brasiliensis* von Huene (Synapsida, Cynodontia, Tritylodontoidea) from the Triassic of Brazil. *Neues Jahrb. Geol. Paläontol. Monatsch.* 5:285–99
- Hopson JA. 1991a. Convergence in mammals, tritheledonts, and tritylodonts. *J. Vertebr. Paleontol.* 11:36A
- Hopson JA. 1991b. Systematics of the nonmammalian Synapsida and implications for patterns of evolution in synapsids. See Schultze & Trueb 1991, pp. 635–93
- Hopson JA. 1994. Synapsid evolution and the radiation of non-eutherian mammals. In *Major Features of Vertebrate Evolution.*, ed. DB Prothero, RM Schoch, pp. 190–219. Knoxville, TN: Paleontol. Soc.
- Hopson JA. 1995. Patterns of evolution in the manus and pes of non-mammalian therapsids. *J. Vertebr. Paleontol.* 15:615–39
- Hopson JA. 1999. Therapsids. In *Encyclopedia of Paleontology*, ed. R Singer, pp. 1256–66. Chicago: Fitzroy Dearborn
- Hopson JA, Barghusen H. 1986. An analysis of therapsid relationships. See Hotton et al. 1986, pp. 83–106
- Hopson JA, Crompton AW. 1969. Origin of mammals. In *Evolutionary Biology*, ed. T Dobzhansky, MK Hecht, WC Steere, pp. 15–71. East Norwalk, CT: Appleton-Century-Croft
- Hopson JA, Kitching JW. 1972. A revised classification of cynodonts (Reptilia; Therapsida). *Palaeontol. Afr.* 14:71–85
- Hopson JA, Kitching JW. 2001. A probainognathian cynodont from South Africa and the phylogeny of non-mammalian cynodonts. *Bull. Mus. Comp. Zool.* 156: In press
- Hotton N. 1991. The nature and diversity of synapsids: prologue to the origin of mammals. See Schultze & Trueb 1991, pp. 598–634
- Hotton N, MacLean PD, Roth JJ, Roth EC, eds. 1986. *The Ecology and Biology of*

- the Mammal-Like Reptiles*. Washington, DC: Smithsonian Inst. Press
- Ivachnenko MF. 1990. Elements of the Early Permian tetrapod faunal assemblages of Eastern Europe. *Paleontol. J.* 1990:102–11
- Ivachnenko MF. 1994. A new Late Permian dromasaurian (Anomodontia) from Eastern Europe. *Paleontol. J.* 1994:77–84
- Ivachnenko MF. 1995. Primitive Late Permian dinocephalian-titanosuchids of Eastern Europe. *Paleontol. J.* 29:120–29
- Ivachnenko MF. 1996a. New primitive therapsids from the Permian of Eastern Europe. *Paleontol. J.* 30:337–43
- Ivachnenko MF. 1996b. Primitive anomodonts, venyukoviids, from the Late Permian of Eastern Europe. *Paleontol. J.* 30:575–82
- Ivachnenko MF. 2000. Estemmenosuchus and primitive theriodonts from the Late Permian. *Paleontol. J.* 34:184–92
- Ivachnenko MF, Golubev VK, Gubin YM, Kalandadze NN, Novikov IV, et al. 1997. *Permian and Triassic Tetrapods of Eastern Europe*. Moscow: GEOS
- Kemp TS. 1969. On the functional morphology of the gorgonopsid skull. *Philos. Trans. R. Soc. London Ser. B* 256:1–83
- Kemp TS. 1978. Stance and gait in the hindlimb of a therocephalian mammal-like reptile. *J. Zool. London* 186:143–61
- Kemp TS. 1979. The primitive cynodont *Procyonosuchus*: functional anatomy of the skull and relationships. *Philos. Trans. R. Soc. London Ser. B* 285:73–122
- Kemp TS. 1980. Aspects of the structure and functional anatomy of the Middle Triassic cynodont *Luangwa*. *J. Zool. London* 191:193–239
- Kemp TS. 1982. *Mammal-Like Reptiles and the Origin of Mammals*. New York: Academic
- Kemp TS. 1983. The relationships of mammals. *Zool. J. Linn. Soc.* 77:353–84
- Kemp TS. 1985. Synapsid reptiles and the origin of higher taxa. *Spec. Pap. Palaeontol.* 33:175–84
- Kemp TS. 1988. Interrelationships of the Synapsida. In *The Phylogeny and Classification of the Tetrapods: Mammals*, ed. MJ Benton, 2:1–22. Oxford: Systematics Assoc. Spec. Vol. No. 35B
