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Phylogenetic interrelationships and pattern of evolution of the therapsids: testing for polytomy

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There is little agreement on the interrelationships of the major therapsid subtaxa because none of the variously proposed sister-group relationships are supported by clearly defined, unambiguously distributed morphological characters. Rather than pursue a new cladistic analysis here, the hypothesis is explored that the lack of an agreed cladogram is because there was a polytomy at the base of the therapsid radiation that is not amenable to positive testing by conventional morphological cladistics, but that can be tested in four ways. The virtually simultaneous appearance of all the lineages except Cynodontia in the Middle Permian stratigraphic record supports the hypothesis. The palaeogeographic record, which shows a combination of taxa with first occurrences in different parts of Pangaea also supports it, though this is not strong evidence. The palaeoenvironmental record supports the polytomous hypothesis strongly by providing evidence of a coincidence between the start of the therapsid radiation and the appearance of a new suite of ecological opportunities for diversification within higher latitudes. Finally, a functional correlation analysis of the characters associated with feeding, and the reconstruction of lineages of functionally integrated organisms offers strong support by indicating that no two of the four respective lineages, Dinocephalia, Gorgonopsia, Anomodontia and Therocephalia, could have shared a functionally feasible common ancestral stage subsequent to a hypothetical ancestor at a biarmosuchian grade. The exception is Cynodontia and Therocephalia, which are inferred to have shared such a more recent common ancestral stage, and therefore to be sister-groups in the taxon Eutheriodonta.

Keywords: Therapsida, Permian tetrapods, Permian palaeoecology, correlated progression.

INTRODUCTION

The amniote clade Therapsida is highly significant in the history of terrestrial tetrapod life for two, no doubt interrelated reasons. One is that the anatomy indicates that from the very start therapsids were evolving the increased energy budgets and activity levels that were to culminate in the mammals, with the latter's huge potential for physiological and anatomical diversification. The second is that it was the nonmammalian therapsids that were primarily responsible for establishing what was to become the standard structure of fully terrestrial tetrapod communities – a fauna dominated by a very large preponderance of diverse amniote herbivore species. This structure was later repeated in essence by the dinosaur-dominated communities of the later Mesozoic, and by the mammalian-dominated communities of the Tertiary right up to the present day.

However, the details of the early radiation of the Therapsida are shrouded in obscurity. The earliest fossil record of several derived lineages occurs approximately simultaneously, and cladistic analysis has so far led only to a number of very weakly-supported and ambiguous interrelationships amongst these lineages. Indeed, the situation is remarkably comparable to the morphological analysis of placental mammal interrelationships. Here the taxon Placentalia on the one hand, and the individual constituent orders on the other, are very well-supported clades, but to a very large extent morphological characters proved unable satisfactorily to resolve the interrelationships between these orders. Only with the advent of sufficient molecular sequence data over the last decade did this resolution become possible, with the by now familiar but at the time utterly unexpected results (e.g. Kemp 2005; Springer *et al.* 2005). Thus the Therapsida are also of interest as a paradigm for how to interpret an evolutionary pattern of a taxon where morphological based cladistic analysis does not generate a well-supported set of sister-group relationships, but where molecular evidence is not available.

CURRENT VIEWS OF THE INTERRELATIONSHIPS OF THERAPSIDS

As reviewed most recently by Rubidge & Sidor (2001) and Kemp (2005), there are six widely recognized undisputed therapsid subtaxa, viz:

- *Biarmosuchia:* medium-sized carnivores retaining several sphenacodontid characters. No clear-cut shared derived characters so this may technically be a paraphyletic group, and certainly close in structure to the hypothetical therapsid ancestor.
- *Dinocephalia:* large to very large carnivores and herbivores but generally quite primitive. Characterized by a tendency to pachyostosis of the skull bones.
  Gorgonopsia: medium to large, highly specialized carnivores, characterized by very large canines and a jaw hinge and musculature capable of an extremely wide gape.
- *Anomodontia: s*mall to large, highly specialized herbivores, although including some quite primitive, basal forms. Apart from the latter, dentition largely or completely replaced by a horny beak, and extreme enlargement of the jaw muscles.
- *Therocephalia: s*mall to large-sized diverse carnivores, with a few specialized omnivores, and in the Triassic

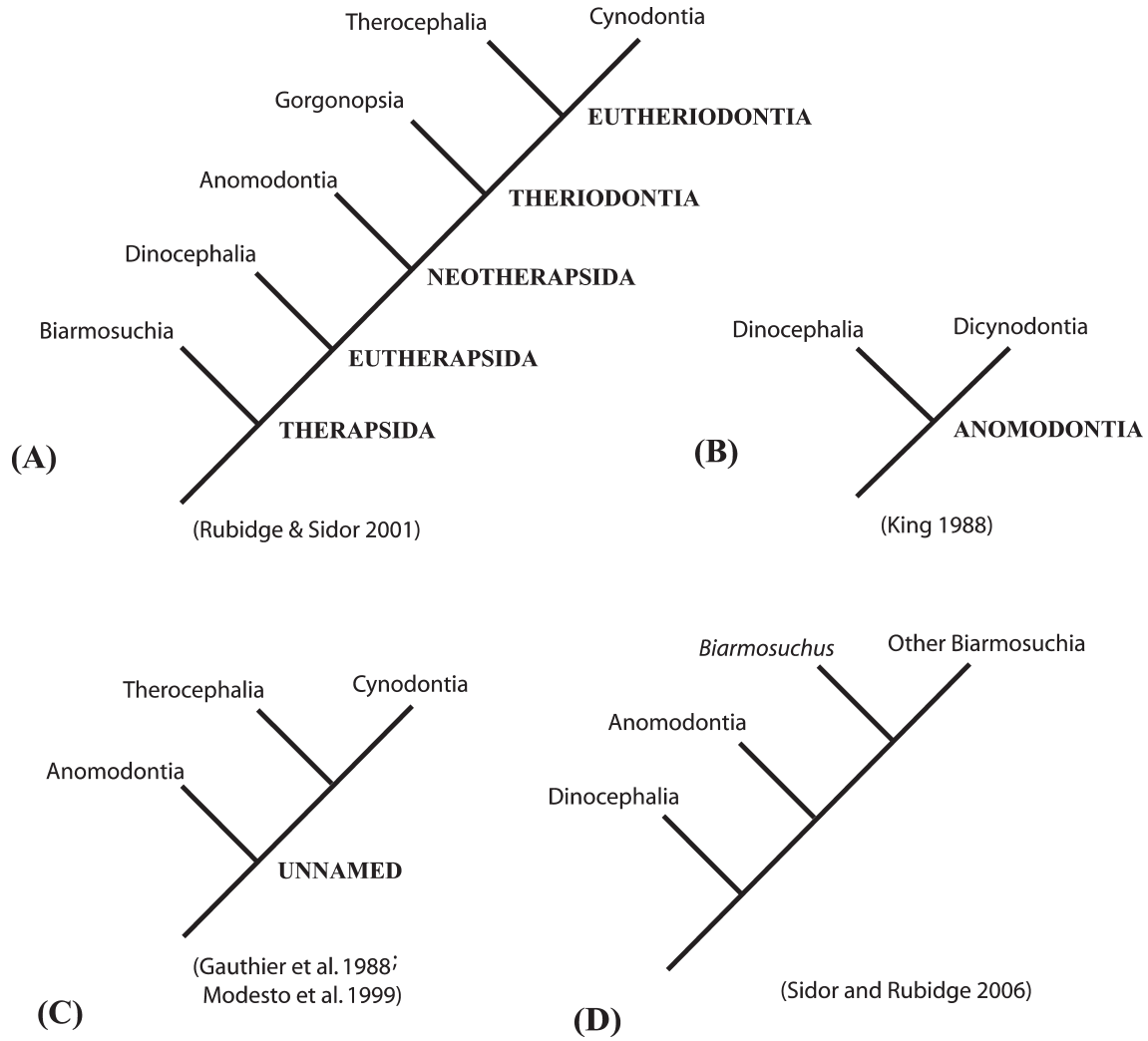


Figure 1. Current hypotheses of the interrelationships of major therapsid sub-taxa. See Table 1 for the characters used by respective authors to define the nodes.

one specialized herbivorous subgroup.

