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The origin and early radiation of the therapsid mammal-like reptiles: a palaeobiological hypothesis

T. S. KEMP

University Museum of Natural History, and St John's College, Oxford, UK

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Abstract

The replacement of the basal synapsid pelycosaurs by the more 'mammal-like' therapsids in the Permian was an important event in the history of tetrapods because it initiated the eventual transition to the mammals. It is also an example of taxon replacement in the fossil record that is unusually amenable to explanation, based on a combination of analysis of the biological significance of the inferred character changes, with the stratigraphic, palaeogeographic and palaeoecological circumstances of the time. An hypothesis is presented in which the origin of the therapsids resulted from a correlated progression of character evolution leading to higher levels of metabolic activity and homeostatic regulation of the body. It was a response to the availability of a seasonally arid, savanna-like biome. The subsequent explosive radiation of therapsids was associated with habitat expansion made possible by the Mid-Permian development of geographical continuity between that biome and the temperate biomes. The final extinction of the pelycosaurs was a case of incumbent replacement by the new therapsid lineages.

Introduction

A common observation of long-term evolutionary patterns witnessed in the fossil record is the replacement of a radiation of one taxonomic group by another of broadly comparable ecological role. Referred to variously as 'ecological replacement', 'clade replacement', 'taxon replacement', or 'competitive replacement', there are numerous examples at various taxonomic levels, some associated with mass extinction events, others not. Explanations offered vary from the extremes of interspecific competition, on the one hand, to ecological opportunism, on the other, but finding appropriate information to test hypotheses about specific cases is difficult (e.g. Benton, 1996). All too often in the past, little more than what amounts to *a priori* extrapolation of well-known ecological time-scale processes to geological time-scale events has passed as causal explanation. The replacement in the middle of the Permian of the basal synapsid pelycosaurs by the more derived, more mammal-like therapsids is an example that is more amenable to palaeobiological analysis than most.

The amniote clade Synapsida consists of the stem and crown group mammals; fossils of several grades are known that together span the morphological distance from the common ancestral amniote to the Mammalia (e.g. Kemp, 2005). For virtually the entire history of their study, synapsids have been divided into the basal group Pelycosauria and the derived group Therapsida. Therapsida is actually nested cladistically within the Pelycosauria, and in turn Mammalia is nested within Therapsida, so that both these mammal-like reptile taxa are technically paraphyletic. However, the situation is sufficiently well known and straightforward that no misunderstanding is likely to arise from using the terms Pelycosauria and Therapsida, rather than the synonymous but awkward expressions 'non-therapsid Pelycosauria' and 'nonmammalian Therapsida'. As discussed later in context, there is also good justification for regarding them as valid evolutionary, even though not cladistic entities.

A good deal of attention has been paid to the biological transition from the therapsid-grade as represented by progressive cynodonts to the mammal-grade. In contrast, the transition from the pelycosaur-grade to

Correspondence: Dr Tom Kemp, Oxford University Museum of Natural History, Parks Road, Oxford OX1 3PW, UK.
Tel.: 44 186 272964; fax: 44 186 272970;
e-mail: tom.kemp@oum.ox.ac.uk

the therapsid-grade has been relatively little discussed, yet this earlier event was of critical biological significance to the history of terrestrial life, involving as it did extensive reorganization of a low-energy, weak-jawed, sprawling-limbed, fully ectothermic, basal amniote into a radically new kind of organism. It was the ancestral therapsid that had crossed the biological threshold on the road that led ultimately to the metabolically more active, versatile and potentially much more adaptable kind of terrestrial organisms represented by the mammals. (A comparable transition occurred within the Archosauria, leading to the birds, but curiously this was far in the future.) The transition seems to have depended on a unique and fortuitous combination of mid-Permian biological and environmental circumstances.

The pioneering work of establishing the timing and palaeogeography of the transition between the pelycosaur radiation, known primarily from the Upper Carboniferous and Lower Permian of North America, and the oldest therapsids from the Middle Permian of Russia was conducted by Olson (1962, 1974, 1986). Since that time the picture has profoundly changed in several respects. First, fragmentary specimens that Olson believed to be Mid-Permian therapsids co-occurring with the youngest pelycosaurs of North America have been reinterpreted as at best indeterminate (Parrish *et al.*, 1986; King, 1988), and almost certainly pelycosaurs (Sidor & Hopson, 1995; Reisz & Laurin, 2004), and in any case they are probably Early Permian in age (Lucas, 2004). Meanwhile, new finds of early therapsids have been made in South Africa (Rubidge, 1995) and China (Li *et al.*, 1996). Secondly, there is a greater knowledge of the morphology, inferred biology, and relationships of the earliest therapsids and their implication for the nature of the hypothetical ancestral form (Ivakhnenko, 2002, 2003a; Kemp, 2005). Thirdly, the stratigraphy, and its correlation between the relevant regions are more or less agreed upon (Golubev, 2000; Izart *et al.*, 2003; Lucas, 2004). Finally, there is a far more detailed understanding of the palaeoclimatic and palaeoecological conditions during the Permian (Parrish *et al.*, 1986; Gibbs *et al.*, 2002; Rees *et al.*, 2002).