- Keyser AW. 1973. A new Triassic vertebrate fauna from South West Africa. *Palaeontol. Afr.* 13:1–15
- Keyser AW. 1993. A re-evaluation of the smaller Endothiodontidae. *Mem. Geol. Surv. S. Afr.* 82:1–53
- Keyser AW, Cruickshank ARI. 1979. The origins and classifications of Triassic dicynodonts. *Trans. Geol. Soc. S. Afr.* 82:81–108
- King G. 1990. *The Dicynodonts: A Study in Palaeobiology*. New York: Chapman & Hall
- King GM. 1988. Anomodontia. In *Encyclopedia of Paleoherpertology*, ed. P Wellnhofer, 17C:1–174. Stuttgart: Fischer
- King GM. 1994. The early anomodont *Venyukovia* and the evolution of the anomodont skull. *J. Zool. London* 232:651–73
- King GM, Jenkins I. 1997. The dicynodont *Lystrosaurus* from the Upper Permian of Zambia: evolutionary and stratigraphic implications. *Palaeontology* 40:149–56
- King GM, Oelofsen BW, Rubidge BS. 1989. The evolution to the dicynodont feeding system. *Zool. J. Linn. Soc.* 96:185–211
- King GM, Rubidge BS. 1993. A taxonomic revision of small dicynodonts with postcanine teeth. *Zool. J. Linn. Soc.* 107:131–54
- Kitching JW. 1977. *The distribution of the Karoo vertebrate fauna*. *Bernard Price Inst. for Palaeontol. Res.*, 1:1–131. Memoir
- Langer MC. 2000. The first record of dinocephalians in South America: Late Permian (Rio do Rasto Formation) of the Paraná Basin, Brazil. *Neues Jahrb. Geol. Paläontol. Abhandlug.* 215:69–95
- Latimer EM, Gow CE, Rubidge BS. 1995. Dentition and feeding niche of *Endothiodon* (Synapsida; Anomodontia). *Palaeontol. Afr.* 32:75–82
- Laurin M. 1998. New data on the cranial morphology of *Lycaenops* (Synapsida, Gorgonopsidae) and reflections on the possible presence of streptostyly in gorgonopsians. *J. Vertebr. Paleontol.* 18:765–76
- Laurin M, Reisz RR. 1995. A reevaluation of

- early amniote phylogeny. *Zool. J. Linn. Soc.* 113:165–223
- Laurin M, Reisz RR. 1996. The osteology and relationships of *Tetraceratops insignis*, the oldest known therapsid. *J. Vertebr. Paleontol.* 16:95–102
- Lepper J, Raath MA, Rubidge BS. 2000. A diverse dinocephalian fauna from Zimbabwe. *S. Afr. J. Sci.* 96:403–5
- Li J, Cheng Z. 1995. A new Late Permian vertebrate fauna from Dashankou, Gansu with comments on Permian and Triassic vertebrate assemblage zones of China. In *Short Papers of Sixth Symposium on Mesozoic Terrestrial Ecosystems and Biota*, ed. AL Sun, YQ Wang, pp. 33–37. Beijing: China Ocean Press
- Li J, Rubidge BS, Cheng Z. 1996. A primitive anteosaurid dinocephalian from China—implications for the distribution of earliest therapsid faunas. *S. Afr. J. Sci.* 92:252–53
- Lucas SG. 1998. Global Triassic tetrapod biostratigraphy and biochronology. *Palaeoogeogr. Palaeoclimat. Palaeoecol.* 143:347–84
- Luo Z. 1994. Sister-group relationships of mammals and transformations of diagnostic mammalian characters. In *In the Shadow of the Dinosaurs: Early Mesozoic Tetrapods*, ed. NC Fraser, H-D Sues, pp. 98–128. New York: Cambridge Univ. Press
- MacLeod KG, Smith RMH, Koch PL, Ward PL. 2000. Timing of mammal-like reptile extinctions across the Permian-Triassic boundary in South Africa. *Geology* 28:227–30
- Maier W, van den Heever J, Durand F. 1996. New therapsid specimens and the origin of the secondary hard and soft palate of mammals. *J. Zool. Syst. Evol. Res.* 34:9–19
- Martinez RN, Forster CA. 1996. The skull of *Probesodon sanjuanensis*, Sp. Nov., from the Late Triassic Ischigualasto Formation of Argentina. *J. Vertebr. Paleontol.* 16:285–91