- *Cynodontia:* initially small to medium-sized carnivores, although a very diverse group in the Triassic. The most progressive taxon with many characters shared with mammals such as complex teeth, enlarged dentary and secondary palate.

The first of these subtaxa, Biarmosuchia, is recognized almost completely by a number of sphenacodontid-like plesiomorphic characters. One or two minor synapomorphies have been claimed for it (Hopson 1991; Sidor & Rubidge 2006), but the taxon may well be paraphyletic and include the ancestry of the rest of the therapsids. The rest of these therapsid subtaxa are well-supported clades.

There are also a few very poorly known forms from the Middle Permian of Russia, such as *Nikkasaurus, Microurania, Phthinosuchus* and *Niaftasuchus* (Ivakhnenko 2003; Kemp 2005). These are ignored here, although with better material they may well prove important. There is also a specimen that has been claimed to represent a very basal therapsid, *Tetraceratops,* which is represented by a single, poorly preserved specimen from the Lower Permian of North America. Laurin & Reisz (1996) described it as possessing certain therapsid features, but several authors have subsequently rejected this claim, and interpreted it as Romer & Price (1940) originally did as an aberrant pelycosaurian grade synapsid.

The most familiar cladogram of the major therapsid subtaxa (Fig. 1A) is that published in their review by Rubidge & Sidor (2001) and based mainly on the analysis and data set of Sidor & Hopson (1998). Although it is expressed as a fully resolved set of dichotomies, the number of characters supporting the major nodes is not only small or very small, but also the significance of many of these characters can be doubted on the grounds of their being either not unique to the taxon, probably non-independent, too vaguely defined for confidence that they are homologous, or based on a very small sample of species within the taxon (Table 1). Meanwhile, other authors have proposed different relationships, although on no more convincing grounds. King (1988) argued for a sister group relationship between the Dinocephalia and Anomodontia (Fig. 1B), to which combined taxon she applied the name 'Anomodontia' in a former usage. Cladistic analyses by Gauthier *et al.* (1988) and by Modesto *et al.* (1999) independently concluded that Anomodontia, is the sister group of Therocephalia plus Cynodontia (Fig. 1C). Recently Sidor & Rubidge (2006) published a cladistic analysis of several new and newly studied biarmosuchian grade therapsids, along with dinocephalians and basal anomodontians, but not including gorgonop-

Table 1. The putative synapomorphies for the proposed monophyletic groups in Fig. 1, extracted from the respective cited works, with comments on ambiguousness of distribution, impreciseness of the definition, or smallness of sample size as appropriate.

EUTHERAPSIDA – Fig. 1A. (all except Biarmosuchia)

Zygomatic arch bowed laterally. *No more so in the brithopodid dinocephalians (Orlov 1958) than in biarmosuchians (Sigogneau-Russell 1989; Ivakhnenko 1999) and not bowed but simply diverging slightly in therocephalians.*

No distinct ossified olecranon process of the ulna. *Prominent process in gorgonopsians (Colbert 1948) and present, if short, in cynodonts (Jenkins 1971).*

Only three phalanges in 5th pedal digit. *Extremely small sample of taxa available.*

NEOTHERAPSIDA – Fig. 1A. (Anomodontia, Gorgonopsia, Therocephalia and Cynodontia)

Ventrally expanded squamosal hiding most of quadrate in posterior view. *Difficult to accept as homologous because of the very different form and mode of attachment of the quadrate* in *gorgonopsians (Kemp 1969a), therocephalians (Kemp 1972b; van den Heever 1994) and anomodontians (King 1981).*

Epipterygoid broadly contacting underside of parietal. *Contact is narrow in gorgonopsians (Kemp 1969a), and anomodontians (King 1988). Ivakhnenko (2003, figs 6 and 9) figures an epipterygoid apparently very similar to that of gorgonopsians and anomodontians in both* Biarmosuchus *and the dinocephalian* Archaeosyodon.

Epiphyses on atlas vertebra. *An extremely small sample; Sigogneau-Russell (1989) states that the atlas of the biarmosuchian* Hipposaurus *is similar to that of gorgonopsians.*

Enlarged obturator foramen of pelvis. *An extremely small sample of biarmosuchians. In dicynodontians wide variation is reported, from minute to large (King 1988).*

THERIODONTIA – Fig. 1A. (Gorgonopsia, Therocephalia and Cynodontia)

Flat, low snout with dorsal surface of nasals horizontal.

Short internarial process. *Relatively long in the basal cynodont Procynosuchus (Kemp 1979), and short in pelycosaurs (Romer & Price 1940).*

Narrow temporal roof, equal or less than interorbital width. *Not the case in gorgonopsians generally (Sigogneau-Russell 1989).*

Greater flaring of zygomatic arch. *Not the case in therocephalians*.

Dentary with free-standing coronoid process. *The gorgonopsian coronoid process differs from those of therocephalians and cynodonts in its triangular rather than flat cross-sectional shape, indicating a different pattern of muscle attachments.*

Dentary with masseteric fossa. *Not present in gorgonopsians or therocephalians.*

Postdentary bones somewhat reduced in height. *Not absolutely in either gorgonopsians or therocephalians, but only relative to the increased height of the dentary due to the coronoid process.*

Humeral head slightly dorsal. *Very vague and just as true of some dicynodontians (King 1988).*

Deltopectoral crest more than 40% of humeral length. *Also in dicynodontians (King 1988)*.

Greater trochanter of femur still small but extends distal to head. *There is little manisfest difference in the greater trochanter of biarmosuchians and gorgonopsians (Sigogneau-Russell 1989).*

EUTHERIODONTA – Fig. 1A. (Therocephalia and Cynodontia)

Narrow intertemporal roof.

No contact between postorbital and squamosal on medial margin of temporal fossa. *Presumably correlated with previous character.*

Sagittal crest on parietal. *Also presumably correlated with the first character.*

Antero-posterior expansion of epipterygoid. *True, but only to a slight extent in most therocephalians.*

Loss of palatal teeth. *Also in anomodontians.*

Postero-ventral part of dentary thickened and angular in trough.

Fenestra between dentary, surangular and angular.

UNNAMED TAXON – Fig. 1C. (Anomodontia, Therocephalia and Cynodontia)

Frontal margins with lappet entering orbital margin. *Virtually identical in most other therapsids, such as brithopian dinocephalians (Orlov 1958) and gorgonopsians, but not true of even basal cynodontians.*

Postfrontal small. *Still substantial in early therocephalians (van den Heever 1994) and the basal anomodontians* Otsheria *(Chudinov 1960) and* Patranomodon (Rubidge & Hopson 1996).