Three palaeobiological aspects of the origin of therapsids are first considered separately:

- the morphological transition and inferred adaptive significance of the evolution of the hypothetical ancestral therapsid from a pelycosaur-grade ancestor;
- the timing and palaeogeography of the decline of the pelycosaurs and the origin and early divergence of the therapsids;
- the environmental conditions of the Early and Mid-Permian.

A macroevolutionary hypothesis is then synthesized, which incorporates all three aspects in an attempt to explain how and why therapsids arose and replaced the pelycosaurs.

Systematics of the Therapsida

The monophyly of the Therapsida, and its sister group

Most contemporary commentators accept the monophyly of the taxon Therapsida, defined as the last common ancestor of biarmosuchians and mammals, plus all its descendants (Fig. 1). Olson (1962) had at one time proposed that the herbivorous therapsid group Anomodontia was independently derived from caseid pelycosaurs, although by 1971 he had revised his opinion (Olson, 1971, figure 161). The only recent author to consider Therapsida, as usually construed, not to be monophyletic is Ivakhnenko (2002, 2003a). On the basis of the structure of the temporal region of the skull, he recognized a monophyletic group 'Eotherapsida', consisting of sphenacodontid pelycosaurs plus the therapsid groups of other authors, except for the Therocephalia and Cynodontia. He grouped these latter two as the 'Eutherapsida', with the implication that they had a separate origin from pelycosaurs more basal than sphenacodontids.

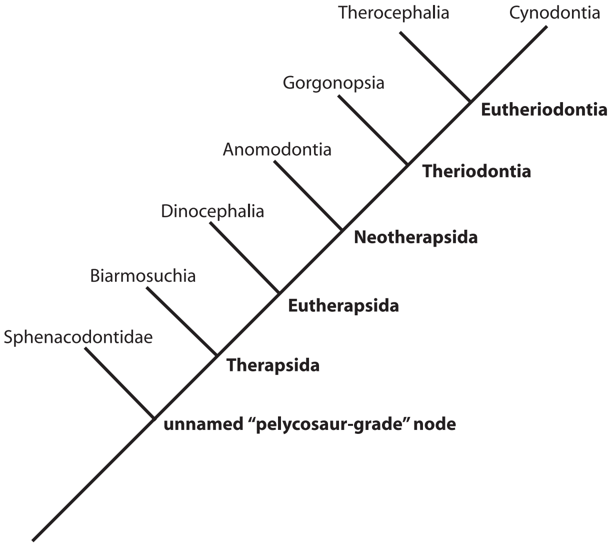

Fig. 1 Rubidge & Sidor's (2001) cladogram of the major therapsid taxa. Characters defining principle nodes. (For the unnamed 'pelycosaur-therapsid' and Therapsida nodes see Table 1.) Eutherapsida: (i) zygomatic arch bowed laterally; (ii) ulna lacks distinct ossified olecranon process; (iii) fifth pedal digit has only three phalanges. Neotherapsida: (i) ventrally expanded squamosal; (ii) epipterygoid broadly contacts underside of the parietal; (iii) epiphyses on atlas vertebra; (iv) enlarged obturator fenestra of pelvis. Theriodontia: (i) dorsal profile of snout nearly straight; (ii) greater flaring of zygomatic arch; (iii) dentary with coronoid process; (iv) dentary with masseteric fossa; (v) post-dentary bones somewhat reduced in height; (vi) humeral head slightly dorsal; (vii) deltopectoral crest more than 40% humeral length; (viii) greater trochanter of femur still small but extends distal to head.

Table 1 The defining characters of (a) Therapsida, (b) the unnamed Sphenacodontidae–Therapsida clade, and (c) Sphenacodontidae (from Sidor & Hopson, 1998 except where otherwise cited).