- Martinez RN, May CL, Forster CA. 1996. A new carnivorous cynodont from the Ischigualasto Formation (Late Triassic, Argentina), with comments on eucynodont phylogeny. *J. Vertebr. Paleontol.* 16:271–84
- McNab BK. 1978. The evolution of endothermy in the phylogeny of mammals. *Am. Nat.* 112:1–21
- McShea DW. 1994. Mechanisms of large-scale evolutionary trends. *Evolution* 48:1747–63
- Modesto SP. 1992. Did herbivory foster early amniote diversification? *J. Vertebr. Paleontol.* 11:49A
- Modesto SP. 1995. The skull of the herbivorous synapsid *Edaphosaurus boanerges* from the Lower Permian of Texas. *Palaeontology* 38:213–39
- Modesto SP, Rubidge BS, Welman J. 1999. The most basal anomodont therapsid and the primacy of Gondwana in the evolution of the anomodonts. *Proc. R. Soc. London Ser. B* 266:331–37
- Modesto S, Rubidge B. 2000. A basal anomodont therapsid from the Lower Beaufort Group, Upper Permian of South Africa. *J. Vertebr. Paleontol.* 20:515–21
- Modesto S, Sidor C, Rubidge B, Welman J. 2001. A second varanopseid skull from the Upper Permian of South Africa: implications for Late Permian ‘pelycosaur’ evolution. *Lethaia* 34:In press
- Munyikwa D. 2001. *Cranial morphology of a primitive dinocephalian (Amniota: Therapsida) from the Madumabisa Mudstone Formation, Zimbabwe*. MSc thesis, Univ. Witwatersrand, Johannesburg, S. Afr. 75 pp.
- Neveling J. 1998. *The biostratigraphy and sedimentology of the contact area between the Lystrosaurus and Cynognathus Assemblage Zones (Beaufort Group: Karoo Supergroup)*. MSc Thesis. Univ. Witwatersrand, Johannesburg, S. Afr. 126 pp.
- Ochev VG, Shishkin MA. 1989. On the principles of global correlation of the continental Triassic on the tetrapods. *Acta Palaeontol. Polon.* 34:149–73
- Olson EC. 1959. The evolution of mammalian characters. *Evolution* 13:344–53
- Olson EC. 1962. Late Permian terrestrial vertebrates, U.S.A. and U.S.S.R.. *Trans. Am. Philos. Soc.* 52:1–224
- Olson EC. 1968. The family Caseidae. *Feldiana Geol.* 17:224–349
- Olson EC. 1989. Problems of Permo-Triassic

- terrestrial vertebrate extinctions. *Hist. Biol.* 2:17–35
- Owen R. 1844. Description of certain fossil crania, discovered by A. G. Bain, Esq., in sandstone rocks at the south-eastern extremity of Africa, referable to different species of an extinct genus of Reptilia (*Dicynodon*), and indicative of a new tribe or suborder of Sauria. *Proc. Geol. Soc. London* 4:500–4
- Parrington FR. 1955. On the cranial anatomy of some gorgonopsids and the synapsid middle ear. *Proc. Zool. Soc. London* 125:1–40
- Parrish JMJ, Parrish JT, Ziegler AM. 1986. Permian-Triassic paleogeography and paleoclimatology and implications for therapsid distribution. See Hotton et al. 1986, pp. 109–31
- Ray S. 2000. Endothiodont dicynodonts from the Late Permian Kundaram Formation, India. *Palaeontology* 43:375–404
- Reisz RR. 1986. Pelycosauria. In *Encyclopedia of Paleoherpetology*, ed. P Wellnhofer, 17A: 1–102. Stuttgart: Fischer
- Reisz RR, Berman DS. 2001. The skull of *Mesenosaurus romeri*, a small varanopseid (Synapsida: Eupelycosauria) from the Upper Permian of the Mesen River Basin, northern Russia. *Ann. Carnegie Mus.* 70:113–132
- Reisz RR, Dilkes DW, Berman DS. 1998. Anatomy and relationships of *Elliotsmithia longiceps* Broom, a small synapsid (Eupelycosauria: Varanopseidae) from the Late Permian of South Africa. *J. Vertebr. Paleontol.* 18:602–11