Postorbital region of skull longer than preorbital region. *Not true of more basal therocephalians, and lengths about equal in basal cynodonts.*

Palatine with separate palatal and choanal rami. *Difficult to distinguish from the gorgonopsian condition (Kemp 1969a; Sigogneau-Russell 1989)*

Mandibular fenestra present. *Different construction in anomodontians (King 1988) compared to therocephalians (Kemp 1972b), for example in the former the dentary extends above and below it, but only above it in the latter.*

Palatine teeth absent.

Teeth on transverse process of pterygoid absent.

Tabular separated from opisthotic by squamosal. *Not the case in basal cynodonts.*

Odontoid fused to axis in adult.

Second intercentrum fused to axis in adult. *Probably functionally correlated with the previous character.*

Atlas neural arch separated from atlas intercentrum. *Doubtful as they function together as a ring (Kemp 1969b).*

Clavicles narrow medially. *They broaden medially in at least the therocephalian* Regisaurus *(Kemp 1986; Fourie & Rubidge 2007) and the basal cynodontian* Procynosuchus *(Kemp 1980)*

Humeral head articular surface bulbous and inflected. *No more so in some therocephalians (Kemp 1986; Fourie & Rubidge 2007) than in gorgonopsians (Kemp 1982).*

Ilium more than twice height of acetabulum. *Not in therocephalians (Kemp 1986).*

Continued on p. 4

Table 1 (*continued*)

Obturator foramen between pubis and ilium, rather than in pubis alone. *Condition unclear in gorgonopsians (Sigogneau-Russell 1989).*

Femoral head oblong and spherical (rather than elongate, subspherical, or protuberant). *Very vague and hard to exclude gorgonopsians or even biarmosuchians (Sigogneau-Russell 1989).*

ANOMODONTIA *sensu* King (1988) – Fig. 1B. (Dinocephalia and Anomodontia *s.s.*)

Loss of coronoid bones.

Non-terminal nostrils and long posterior spur of premaxillae. *Also in biarmosuchians (Sigogneau-Russell 1989; Ivakhnenko 1999) and the basal cynodontian* Procynosuchus (*Kemp 1979).*

Grooved or troughed palatal exposure of vomers. *Difficult to see a significant difference between biarmosuchians and dinocephalians, and complicated by the evolution of a secondary palate in anomodontians.*

Reduction or loss of internal trochanter of femur.

sians, therocephalians or cynodonts (Fig. 1D). Their strict consensus tree of nine equally parsimonious trees included a fourfold polytomy of, respectively, Dinocephalia, Anomodontia, the genus *Biarmosuchus* alone, and the other biarmosuchians. A majority rule consensus of the nine trees generated Dinocephalia as the most basal and Anomodontia and Biarmosuchia as sister groups.

It is, of course, possible that a new cladistic analysis with more thoughtful selection of characters would produce a more strongly supported set of resolved interrelationships. However, in the absence of radical new material, and in the light of the universal problem of how objectively to recognize unit morphological characters, this is unlikely, and is not attempted here. Rather, it is the purpose of this paper to propose that the failure to discover a well-supported and fully resolved tree of therapsid interrelationships lies in the inability of cladistic methodology to deal with a situation where the real evolutionary pattern may have been a virtually simultaneously polytomous splitting of several lineages from the ancestor. In such a case, alternative, non-cladistic tests for true polytomy need to be considered.

TESTING FOR POLYTOMY

It must be accepted as a matter of evolutionary biology that in principle a polytomous split of several lineages from a low taxonomic level can occur. At the extreme the multiple lineages would all arise directly from a single ancestral species, although more plausibly perhaps they would arise from different respective species sharing the typical morphological disparity of a single genus, or from different genera sharing the typical disparity of a taxonomic family. As has always been understood, such a situation creates difficulties in principle for cladistic analysis (e.g. Maddison 1989). If there are no characters defining successive nodes on the tree, cladistic methodology is required to attribute this to a failure to find them, not to their absence. Put another way, for cladistics the null hypothesis is unresolved polytomy and therefore polytomy cannot itself be a testable hypothesis, but only an expression of ignorance of enough characters (e.g. Maddison 1989; Walsh *et al.* 1999). Hence the response to such a situation is to continue the search for defining characters, and in the meanwhile accept provisionally the best supported tree, however weak and unconvincing the support is.

Several molecular systematists (Walsh *et al.* 1999; Poe & Chubb 2004; Whitfield & Lockhart 2007) have addressed the problem of resolving the interrelationships amongst lineages of modern taxa that appear to have arisen by an 'explosive', polytomous radiation. The issue is that the external branches (major subtaxa) of the tree are much longer (i.e. greater molecular differences between them) than the internal branches (the inferred initial diversifications at the base of the tree), to the extent that the molecular evidence lacks the resolving power to distinguish between a succession of finely spaced dichotomies (a 'soft polytomy') on the one hand (Fig. 2B) and a single polytomous split (a 'hard polytomy') on the other (Fig. 2A).

The molecular situation described is clearly analogous to the morphological problem of therapsid interrelationships, and the same terminology is appropriate: therapsids exhibit a soft polytomy in that the morphology can reveal the major subtaxa, but cannot satisfactorily resolve a complete set of dichotomous nodes between them, and therefore cannot discriminate between soft and hard polytomies. In the case of molecular sequence based systematics, there are a number of possible statistical tests of the likelihood that a soft polytomy actually is a hard or true polytomy, because of the ease of recognizing a very large number of objectively definable 'unit' characters (i.e. nucleotides). In the case of a soft polytomy that is based solely on the morphology of fossils, other positive tests for hard polytomy need to be considered, of which there are four kinds.

The stratigraphy test

A polytomy implies a virtually simultaneous origin of the separate lineages. If the stratigraphic sequence covering the time of the event has both adequate temporal resolution, and a dense enough fossil record it can offer support for the polytomy hypothesis.

The relative dating of the first appearance of the major therapsid subtaxa has been reviewed most recently by Lucas (2006), Kemp (2006a) and Abdala *et al.* (2008) (Fig. 3). They are currently known from Middle Permian deposits of three areas: the lower part of the Beaufort Group of South Africa, the cis-Uralian region of Russia, and a sparse fauna from the Xidagou Formation of Dashankou, China. There are disagreements about the dating of Middle Permian continental localities relative to the standard, marine-based sequence (Rubidge 1995; Izart *et al.* 2003; Lucas 2004; Tverdokhlebov *et al.* 2005), but from the nature of the fossil faunas, two aspects of the temporal