(a) Characters of Therapsida
- *Cranial*
  - Premaxilla internarial process long (cf. short)
  - Premaxilla alveolar margin slightly upturned (cf. downturned)
  - Septomaxilla facial process present (cf. absent)
  - Maxilla contact with prefrontal present (cf. absent)
  - Temporal fenestra enlarged (cf. smaller) (Ivakhnenko, 2002)
  - Periotic with ridges for muscle attachments (cf. smooth) (Ivakhnenko, 2002)
  - Temporal fenestra muscle attachment on border of lateral temporal fenestra (cf. no muscle attachment there)
  - Parietal foramen raised on tall 'chimney' (cf. flush with roof)
  - Supratemporal absent (cf. present)
  - Vomer internarial shape widest near middle (cf. slightly widest posteriorly)
  - Vomer ventral surface with lateral ridges and median trough (cf. flat)
  - Choanae elongated posteriorly (cf. no extension). (Sidor, 2003)
  - Post-choanal trough deep to palatal surface (cf. mid-palatal surface flat) (Sidor, 2003)
  - Crista choanalis present (cf. absent) (Sidor, 2003)
  - Bosses or ridges on palate present (cf. absent)
  - Teeth on ectopterygoid absent (cf. present)
  - Degree of anterior rotation of occiput moderate (cf. none)
  - Squamosal external auditory meatus groove shallow (cf. absent)
  - Quadrate reduced in height (cf. quadrate almost as high as temporal fenestra)
  - Quadrate contacts paroccipital process and squamosal about equally (cf. primarily paroccipital process)
  - Paroccipital process orientation moderately postero-ventral and lateral (cf. strongly postero-ventral and lateral)
  - Basicranial joint fused (cf. unfused)
  - Stapes reduced in mass, with large stapedial foramen (cf. massive with small foramen) (Sigogneau & Chudinov, 1972; Maier & Heever, 2002)
  - Stapedial dorsal process distal (cf. proximal)
  - Anterior coronoid absent (cf. present)
  - Splenial position confined medially (cf. exposed medially and laterally)
  - Size of angular reflected lamina posterior emargination long (cf. short)
  - Reflected lamina pattern of radiating ridges and grooves present (cf. absent)
  - Articular glenoid not screw-shaped (cf. screw-shaped)
- *Dental*
  - Enlarged dentary tooth present in caniniform position (cf. present at anteriormost position)
  - Incisors similar sized (cf. some enlarged)
  - Precanine maxillary teeth absent (cf. present)
  - Number of post-canines fewer than 12 (cf. 12 or more)
- *Post-cranial*
  - Vertebral type platycoelous (cf. amphicoelous)
  - Glenoid shape more rounded and facing postero-laterally (cf. anteroposteriorly elongate and screw-shaped)
  - Scapula blade shape constricted (cf. broad above glenoid)
  - Clavicle width at medial end relative to total length less than one-third (cf. greater than one-half)
  - Humerus spinator process absent (cf. present)
  - Humeral head shape elongate oval (cf. broad and strap-like)
  - Manual intermedium size relative to lateral centrale smaller (cf. larger)
  - Distal carpal 5 present but fused with carpal 4 (cf. present)
  - Manual digit III shape of second phalanx short and disc-like (cf. long)
  - Manual digit IV shape of second and third phalanges short (cf. long)
  - Acetabulum shape circular (cf. irregular oval)
  - Acetabulum depth deep (cf. shallow)
  - Intertrochanteric fossa of femur absent (cf. prominent)
  - Femoral head shape inflected medially (cf. terminal)
  - Femoral head articular shape oval (cf. elongate and irregular)
  - Posterior distal condyle of femur relative to anterior distal condyle extends slightly further distally or level (cf. extends much further distally)
  - Greater trochanter present (cf. absent) (Kemp, 2005)
  - Intertarsal joint between astragalus and calcaneum highly mobile (cf. no specific joint) (Kemp, 2005)
  - Foot plantigrade (cf. digitigrade) (Kemp, 2005)
  - Pedal digit III shape of second phalanx short and disc-like (cf. long)
  - Pedal digit IV shape of second and third phalanges short (cf. long)
  - Pedal digit V shape of second phalanx short (cf. long)

(b) Characters of the unnamed Sphenacodontidae–Therapsida clade
- Maxilla contact with nasal present (cf. absent)
- Maxillary tooth row ends anterior to orbit (cf. under orbit)
- Teeth on vomer absent (cf. present)
- Position of transverse flange of pterygoid beneath or anterior to orbit (cf. posterior to orbit). Also in *Haptodus*
- Dentary anterior occlusal margin strongly offset above rest of dentary (cf. horizontal or slightly inclined)
- Angular reflected lamina posterior emargination present (cf. absent)
- Incisor serrations present (cf. absent)
- Canine serrations present (cf. absent)
- Sacral rib number three (cf. two). Also in *Haptodus*
- Femur proximo-distal curvature present (cf. absent)

(c) Characters of Sphenacodontidae
- Incisors variable in size
- Second dentary tooth enlarged
- Weak development of the adductor ridge of the femur

However, Ivakhnenko's classification is based on only a few selected characters. The total number of synapomorphies supporting therapsid monophyly is very considerably larger (Table 1). Hopson & Barghusen (1986) listed 11 characters, all cranial. In an unpublished manuscript, Rowe (1986) listed 41, of which 20 are post-cranial. Sidor & Hopson (1998) increased this to as many as 48 cranial, dental and post-cranial characters defining the therapsid node on their most parsimonious tree. A number of other characters have since been shown to be at least highly probable therapsid synapomorphies, including several of the palate (Sidor, 2003), the middle ear (Maier & Heever, 2002), the temporal fenestra (Ivakhnenko, 2002), and the post-cranial skeleton (reviewed by Kemp, 2005).

The sister group of the Therapsida is also agreed almost universally to be the sphenacodontid pelycosaurs (excluding the genus *Haptodus*, which shares only two characters with Sphenacodontidae *sensu stricto* plus Therapsida, and is therefore taken to be the basal sister group of the latter two). Reisz (1986) found four cranial characters, and Sidor & Hopson (1998) increased this to eight unambiguous synapomorphies of the skull, dentition and post-cranial skeleton of therapsids and sphenacodontids (Table 1). Referring again to Ivakhnenko's (2002) comparison, the temporal region of the skull provides additional support for the relationship. However, it should be noted that compared with the considerable number of synapomorphies of the Therapsida, the character support for the relationship of the latter to the Sphenacodontidae is much less strong. The implication is that, as discussed later, the origin of the hypothetical ancestral therapsid from a sphenacodontid-grade pelycosaur was indeed a major evolutionary transition affecting many parts and functions of the organisms.