- Reisz RR, Sues H-D. 2000. Herbivory in Late Paleozoic and Triassic terrestrial vertebrates. In *Evolution of Herbivory in Terrestrial Vertebrates*, ed. H-D Sues, pp. 9–41. New York: Cambridge Univ. Press
- Renaut AJ. 2000. *A re-evaluation of the cranial morphology and taxonomy of the Triassic dicynodont genus Kannemeyeria*. PhD thesis, Univ. Witwatersrand, Johannesburg, S. Afr. 266 pp
- Romer AS. 1969a. The Brazilian Triassic cynodont reptiles *Belesodon* and *Chiniquodon*. *Breviora* 332:1–16
- Romer AS. 1969b. The Chañares (Argentina) Triassic reptile fauna V. A new chiniquodontid cynodont, *Probelesodon lewisi*—cynodont ancestry. *Breviora* 333:1–24
- Romer AS. 1970. The Chañares (Argentina) Triassic reptile fauna VI. A chiniquodontid cynodont with an incipient squamosal-dentary jaw articulation. *Breviora* 344:1–18
- Romer AS, Price LI. 1940. Review of the Pelycosauria. *Geol. Soc. Am. Spec. Pap.* 28:1–538
- Rowe T. 1986. *Osteological diagnosis of Mammalia, L. 1758, and its relationship to extinct Synapsida*. PhD thesis, Univ. Calif. 446 pp.
- Rowe T. 1988. Definition, diagnosis, and the origin of Mammalia. *J. Vertebr. Paleontol.* 8:241–64
- Rowe T. 1993. Phylogenetic systematics and the early history of mammals. See Szalay et al. 1993, pp. 129–45
- Rowe T, van den Heever JA. 1988. The hand of *Anteosaurus magnificus* (Dinocephalia: Therapsida) and its bearing on the origin of the mammalian manual phalangeal formula. *S. Afr. J. Sci.* 82:641–45
- Ruben J. 1995. The evolution of endothermy in mammals and birds: from physiology to fossils. *Annu. Rev. Physiol.* 57:69–95
- Rubidge BS. 1990a. A new vertebrate biozone at the base of the Beaufort Group, Karoo Sequence (South Africa). *Palaeontol. Afr.* 27:17–20
- Rubidge BS. 1990b. Redescription of the cranial morphology of *Eodicynodon oosthuizeni* (Therapsida: Dicynodontia). *Navors. Nas. Mus. Bloemfontein* 7:1–25
- Rubidge BS. 1991. A new primitive dinocephalian mammal-like reptile from the Permian of southern Africa. *Palaeontology* 34:547–59
- Rubidge BS. 1994. *Australosyodon*, the first primitive anteosaurid dinocephalian from the Upper Permian of Gondwana. *Palaeontology* 37:579–94
- Rubidge BS. 1995. *Biostratigraphy of the Beaufort Group (Karoo Supergroup)*. Pretoria, S. Afr.: Gov. Printer
- Rubidge BS, Hancox PJ, Catuneanu O. 2000. Sequence analysis of the Ecce-Beaufort

- contact in the southern Karoo of South Africa. *S. Afr. J. Geol.* 103:81–96
- Rubidge BS, Hopson JA. 1996. A primitive anomodont therapsid from the base of the Beaufort Group (Upper Permian) of South Africa. *Zool. J. Linn. Soc.* 117:117–39
- Rubidge BS, Kitching JW, van den Heever JA. 1983. First record of a therocephalian (Therapsida: Pristerognathidae) from the Ecca of South Africa. *Navors. Nas. Mus. Bloemfontein* 4:229–35
- Rubidge BS, Modesto SP, Sidor CA, Welman J. 1999. *Eumotosaurus* from the Ecca-Beaufort contact in the Northern Cape: implications for Karoo Basin development. *S. Afr. J. Sci.* 95:553–55
- Rubidge BS, van den Heever JA. 1997. Morphology and systematic position of the dinorocephalian *Styracocephalus platyrhinus*. *Lethaia* 30:157–68
- Rybczynski N. 2000. Cranial anatomy and phylogenetic position of *Suminia getmanovi*, a basal anomodont (Amniota: Therapsida) from the Late Permian of Eastern Europe. *Zool. J. Linn. Soc.* 130:329–73
- Schultze H-P, Truab L, eds. 1991. *Origins of the Higher Groups of Tetrapods: Controversy and Consensus*. Ithaca, NY: Comstock
- Sidor CA. 2000. *Evolutionary trends and relationships within the Synapsida*. PhD thesis, Univ. Chicago. 370 pp.