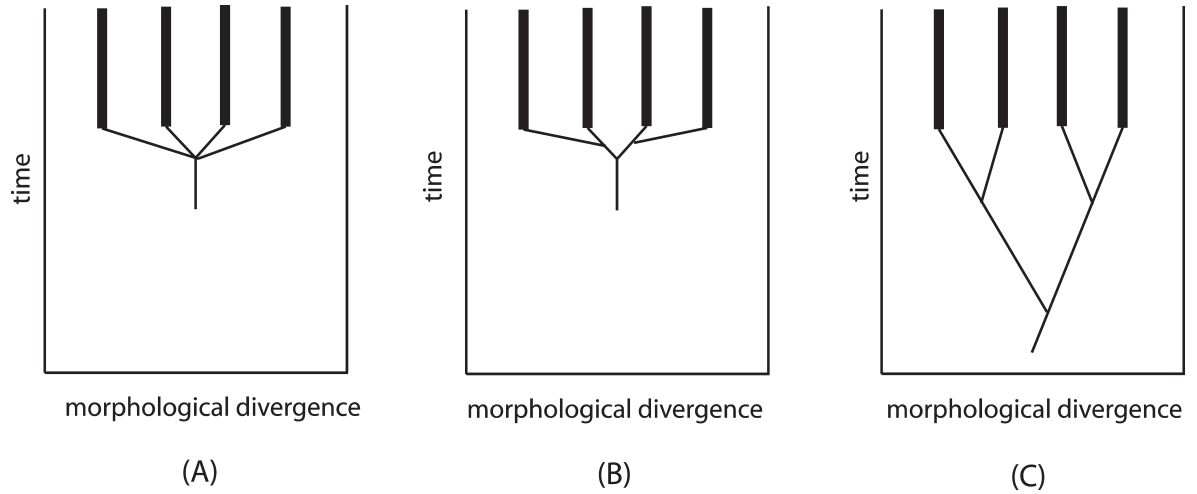


Figure 2. Possible patterns of evolution; thick lines represent the fossil record, thin lines the true phylogenetic lineages. **A**, A 'hard' or true polytomy. **B**, A 'soft' polytomy in which the internal branches are too short to be resolvable by morphological characters. **C,** A sequence of dichotomies with long ghost lineages.

pattern of occurrence of early therapsids are generally agreed upon. First, the three formations that have so far yielded early, Guadalupian-aged therapsids are closely spaced in time. Abdala *et al.* (2008) believe that the South African *Eodicynodon* Assemblage-Zone is around the Roadian-Wordian boundary, and that both the Russian Ocher Assemblage and the Chinese Xidagou Formation fauna are Roadian, and so slightly older. The actual therapsids currently known from this time include all the major subtaxa except one. The Cynodontia did not appear until some 6–7 million years later, in the Late Permian Tatarian of Russia and the approximately contemporaneous *Tropidostoma* Assemblage Zone of South Africa (Botha-Brink & Abdala 2008). Second, it is believed that there is a significant hiatus between the last occurrence of the North American pelycosaurs and these earliest therapsids. It has been termed 'Olson's Gap' by Lucas (2004), after E.C. Olson who first proposed its existence (Olson 1962), and is perhaps about five million years in length.

There is also a general belief that a very considerable therapsid ghost lineage of about 35 million years must have existed, from the first appearance of therapsids in the Middle Permian right back to the first appearance of their presumed sister-group, the sphenacodontid pelycosaurs in the Late Carboniferous (Abdala *et al.* 2008). However, as Kemp (2006a) has pointed out, on the currently available evidence the possibility cannot be ruled out that Sphenacodontidae is paraphyletic, and that Therapsida is the sister-group of a much later, Early Permian member of that taxon. If this is so, then at the minimum the ghost lineage need be scarcely any longer than that of the the five million years of Olson's Gap. The temporal pattern of first appearances of fossil therapsids is completely compatible with a simultaneous splitting of an ancestral therapsid into all the major subtaxa except Cynodontia in Roadian times. This support for the polytomy hypothesis must nevertheless be treated with some caution because of the existence of Olson's Gap, and because of the impossibility on the basis of presently known characters of knowing the precise relationships of Therapsida to the sphenacodontian pelycosaurs, and therefore how long the therapsid ghost lineage really is.

The palaeobiogeography test

A second implication of polytomy is that all the lineages first appeared in the same geographical region. The fossil record of a radiation could in principle be compatible with such a pattern. Alternatively, it could suggest a pattern of separate regions of origin for different combinations of taxa, implying a succession of dichotomies.

The earliest therapsid fossils occurring in the three regions of mid-Permian Pangaea do not show a clear taxonomic differentiation between the areas. Four of the lineages occur together in South Africa, Dinocephalia, Anomodontia, Gorgonopsia and Therocephalia (Rubidge 1995). In Russia there are three, Biarmosuchia, Dinocephalia and Anomodontia (Ivakhnenko 2003), and in China only two, Biarmosuchia and Dinocephalia (Li & Cheng 1996; Li *et al.* 1997). Thus the palaeogeographic pattern tends to support a polytomy rather than pointing to possible vicariant or dispersal events separating successive dichotomies. However, the very small number of localities, and the paucity of fossils within them renders the pattern too weak to be regarded as particularly significant.

The palaeoenvironmental test

A polytomous divergence of several lineages virtually simultaneously is a realistic possibility, and such an event can be presumed to have a potentially discoverable cause. Explanations of explosive radiations have long been sought, in terms of such concepts as key innovations (Hunter 1998) and ecological opportunities (Kemp 2007b). For example, it is suggested that the Cambrian explosion is related to increase in oxygen levels (e.g. Marshall 2006), and that the Tertiary radiation of placental mammals was facilitated by the removal of competitive exclusion by dinosaurs (e.g. Kemp 2005). A hypothesis of polytomy may in principle be supported by evidence of the sudden origin in the ancestral taxon of a novel biological potential, or evidence of the coincidental origin of a series of new ecological opportunities.