The only possible disturbance to this clear distinction between sphenacodontids and therapsids concerns a single, poorly preserved specimen of *Tetraceratops*. Attributed to the Pelycosauria, possibly the basal group Eothyrididae, by Romer & Price (1940), and to the Pelycosauria *incertae sedis* by Reisz (1986), it occurs much earlier than any therapsid, in the Lower Permian Leonardian Stage of Texas. Laurin & Reisz (1996) re-described it and claimed that it possesses a number of characters, eight in all, that are otherwise unique to the therapsids. Their conclusion is that *Tetraceratops* is a basal member of the Therapsida, and illustrates a transitional grade between the sphenacodontids and the remainder of the therapsids. If so, then this is a most important form for understanding the evolution of the therapsids. Unfortunately, *Tetraceratops* is still represented to date by the one incomplete and badly crushed skull and jaws. Furthermore, Conrad & Sidor (2001) briefly reported that the therapsid characters claimed are not entirely unambiguous; they suggested that it is actually a basal sphenacodontid pelycosaur.

Inter-relationships of the therapsid subtaxa

The cladistic inter-relationships of the therapsid lineages are contentious. Sidor & Hopson (1998) have published the most comprehensive cladistic analysis to date, and in their more recent review Rubidge & Sidor (2001) accepted its major dichotomies as the best-supported hypotheses of higher level relationships. However, inspection of the synapomorphies associated with several of the proposed nodes causes considerable misgivings about how accurately the cladogram represents the real phylogeny (Fig. 1). A good deal of caution, if not outright scepticism, is appropriate towards relationships supported by so few, often minor or vaguely defined characters. Indeed, as noted by Rubidge & Sidor (2001), several other authors have expressed various different arrangements, based on scarcely less evidence. King (1988) regarded the Dinocephalia and Anomodontia as sister groups; Kemp (1988) was reluctant to accept that Gorgonopsia were part of a monophyletic Theriodontia; Gauthier *et al.* (1988) went further and placed the Anomodontia with the Theriodontia, again to the exclusion of Gorgonopsia; Modesto *et al.* (1999) suggested that Anomodontia and Therocephalia formed a clade. The classification of Ivakhnenko (2002, 2003a) relates the Gorgonopsia, Dinocephalia and Anomodontia, to the exclusion of the Therocephalia and Cynodontia.

In addition to the problem of these well-known groups of therapsids, there are several early and short-lived taxa in the Russian Middle Permian fauna whose precise relationships are as yet obscure. Niaftasuchids and nikkasaurids are two groups of small, presumed herbivores, and there are a number of poorly known specimens of carnivores (Ivakhnenko, 2003a).

An analogy with current understanding of the inter-relationships of the orders of placental mammals suggests itself. The accumulation over the last half decade of molecular sequence data, and the development of statistical methods for analysing it, have led to the rejection of several supraordinal groups based on earlier morphological studies, while at the same time resolving the hitherto unresolved polychotomies (e.g Springer *et al.*, 2003; see Kemp, 2005 for a review). The extent of this new evidence is sufficient now to lead to the virtually unassailable conclusion that morphology, even of such an intensively studied group as modern mammals, is inadequate for revealing cladistic relationships at the ordinal level. The shared derived morphological characters that might be expected to have resolved these relationships must have been too minor, or in some cases perhaps too subject to convergence, to have remained discernable in the known living or fossil representatives. The pattern of divergence of the major therapsid lineages, where the morphological support for relationships amongst its constituent groups is similarly so sparse, appears to have been comparable with that of placentals, reducing yet further the confidence with which even the technically best supported cladogram of the group can be accepted as an accurate representation of the true phylogeny. At the poor morphological resolution available, and in the absence of molecular sequence data, the early radiation of therapsids is virtually indistinguishable from a polychotomous 'star' phylogeny. The most likely explanation for this is that the therapsids radiated rapidly and more or less simultaneously into the several constituent groups, as discussed later.

The nature and origin of the ancestral therapsid

The characters that define the Therapsida (Table 1) are taken to be the characters that evolved during the transition from the hypothetical common ancestor of sphenacodontids and therapsids to the hypothetical ancestral therapsid. As so interpreted, they permit a morphological reconstruction (Fig. 2) and interpretation

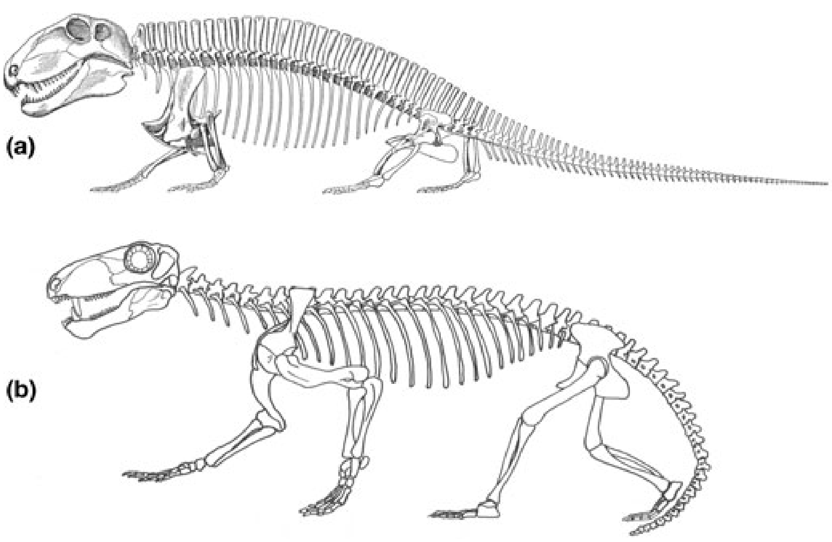

Fig. 2 Skeletal reconstructions of (a) *Sphenacodon* (from Romer & Price, 1940), (b) hypothetical ancestral therapsid (skull modified from *Biarmosuchus*, after Ivakhnenko (-1999); post-cranial skeleton modified after Colbert's (1948) reconstruction of the gorgonopsian *Lycaenops*.

of the biology of the latter. The characters are found to relate to a variety of separate functions of the organism, as briefly described here.