- Sidor CA. 2001. Simplification as a trend in synapsid cranial evolution. *Evolution* 55: 1419–42
- Sidor CA, Hopson JA. 1995. The taxonomic status of the Upper Permian eotheriodont therapsids of the San Angelo Formation (Guadalupian), Texas. *J. Vertebr. Paleontol.* 15:53A
- Sidor CA, Hopson JA. 1998. Ghost lineages and “mammalness”: assessing the temporal pattern of character acquisition in the Synapsida. *Paleobiology* 24:254–73
- Sigogneau D. 1970. *Révision Systématique des Gorgonopsiens Sud-Africains*. Paris: Cahiers Paléontol.
- Sigogneau-Russell D. 1989. Theriodontia I. In *Encyclopedia of Paleoherpétology, Part 17B*, ed. P Wellnhofer, pp. 1–127. Stuttgart, Ger.: Fischer
- Smith RMH. 1993. Vertebrate taphonomy of Late Permian floodplain deposits in the southwestern Karoo Basin of South Africa. *Palaios* 8:45–67
- Smith RMH. 1995. Changing fluvial environments across the Permian-Triassic boundary in the Karoo Basin, South Africa and possible causes of tetrapod extinctions. *Palaeogeogr. Palaeoclimat. Palaeoecol.* 117:81–104
- Smith RMH, Eriksson PG, Botha WJ. 1993. A review of the stratigraphy and sedimentary environments of the Karoo-aged basins of southern Africa. *J. Afr. Earth Sci.* 16:143–69
- Smith RMH, Kitching JW. 1997. Sedimentology and vertebrate taphonomy of the *Tritylodon* Acme Zone: a reworked palaeosol in the Lower Jurassic Elliot Formation, Karoo Supergroup, South Africa. *Palaeogeogr. Palaeoclimat. Palaeoecol.* 131:29–50
- Sues H-D. 1985. The relationships of the *Tritylodontidae* (Synapsida). *Zool. J. Linn. Soc.* 85:205–17
- Sues H-D. 1986. The skull and dentition of two tritylodontid synapsids from the Lower Jurassic of western North America. *Bull. Mus. Comp. Zool.* 151:217–68
- Sumida SS, Martin KLM, eds. 1997. *Amniote Origins: Completing the Transition to Land*. New York: Academic. 510 pp.
- Surkov MV. 2000. On the historical biogeography of Middle Triassic anomodonts. *Paleontol. J.* 34:79–83
- Szalay FS, Novacek MJ, McKenna MC, eds. 1993. *Mammal Phylogeny: Mesozoic Differentiation, Multituberculates, Monotremes, Early Therians, and Marsupials*. New York: Springer-Verlag
- Tatarinov LP. 1968. Morphology and systematics of the Northern Dvinia cynodonts (Reptilia, Therapsida; Upper Permian). *Postilla* 126:1–15
- Tatarinov LP. 2000. A new gorgonopid (Reptilia, Theriodontia) from the Upper Permian of the Vologda region. *Paleontol. J.* 34:75–83
- Tatarinov LP, Matchenko EN. 1999. A find of

- an aberrant tritylodont (Reptilia, Cynodontia) in the Lower Cretaceous of the Kemerovo region. *Paleontol. J.* 33:422–28
- van den Heever JA. 1994. The cranial anatomy of the early Therococephalia (Amniota: Therapsida). *Univ. van Stellenbosch Ann.* 1: 1–59
- Wagner PJ. 2000. The quality of the fossil record and the accuracy of phylogenetic inferences about sampling and diversity. *Syst. Biol.* 49:65–86
- Ward PD, Montgomery DR, Smith RMH. 2000. Altered river morphology in South Africa related to the Permian-Triassic extinction. *Science* 289:1740–43
- Watson DMS, Romer AS. 1956. A classification of therapsid reptiles. *Bull. Mus. Comp. Zool.* 114:37–89