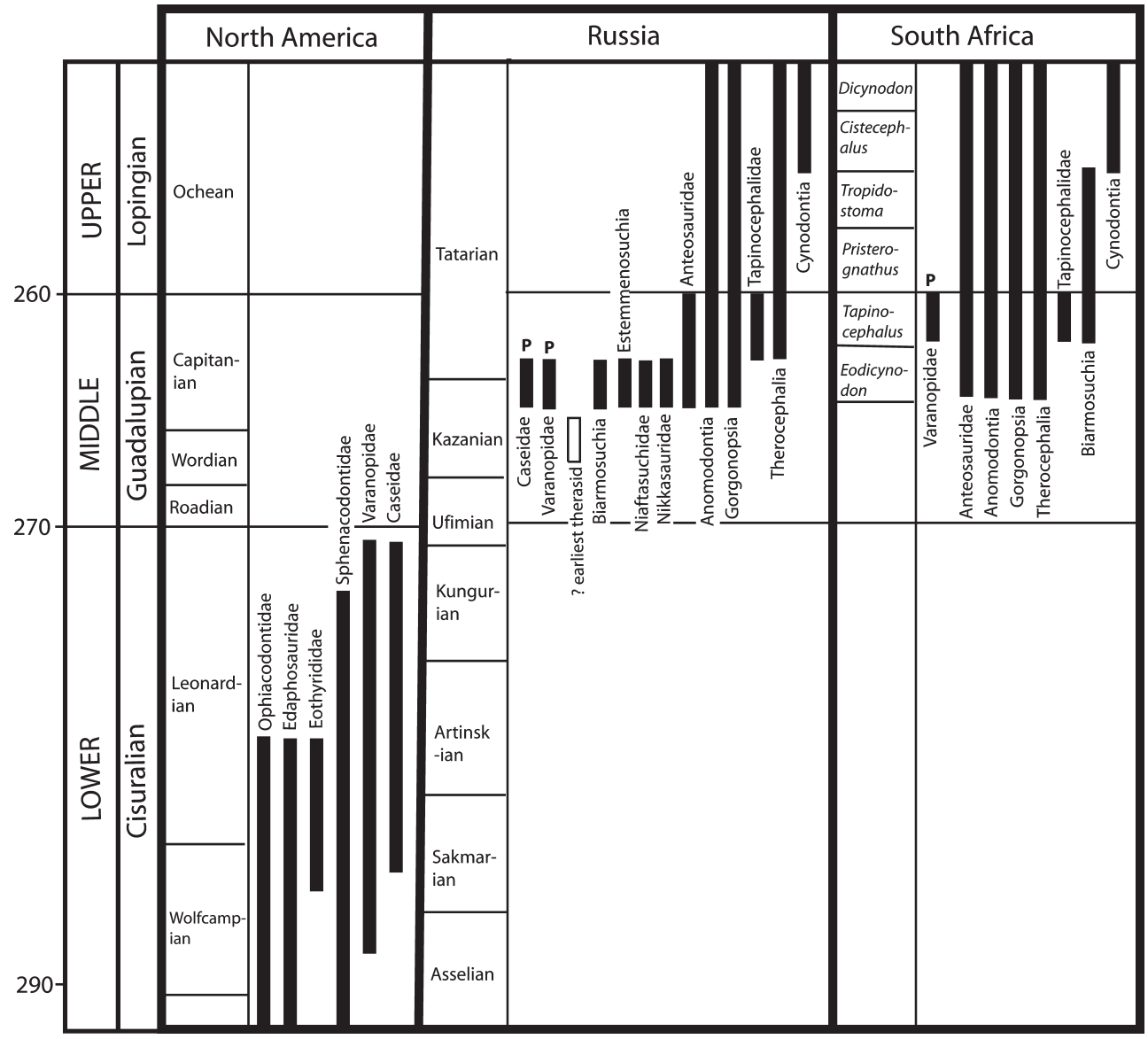


Figure 3. Stratigraphic occurrences of synapsid taxa indicating the virtually simultaneous first appearance of the major therapsid subtaxa in the Middle Permian. The earliest Dinocephalia are indicated by Anteosauridae. **P** indicates pelycosaurian taxa surviving into the Middle Permian. The open box labelled '?earliest therapsid' refers to some extremely poorly preserved fragments from the Copper Sandstones of Russia that have been dubiously claimed to be therapsid limb bones (see Kemp 2006a). The exact stratigraphic correlation between these three regions and also the Xidagou Formation of China, which is not shown, are not yet agreed (see Izart *et al.* 2003; Rubidge 2005; Lucas 2006; Abdala *et al.* 2008). Reproduced with slight modifications from Kemp (2006a).

In the case of the Therapsida, Kemp (2006a) proposed an explicit palaeoenvironmental model for both the origin of basal therapsids, and for their divergence in the Middle Permian into a series of subtaxa (Fig. 4). To summarize briefly, the evidence that was adduced for the model is in part functional interpretation of therapsids as tetrapods with higher energy budgets, and greater internal thermoregulatory and chemoregulatory abilities (Kemp 2007b). This supposedly allowed them to remain continuously active in highly seasonal environments, notably the Summerwet Biome that occupied the tropical zones of Early Permian Pangaea (Rees *et al.* 2002). The second line of evidence is a shift in the palaeoclimatic zones at the start of the Middle Permian. Hitherto, extensive desert zones had isolated the tropical regions from the temperate regions in both hemispheres, but at this time the Summerwet Biome appears to have expanded northwards and southwards along the eastern edge of Pangaea (Rees *et al.* 2002) . For the first time it became possible for therapsids to disperse from tropical into temperate regions. According to the model, this new ecological opportunity for a taxon already adapted for fluctuating, seasonal conditions resulted in the explosive radiation of the group. Rapidly and simultaneously several lineages diverged into a series of new niches – large and small body sizes, carnivores, herbivores and omnivores.

Thus the hard polytomy hypothesis of the interrelationships of therapsids is corroborated by this evidence of a plausible environmental cause occurring coincidentally in time and place with the fossil record of the radiation.

The functional systems test

However plausible an evolutionary scenario can be built on the basis of stratigraphic, biogeographical and palaeoenvironmental evidence, any hypothesis of phylogenetic relationships of organisms must be supported

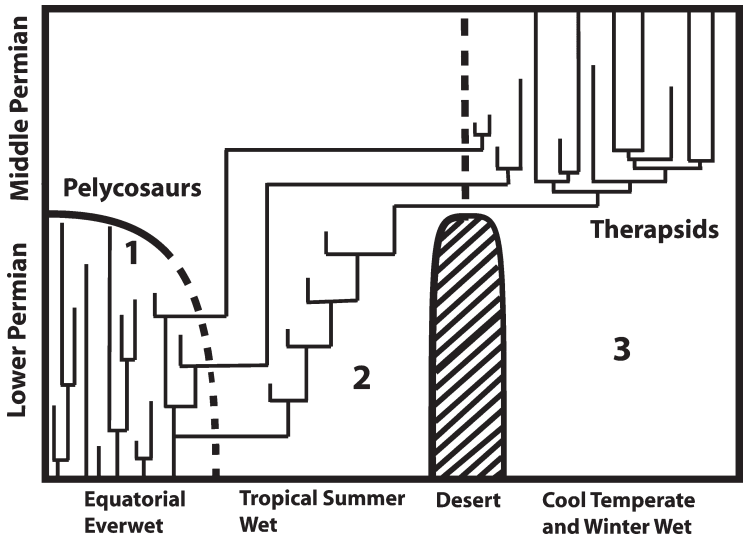


Figure 4. Model of the origin of Therapsida. **Phase 1**: radiation of pelycosaur-grade synapsids in an Everwet biome existing in the equatorial regions of Lower Permian Pangaea. **Phase 2**: evolution of adaptations for remaining active throughout the seasonal fluctuations in the Tropical Summerwet biome, leading to basal therapsids. **Phase 3**: retraction of the mid-latitudal desert zones along the eastern margin of Pangaea opened new dispersal routes to the northerly and southerly temperate biomes, within which therapsids rapidly radiated into a variety of new taxa. Reproduced from Kemp (2006a), which should be consulted for details.

primarily by the analysis of characters. The impasse between the realistic possibility of polytomous branching having occurred on the one hand, and the logical inability of standard cladistic methodology to provide a positive test for it on the other has been pointed out. There is, however, an alternative way of treating characters that in principle at least could detect a polytomy.

Cladistic analysis of morphological characters assumes that the organism can be atomized into a set of objectively recognizable discrete, independent, and initially equally weighted characters. The most parsimonious distribution of these characters amongst the organisms being analysed is then taken to indicate the best estimate of relationships – the best supported tree. However, all these assumptions are to a degree unrealistic, because of course organisms are actually integrated wholes in which the parts are structurally and/or functionally integrated, and they act together to produce the biological attributes of the phenotype (e.g. Dullemeijer 1974; Schwenk 2001). Where large amounts of character data give strongly supported relationships, there is no reason not to accept the most parsimonious tree as a good estimate. However, when there is poor support for any one tree, and little or no agreement amongst different authors concerning which is the best supported tree, then the probability that characters are being over-interpreted is high.

An alternative to the atomistic model of cladistic methodology is the much more realistic correlated progression model (Kemp 2006b, 2007a,b). Here it is assumed that characters are indeed functionally interdependent on one another within an integrated organism. They evolve in loose correlation with one another, and the probability of a change in one particular character depends on what changes have already occurred in others. Meanwhile the coordinated changes amongst the characters always maintain a fully integrated, well-functioning organism.