Feeding

The dentition was that of a specialist carnivore, and consisted of a set of even-sized upper and lower incisors that interdigitated to create a more effective carnivorous bite, followed by single enlarged canines in upper and lower jaws that also interacted with one another. The post-canine teeth were more modest in size, and had a mainly food-holding function.

In order to generate the increased bite forces required by the new arrangement of the dentition, the temporal fenestra was elongated in the posterodorsal direction (Barghusen, 1973). Its medial wall, consisting of the quadrate, was reduced in height, exposing a broad area of the squamosal and braincase for attachment of additional adductor musculature, and its dorsal boundary, consisting of the postorbital bone, had become a lateral-facing area for muscle origin (Ivakhnenko, 2002). Thus the mass of the adductor jaw musculature had greatly increased, and its main component, the temporalis, acted at a greater perpendicular distance from the jaw articulation, together increasing the torque available to the lower jaw. The lower jaw accommodated this increased musculature, and the greatly enlarged reflected lamina of the angular probably received the insertion of enlarged and reorganized pterygoideus and other ventral musculature responsible for food manipulation and active jaw opening (Kemp, 2005). The jaw articulation was simplified, consisting of a roller hinge joint allowing only orthal movements of the jaw while offering resistance to disarticulation of the jaw by struggling prey.

Several anatomical features of the skull were designed to strengthen the structure against the increased feeding forces, although little of this has been studied in detail. The elongated internarial processes of the premaxillae, and the enlarged maxillae are associated with the massive upper canines. Changes in the structure of the palate reflect mechanical strengthening, with the development of lateral and medial ridges on the ventral surface of the vomer, and the appearance of a post-choanal trough presumably stiffening the ventral parts of the skull. In the posterior region of the skull, the more transverse orientation of the paroccipital processes, loss of the supratemporal, and fusion of the basipterygoid articulation clearly relate to strengthening the load-bearing capacity of the parts of the skull on which the muscles most directly acted.

Ventilation

The development of an elongated choana, continuous behind with a post-choanal trough deep to the palatal surface indicates that there was a dedicated air passage in the roof of the oral cavity, while the presence of lateral ridges on the trough in several groups of therapsids suggests that a soft secondary palate may already have evolved in the ancestral therapsid (Sidor, 2003).

It has also been argued by Carrier (1987) that the modification to the stance and gait of therapsids had the function of increasing ventilation volume, by removing the constraint imposed by the lateral undulatory component of the primitive stride. Also, by raising the thorax off the ground a mammalian type of diaphragm could have functioned, although there is no direct osteological evidenced for the latter in the basal therapsids (Bennett & Ruben, 1986).

Locomotion

The post-cranial skeleton of the pelycosaurs was very considerably modified, in structure and inferred function, during the course of evolution of the hypothetical ancestral therapsid. The head was capable of increased dorso-ventral mobility on the atlas vertebrae, the atlas-axis joint permitted rotation about the longitudinal axis, and the neck as a whole was more flexible (Kemp, 1969b). In the appendicular skeleton, the shoulder girdle was far less massively built, and capable of extensive movement relative to the vertebral column, thereby contributing an additional component to stride length. The forelimb was longer and more gracile, and capable of a wider range of movements compared with the highly restricted protraction–retraction cycle imposed by the spiral form of the pelycosaur shoulder joint (Jenkins, 1971). The hind limb was also more gracile and no longer dependent on a massive, ventrally situated caudi femoralis muscle for retraction. Instead, much of its musculature was high up on the pelvis, reducing the overall moment of inertia of the limb. This shift in the musculature, the sigmoid shape and proximo-medial twist of the femur, and the structure of the ankle joint in therapsids, including the biarmosuchians (Sigogneau & Chudinov, 1972) indicates that facultatively alternative gaits, sprawling and parasagittal, existed (Kemp, 1978; Blob, 2001). Basal therapsid locomotory performance was faster, more versatile, and presumably more energetic than its pelycosaurian predecessor.

Hearing

The function of sound reception in basal therapsids is not well understood. Some authors have argued that the space enclosed by the enlarged reflected lamina of the angular of the lower jaw contained an air-filled diverticulum of the middle ear. This acted as a resonance chamber, in association with sound conduction via the jaw hinge and stapes, in principle as in mammals (Allin, 1975; Allin & Hopson, 1992; Ivakhnenko, 2003b). Others have attributed the early evolution of the angular region of the basal therapsid jaw solely to elaboration of the jaw musculature, and that its association with hearing did not evolve until more progressive therapsids (Barghusen, 1973; Kemp, 1982). However, in view of the reduction of the mass of the stapes, as well as the subsequent evolution of this region in synapsids, it is probable that sound reception involving lower jaw elements was indeed enhanced in the hypothetical ancestral therapsid (Allin & Hopson, 1992), although a detailed mechanical analysis is yet to be undertaken of quite how, and how effectively such an arrangement might function (Carroll, 1986).

Nasal cavity contents

Ridges on the posterior part of the internal surface of the snout in the sphenacodontid *Dimetrodon* (Romer & Price, 1940) are usually assumed to be the sites of attachment of cartilaginous nasoturbinals, increasing the area of olfactory epithelium. They are further elaborated in therapsids, and in the more progressive groups there are additional, more anteriorly placed ridges as well, which Hillenius (1992, 1994) suggested may in some cases have carried mucous membrane for warming and humidifying inspired air, a requirement of endothermic tetrapods. However, while possible, there is no direct evidence for such maxillo-turbinals in the hypothetical ancestral therapsid.

Brain size

There is no unambiguous osteological evidence that the hypothetical ancestral therapsid had an enlarged brain compared with pelycosaurs, because the brain of non-mammalian synapsids is not completely enclosed in bone. An estimate of length and longitudinal differentiation is possible, but neither the height, nor the maximum width can be measured. Hopson (1979, 1980) and Quiroga (1979) both estimated the volume of more advanced, cynodont therapsids as at the upper end of the range of modern reptiles. The only attempt at a complete brain reconstruction of a more basal therapsid available is that of Kemp (1969a) for a gorgonopsian, which also suggests a brain that was above the average size for ectothermic amniotes generally. The possibility that the hypothetical ancestral therapsid had undergone a significant increase in relative brain size from that of a pelycosaur certainly exists.

Bone histology

The relationship between bone histology and various aspects of the biology of vertebrates has long been discussed (e.g. Ricqlès, 1976; Chinsamy, 1997). The cortical bone of pelycosaurs is generally poorly vascularized lamella-zonal bone, similar to that of most primitive tetrapod groups. In marked contrast, cortical bone of therapsids, including the basal form *Biarmosuchus*, contains a high level of well-vascularized fibrolamellar bone, with extensive Haversian replacement (Ricqlès, 1976). This is altogether more characteristic of mammals, although the exact biological significance of the shift is not clear (Bennett & Ruben, 1986). There is no unambiguous relationship between this kind of bone histology and temperature physiology in modern tetrapods, and the most direct functional link seems to be with rate and pattern of growth. Ray *et al.* (2004) interpreted the histology of several therapsids in terms of rapid osteogenesis, although noting varying degrees of secondary remodelling and cyclical growth in different taxa. At any event, whatever the exact physiological significance, therapsid bone histology is far more comparable to that of mammals, particularly larger bodied forms, than to that of pelycosaurs.

Body size

The body size of the hypothetical ancestral therapsid is difficult to estimate confidently. The estimates of skull length, total length and body weight of pelycosaurs given by Romer & Price (1940, their table 5) show that the basal sphenacodontid-therapsid *Haptodus longicaudus*, has a skull length of about 70 mm, total body length of 588 mm and estimated weight of 3 kg. However it is extremely small for the group, and the poor level of ossification indicates that the specimens are very immature. Amongst the strictly sphenacodontid genera, *Sphenacodon* specimens have a skull length range of 297–403 mm, body length of 1785–2231 mm and estimated weight of 52–83 kg. Most *Dimetrodon* specimens are even larger, with *Dimetrodon grandis* reaching a skull length of 482 mm, body length of 3195 mm and estimated weight of 254 kg.

As for the therapsids, a growth series of specimens of the basal form, *Biarmosuchus tener* range in skull length from 165 to 345 mm (Ivakhnenko, 1999). Assuming a similar ratio of skull length to body weight as in pelycosaurs, this would correspond to a maximum weight of around 70 kg. Early anteosaurid dinocephalians are within the same size category, whilst the estemmenosuchids are larger, with skull lengths over 500 mm. Conversely, niaftasuchids, nikkasaurids, and the basal anomodontians are a good deal smaller than *B. tener*.

From these figures, the most parsimonious estimate of the size of the ancestral therapsid is between 50 and 100 kg, making it medium to large for a terrestrial tetrapod.

The biological nature of the hypothetical ancestral therapsid

It has always been recognized that therapsids are in a general way more 'advanced', or 'progressive' in their biology than their pelycosaurian forebears, as for example in the reviews of Olson (1969, 1986), Kemp (1982), and Bennett & Ruben (1986). Most of the discussion has centred on the extent to which endothermic temperature physiology had evolved, but there has been little agreement on what was the primary function of endothermy, how it evolved, and to what extent it had been achieved in therapsids.