Applying the correlated progression model as a test for polytomy requires an understanding of the functional interrelationships between the known characters of a derived phenotype. Once this is achieved, a more primitive hypothetical stage can be reconstructed, in which the individual parts are more plesiomorphic but between which the functional relationships are maintained. For example, there must always be correlation between the size and orientation of the inferred site of origin and site of insertion of a muscle; between the form of the dentition and the mandibular mobility permitted by the shape of the jaw articulation; between the inferred action of the forelimb and the action of the hindlimb; between body size and various allometrically related structures, and so on. By performing such an analysis several times, a hypothetical sequence of successively more plesiomorphic, ancestor-like stages can be reconstructed all the way back to the inferred ancestral state of the whole lineage. The third step is to compare this sequence of reconstructed historical stages for one lineage with those of other lineages, in order to see if there is a possible coincidence of structure and function at any point. Absence of such coalescence implies that the two lineages evolved independently from the common ancestor of the whole taxon, even if in a cladistic analysis there are certain isolated characters in common. And if several lineages lack coalescence with any others, then a hypothesis of polytomy is corroborated.

The most comprehensively studied functional aspect of therapsids is the feeding mechanism, which involves numerous integrated structures. The architecture of the jaw musculature is related to the size and shape of the temporal fenestrae, the posterior palate, and such structural features as a coronoid eminence, a discrete coronoid process of the dentary, fossae on the angular and dentary bones, ridges on the reflected lamina of the angular, and the form of the retroarticular process of the articular. Also integrated with the jaw muscle forces and directions are dental features such as interdigitating incisors, large, reduced or absent canines, reduced or elaborated post-

canines, and inferred keratinous beaks. The jaw articulation may vary in form and degree of robustness for stress resistance, and in design for size of gape, and often propalinal movements of the mandible. The nature of the attachment of the quadrate to the squamosal is surprisingly variable amongst therapsids, which reflects the vectors of the stresses generated by the jaw muscles, and mobility in some groups. There are also various structural elements of the skull associated with stress resistance, such as the epipterygoid and parocciptal process.

Much less is currently understood about the mechanics of the postcranial skeleton and locomotory system of therapsids, so although in principle this part of the phenotype could equally well be incorporated into a correlated functional analysis, for the present purpose attention is restricted to the skull and jaws.

The ancestral state (Fig. 5A)

The Russian biarmosuchian *Biarmosuchus* (Chudinov 1960; Ivakhnenko 1999) combines therapsid characters with sphenacodontid characters, and has few if any significant autapomorphies (Hopson 1991; Rubidge & Sidor 2001; Sidor & Rubidge 2006). It is therefore a good model for an ancestral therapsid-stage from which the remaining major taxa evolved. The long, convex preorbital region, relatively small temporal fenestra, modest coronoid eminence of the mandible, and well-developed postcanine dentition are all comparable to features of the sphenacodontid pelycosaurs. The more striking of the many detailed differences from the sphenacodontid are the much larger upper canine tooth, a degree of dorso-ventral expansion of the temporal fenestra, enlargement of the reflected lamina of the angular, and an anterior rotation of the occiput. Kemp (2005) attempted a simple reconstruction of the jaw musculature, concluding that the adductor mandibuli consisted mainly of a single muscle mass originating on the medial and posterior edges of the temporal fenestra, and no doubt from an aponeurotic sheet of connective tissue across it (Barghusen 1976b). It inserted in primitive sphenacodontid fashion along the dorsal and medial parts of the coronoid region of the jaw, and had not invaded the lateral surface of the jaw at all. The incisor teeth may have interdigitated, although this is not certain. The jaw articulation was a simple, roller-like hinge between the quadrate and articular bones. No attention has yet been paid to the mechanical structure of the skull, but it seems likely from the estimated muscle sizes that the stresses generated by the biting action were small compared to most of the more derived therapsids. Stress transmission between skull and mandible was probably adequately accommodated by the relatively firm attachment of the large quadrate to the squamosal, and by the generally robust intertemporal and occipital regions of the skull.

Dinocephalia (Fig. 5B)

No comprehensive review of the jaw musculature of a dinocephalian has yet been undertaken, although Barghusen (1976a) and Kemp (1982) reconstructed the likely general features. The skull of *Titanophoneus* is presumed to have a structure close to that of the ancestral dinocephalian (Orlov 1958). The temporal fenestra has enlarged by dorso-ventral expansion compared to the ancestral therapsid condition, but there is no significant lateral or posterior expansion. The main distinction is an extension of the area of origin of adductor musculature onto a broadened lateral-facing surface of the intertemporal region. In this latter respect, the temporal fenestra of dinocephalians is entirely unlike that of gorgonopsians and the less specialized of the anomodontians. The form of the mandible indicates clearly that the insertion of this part of the adductor musculature had remained on the dorsal and medial parts of the lower jaw, much as in the ancestral stage, with no expansion onto the lateral jaw surface (Barghusen 1976a; Kemp 1982).

A reconstruction of the functional evolution of the ancestral dinocephalians from the ancestral therapsid condition consists only of the dorso-ventral expansion of the origin of the adductor muscles, which is entirely different from what occurred in any of the other main therapsid subtaxa. Indeed, none of the integrated jaw function features characteristic of any of the other taxa are found in dinocephalians. This absence of coalescence of derived functional organization supports the hypothesis of an independent evolutionary lineage for Dinocephalia.

Anomodontia (Fig. 5C)

The majority of anomodontians are the dicynodontians, which are the most modified of all therapsids, especially in terms of feeding function (Crompton & Hotton 1967; King 1981, 1988). The temporal fenestra is vastly increased in size by expansion both antero-posteriorly and, to varying extents, medially in different taxa. Furthermore, the posterior part of the skull has extended ventrally, which has the effect of lowering the position of the jaw articulation and so increasing the torque generated by the adductor musculature. It also creates another large area of origin for this musculature. Novel areas for insertion of the muscles on the lower jaw are also present. These are a broadened dorsal surface of the jaw, and shelves on the lateral surface of the dentary, often placed very far forwards (King 1988). The jaw articulation is modified to permit propalinic shifts, correlated with the evolution of a horny tooth beak. Of the dentition, at the most only upper, tusk like canines and a few very small postdentary teeth are present.