Kemp (in press) has reviewed the adaptive significance of endothermy and its origin in synapsids. Contrary to other authors, he argued that no single function can be considered primary, but that the several functions of endothermic temperature physiology manifested in modern endotherms evolved in correlation with one another, by a series of small, incremental shifts in all of them, hand in hand as it were, by the process referred to as correlated progression. The functions include thermoregulation, which allows both an expansion of the temporal and geographical range of activity, and a more complex internal organization of the body, particularly though by no means exclusively the central nervous system. The functions also include behaviour associated with an increased maximum aerobic activity level, and an enhanced level of juvenile provision and hence growth rate. The evidence for the correlated progression model consists in part of a consideration of the integrated nature of organisms in general, and in part of the observed pattern of acquisition of mammalian characters seen in the fossil record. At every grade represented by fossils, there has been an incremental shift towards the mammalian state in characters associated with several different functions, but never a large shift in any one of them alone.

Applying the correlated progression model specifically to the origin of the therapsids, the transition from the common ancestor of sphenacodontids and therapsids to the hypothetical ancestral therapsid appears to have been the most significant step in the whole sequence from basal amniote to mammal, because it was the first substantial shift away from the basic physiology of all previous, and most subsequent amniotes. The inferred attributes of the hypothetical ancestral therapsid briefly described above indicate that it had evolved a higher rate of food assimilation and of ventilatory capacity, a more agile, faster, more energetic mode of locomotion, more elaborate and therefore more sensitive olfaction and hearing, and an increased growth rate. While little more can be said from direct palaeontological evidence, it follows inevitably from the correlated progression model that many other characters must have also undergone an incipient change towards the mammalian state. Higher aerobic activity levels, double circulation of the blood system, more precise chemoregulation, more elaborate brain function, maternal provision, and so on must all be expected to have evolved.

As so interpreted, the hypothetical ancestral therapsid differed from the sphenacodontid-therapsid common ancestor in all the necessary attributes for a higher rate of resource utilization associated with a higher aerobic metabolic rate. This in turn related to a higher level of internal homeostasis, manifested by greater independence of environmental fluctuation of ambient temperature and humidity.

The tempo of the origin and early diversification of the therapsids

The hypothetical ancestral therapsid has been reconstructed as an actively hunting predator, of medium body size, which also proved to have had the potential to give rise to a range of different kinds of carnivores and herbivores. The earliest appearance of possible therapsids in the fossil record is the Russian early Kazanian (Fig. 3), dated approximately 267 Ma (Lucas, 2004). Unfortunately they are very poorly preserved and fragmentary (Efremov, 1954; Chudinov, 1983), leaving their true identification in doubt. However, by the later Kazanian-early Tatarian of Russia, about 265 Ma, at least seven therapsid lineages are known to have existed (Ivakhnenko, 2003a). Carnivores are represented by biarmosuchians, basal gorgonopsians, and anteosaurid (brithopodid) dinocephalians. There were also the large,