The functional evolution of anomodontians is better understood than that of other taxa because of a number of more basal anomodonts known from the Middle Permian of South Africa and Russia (King *et al.* 1989; Modesto *et al.* 1999; Reisz & Sues 2000). The cranial anatomy of *Patranomodon* (Rubidge & Hopson 1996), for example, illustrates a stage between the hypothetical ancestral therapsid and a basal dicynodontian such as *Eodicynodon* (Rubidge 1990). *Patranomodon* has retained a relatively long preorbital region, and its temporal fenestra is relatively small and little expanded medially. Incisor teeth are also retained. The lack of significant medial expansion of the temporal fenestra, or of any spread of the attachment of

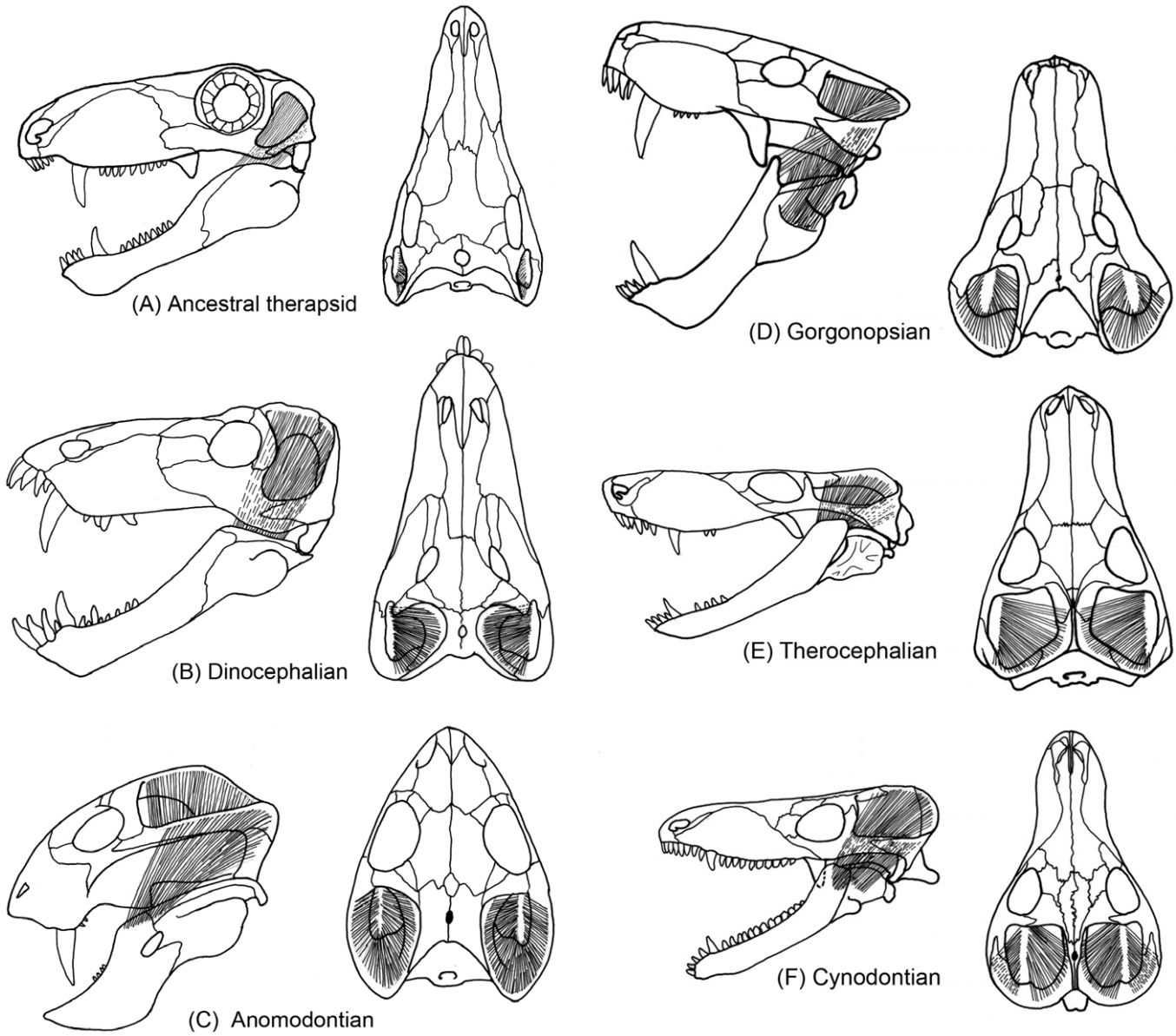


Figure 5. Reconstruction of the main adductor mandibuli musculature of the six major therapsid subtaxa. Outlines of skulls based on (**A**) *Biarmosuchus* (Ivakhnenko 1999); **B**, anteosaurid dinocephalian *Titanophoneus* (Orlov 1958); **C**, dicynodontian anomodontian *Eodicynodon* (Rubidge 1990); **D**, gorgonopsian *Arctognathus* (Kemp 1969a); **E**, therocephalian *Olivierosuchus* (Brink 1965); **F**, cynodontian *Procynosuchus* (Kemp 1979).

adductor musculature to a laterally-facing area of the edge of the intertemporal roof, but the presence already of the depression of the jaw articulation all indicate that functionally the anomodontian lineage could not have shared a common ancestry with either the dinocephalian or the therocephalian lineages, in which none of these features occur. Indeed, the reconstructed evolutionary trajectory from the ancestral anomodontian back to the hypothetical ancestral therapsid stage shows no sign of coalescence with that of any other taxon.

Gorgonopsia (Fig. 5D)

Kemp (1969) undertook a detailed analysis of the highly specialized jaw function system of gorgonopsians. The temporal fenestra was expanded posteriorly and laterally, but scarcely at all medially, and this is correlated with new areas of insertion on the lower jaw. There is a discrete coronoid process, which is obtusely triangular in cross-section, and part of the adductor musculature gained an insertion on the external face of the lower part. The lateral part of the adductor musculature expanded its area of origin onto the inside face of the broad, outwardly bowed zygomatic arch, and acquired a unique insertion onto a strong ridge occupying the reflected lamina of the angular. The part of the adductor musculature attached to the still narrow medial edge and the undersurface of the intertemporal roof corresponds to the ancestral temporalis musculature, and it still inserted on the medial side of the lower jaw.

This radical reorganization of the posterior and external parts of the adductor musculature is correlated with the ability of the lower jaw to open extremely widely, by more than 90°, and this was also reflected in a very specialized jaw articulation that permitted a wide gape while retaining a tight connection between the articular and quadrate (Parrington 1955). Finally, notwithstanding Laurin's (1998) claim that this was not the case, it is clear from well-preserved and fully prepared specimens that the

quadrate was moveably attached to the squamosal in such a way as to allow propalinal movement of the lower jaw (Kemp 1969a). The jaw could shift forwards to allow the upper and lower incisor teeth to interdigitate, and backwards to allow unencumbered energetic use of the huge opposing canines.

The various structures associated with gorgonopsian jaw action were integrated with one another within a functional system designed for highly active predation. Reconstruction of hypothetical evolutionary stages leading to the fully expressed gorgonopsian arrangement is constrained by the requirement that no one of the individual derived elements can be fully expressed in the absence of others, and in this case the correlations are especially apparent. Of particular relevance, the gorgonopsian coronoid process can only have evolved in correlation with a simultaneous posterior expansion of the temporal fenestra, since its function is to act as the insertion of that part of the adductor jaw musculature originating from the hind region of the fenestra (Kemp 1969a). This achieved an increased length of the musculature connecting them, which prevented undue restriction of the gape, and at the same time increased the torque applied to the lower jaw to increase the velocity of jaw-closing. A simultaneous expansion of the lateralmost part of the adductor mandibuli, was also necessary for generating a force adequate to operate the large canines.

Therocephalia (Fig. 5E)

The temporal fenestra was enlarged in a manner entirely unlike that of any of the previous groups. Medial expansion led to a narrowing of the intertemporal roof, but there is little development of the zygomatic arch. Kemp (1972b) interpreted the posteriormost root of the zygomatic arch as the area of origin of the homologue of the cynodontian and mammalian masseter muscle, although at this stage it did not extend anteriorly along the arch. The coronoid process is constructed differently from that of gorgonopsians, and is associated with medially and postero-medially directed musculature attached to the intertemporal region of the skull, rather than with posteriorly directed musculature as in gorgonopsians.

The jaw articulation (Kemp 1972b) is quite different from that of other groups, not allowing propaliny, but instead resisting a large postero-medially directed reaction from the temporalis and incipient masseter muscles.

The different arrangement of the adductor musculature between gorgonopsians and therocephalians implies independent modification from the hypothetical ancestral stage. The expansion of the temporal fenestra must have occurred independently in the two taxa because it is correlated with quite different parts of the adductor mandibuli muscle. Similar, the discrete coronoid process differs in form, and in the part of the musculature attached to it. The very different form of the jaw articulation reflects different reaction force regimes between the two. Therefore there is no sign of coalescence in the reconstructed morphological sequence between the hypothetical lineages leading to the therocephalians and the gorgonopsians, respectively.

Cynodontia (Fig. 5F)

Several authors have published reconstructions of the basal cynodontian jaw musculature (Barghusen 1968; Kemp 1979; Abdala & Damiani 2004). Most striking is the medial expansion of the temporal fenestrae creating a deep sagittal crest, and a simultaneous lateral expansion forming a bowed zygomatic arch. The latter was associated with a masseter muscle, which inserted into the lateral fossa of the broad coronoid process. According to Kemp (1979), in the basal cynodontian *Procynosuchus* this fossa was for the lateralmost part of the temporalis muscle and was only invaded by masseter muscle originating along the zygomatic arch in more derived forms. Abdala & Damiani (2004) differed in believing that the fossa was for the insertion of a true masseter muscle all along. However this does not greatly affect the reconstruction. The jaw articulation of the basal cynodontians is very similar to that of therocephalians, with the antero-laterally facing condyle of the quadrate designed to resist a postero-medially directed net reaction force applied by the articular. The epipterygoid of cynodontians is very broad, and together with the narrow intertemporal roof above and the basicranial axis below formed a box-girder, to strengthen the skull against the increased stresses arising from the enlarged adductor musculature (Kemp 1972a).

Thus the arrangement of the adductor musculature of the medial and posterior parts of the temporal fenestra of the basal cynodont *Procynosuchus* is very similar to that of therocephalians. The main difference between the two taxa lies in the absence of a muscle-bearing zygomatic arch and correlated invasion of the lateral surface of the mandible by adductor musculature in therocephalians. However, the coronoid process of both taxa is associated with a comparable medial expansion of the temporal fenestra. Therefore a functionally integrated common stage for the two lineages can be reconstructed, which is essentially therocephalian in nature. The recent description of an early and even more basal cynodontian *Charassognathus* (Botha *et al.* 2007) supports the hypothesis that the cynodontian and therocephalian lineages coalesce. Unlike *Procynosuchus,* it lacks an adductor fossa on the lateral surface of the coronoid process, but it does have a notch in the lower edge of the process that apparently represents an incipient invasion of the outer surface of the dentary from what would have been an essentially therocephalian-like arrangement of the musculature. The structure of the jaw articulation is very similar in therocephalians and *Procynosuchus,* and is correlated with the greater development of the medial and posterior parts of the adductor mandibuli. Even the expansion of the epipterygoid, to a modest degree in most therocephalians but more extensively in cynodonts and the therocephalian family Whaitsiidae, corroborates the essential similarity between the two of the integrated feeding system. Functional considerations therefore support a relationship between these two major therapsid subgroups.

Conclusion

Functional analysis of the skull and inferred mandibular musculature reveals that the integrated feeding system in

four of the five major derived therapsid subtaxa differed radically from one another. Each one evolved its own unique combination of characters from an hypothetical ancestral therapsid stage, approximately represented by the highly plesiomorphic *Biarmosuchus*. Furthermore, on reconstructing functionally integrated back-trajectories for the four, no two of them appear to have shared a common stage – to have coalesced – at any point subsequent to the common ancestor. This evidence corroborates the hypothesis that, at least at the level of morphological resolution available, there was a fourfold polytomy at the base of the therapsids, consisting of the dinocephalian, gorgonopsian, anomodontian and therocephalian lineages respectively.

By contrast, the Cynodontia possessed an integrated system that had several features also occurring in similar combination in the Therocephalia, and in this case evolutionary back-trajectories of the functional morphology of these two lineages appear to have coalesced at a common point subsequent to the biarmosuchian-grade ancestral stage. This supports the hypothesis that Therocephalia and Cynodontia are sister groups, constituting a monophyletic taxon Eutheriodonta.

These observations indicate that certain of the characters used in formal cladistic analyses to define various interrelationships cannot be regarded as homologous. A notable example is the presence of a coronoid process of the dentary used to support a monophyletetic Theriodontia, consisting of Gorgonopsia, Therocephalia and Cynodontia. It was concluded on functional grounds that this stucture must be convergent in the gorgonopsians and therocephalians because it is associated with different parts of the adductor musculature in the two. Another example is the character used to support a relationship between Anomodontia and Eutheriodontia (Fig. 2C), the increased postorbital length of the skull. Again this can hardly be regarded as a homologous character because it is associated with quite different ways of enlarging the temporal fenestra, and with different associated patterns of reorganization of the musculature, a conclusion confirmed by the discovery of the basal anomodontian *Patranomodon*.

CONCLUSIONS

The question posed in this essay is whether the weak support for, and extensive lack of agreement on a well-resolved phylogenetic tree of the major therapsid subtaxa is because of the failure yet to discover adequately known discriminating characters, or because there was a true polytomy in which several therapsid lineages diverged virtually simultaneously from a low-level ancestral therapsid taxon. The standard test for proposed phylogenetic relationships is formal cladistic analysis, but methodologically this is designed only to discover the best supported, fully dichotomous tree, however weak that support may be. Logically cladistics cannot be used positively to corroborate a hypothesis of therapsid polytomy. Four valid non-cladistic, non-tautological tests of polytomy are however available in principle, and when applied to the therapsid radiation three of them offer positive support for a fourfold polytomy from a biarmosuchian-like common ancestral taxon. The remaining one, the palaeobiogeographic test, is consistent with polytomy.

Of the three positive tests, it would be disingenuous to place too much weight on the stratigraphic relationships, but nevertheless this evidence offers very clear positive support for a fourfold polytomy. Only the Cynodontia appear in the fossil record significantly later and therefore, on this evidence, this taxon is a candidate for sharing a common ancestor with one of the other lineages.

The palaeoenvironmental evidence for polytomy is impressive, with the appearance in the fossil record of all the major lineages except Cynodontia coinciding with the appearance of a potential dispersal route to higher latitudes, north and south, areas of the globe that would suit well a group of tetrapods adapted to remain active throughout fluctuating seasonal conditions.

The most important test of polytomy is the functional correlation analysis of the morphology. In so far as this method of analysing morphology owes it origin to a much more realistic model of character evolution than that underpinning cladistics, it is potentially a more effective method for discovering true phylogenetic patterns including, critically, the power to detect polytomy. In the case of the therapsids, the correlated progression analysis unambiguously supports the hypothesis that four major lineages diverged independently from a biarmosuchian-grade ancestor. These are Dinocephalia, Gorgonopsia, Anomodontia and Therocephalia. Only one major subtaxon, Cynodontia, is inferred to have shared a common ancestor with another. Cynodontia and Therocephalia constitute the monophyletic taxon Eutheriodontia. All other proposed clades are rejected.

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