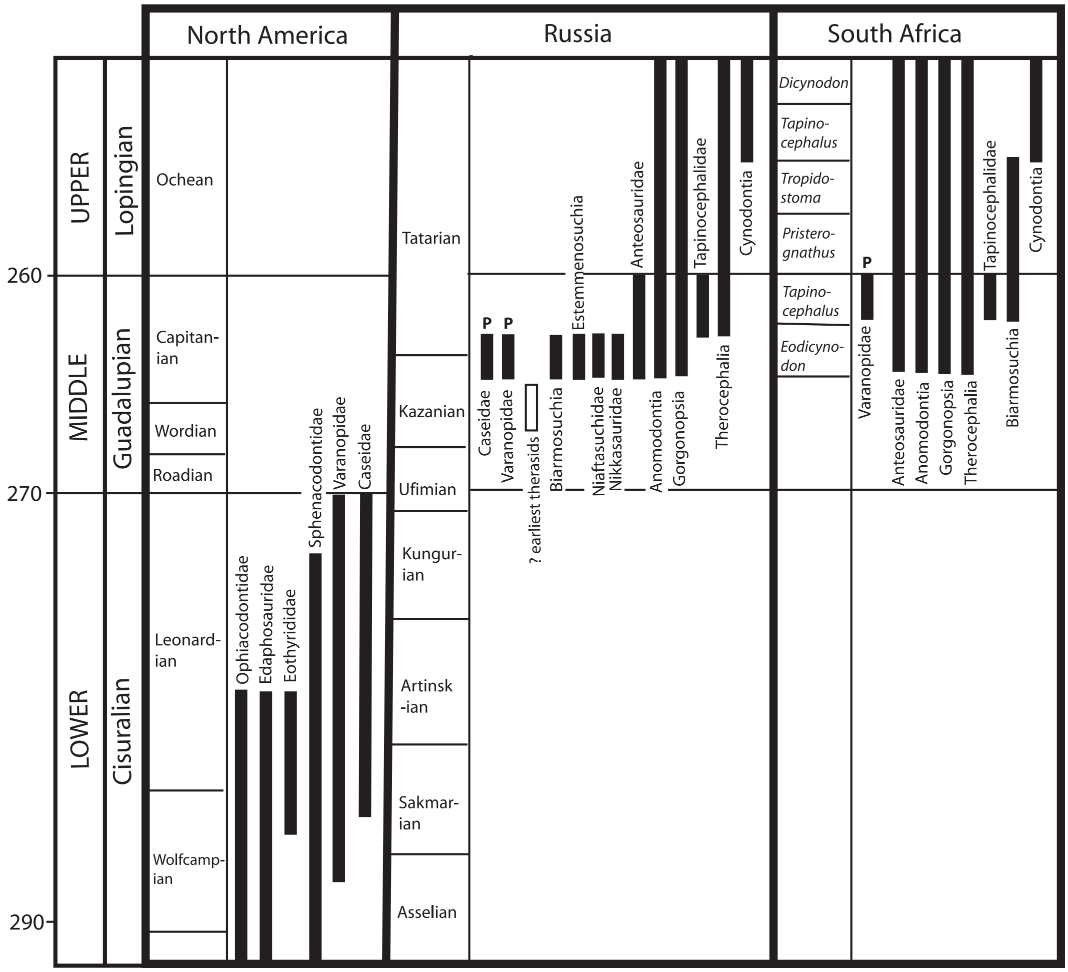

Fig. 3 Dates and geographical occurrences of the main Permian synapsids. (Compiled from Rubidge, 1995; Golubev, 2000; Izart *et al.*, 2003; Lucas, 2004; Tverdokhlebov *et al.*, 2005).

herbivorous estemmenosuchids, and three kinds of small herbivores, basal anomodontians and the as yet little known niaftasuchids and nikkasaurids. In the contemporary South African record there are also the more progressive, larger carnivorous therocephalians and herbivorous dicynodont anomodontians (Rubidge, 1995).

Prima facie, therefore, the fossil record shows a very rapid therapsid radiation, about 267 Ma, into at least nine groups. This is consistent with the analysis of the phylogenetic inter-relationships of the major therapsid taxa indicated earlier. The paucity of shared derived characters categorizing most of the variously proposed higher-level clades indicates that the radiation occurred by the divergence of the separate lineages from the same basal stock over a very narrow window of time, indeed, geologically speaking, virtually simultaneously. On the other hand, sphenacodontid pelycosaurs are known from the Late Carboniferous Stephanian, about 300 Ma. As its presumed sister group, this dates the origin of the clade Therapsida to more than 30 Ma before its actual appearance in the fossil record.

There are three principal possible explanations for the discrepancy between date of origin of the clade and the date of its appearance in the fossil record.

A ghost radiation

It may be that the origin of therapsids and their subsequent diversification occurred gradually throughout the Lower Permian, but that these earlier members of all the lineages remain undiscovered as fossils. This is implausible because, with the single and dubiously possible exception of *Tetraceratops*, not a single synapsid specimen from the Lower Permian is known to have any therapsid characters at all. This is despite the fact that Lower Permian tetrapods have been sampled from three different facies, in three widely separate areas of the world (Behrensmeyer *et al.*, 1992; Milner, 1993; Berman *et al.*, 1997). First, far the largest is Milner's (1993) edaphosaurid-nectridean province of the then equatorial North America and central and western Europe, with its abundant fauna of pelycosaurs and many other amniote and amphibian taxa. Secondly, there is the mesosaur province of southern Gondwana, which contains the aquatic amniote *Mesosaurus* and tetrapod footprints. Thirdly, there is the north temperate fauna of what today is Kazakhstan, which contains freshwater seymouriamorphs tetrapods.

The short fuse

It may be that no significant evolutionary transition towards the ancestral therapsid occurred until late in the Early Permian, that it was completed within a short period of time, and that the divergence into the major lineages occurred very rapidly at the start of the Mid-Permian, over the course of a few million years.

Even if it is correct that the sphenacodontids constitute the monophyletic sister group of Therapsida, and therefore that the two had diverged before the start of the Permian, it does not necessarily follow that the therapsid lineage had immediately commenced to evolve new characters. They may have remained phenetically virtually indistinct from sphenacodontids proper until well into the Early Permian. Indeed, there are so few characters supporting the monophyly of Sphenacodontidae (Table 1) that the possibility can hardly be discounted that it is paraphyletic, and that the therapsids evolved from a 'sphenacodontid' ancestor towards the end of the Early Permian.

If the short fuse model is correct, then no basal therapsid fossils are to be expected throughout the Early Permian, which is the case. However, the model further implies that there was a very rapid correlated evolution of the many characters that changed in the short time available. One argument against this is Sidor & Hopson's (1998) demonstration of a significant correlation between the numbers of new synapomorphies found at, and the estimated time spans between successive nodes in their cladogram of synapsids. They interpreted the relationship as evidence for an approximately constant rate of acquisition of mammalian characters. If correct, it would have required a considerable period of time for almost 50 new osteological, and by inference very many more non-osteological characters to evolve between a sphenacodontid ancestor and a therapsid. Perhaps more convincingly, the correlated progression model for the origin of a major new taxon also implies a relatively slow, gradual acquisition of characters (Kemp, in press).

The long fuse

It is more plausible therefore that the evolution of the ancestral therapsid was a lengthy, gradual process occupying much of the Early Permian, during which all the therapsid characters gradually accumulated. Furthermore, the lineage may have remained as a group of ecologically restricted, conservative carnivores that did not give rise to any other ecotypes until the start of the Mid-Permian, when a rapid radiation into a variety of derived therapsid groups occurred. The absence of any fossil record of what is thus assumed to have been a single, low diversity lineage throughout the Lower Permian becomes a great deal more plausible.

The long fuse model predicts that intermediate grade fossils will eventually be found in Lower Permian sediments; despite the scepticism expressed, more complete material of *Tetraceratops* might yet reveal that it is in fact one such grade. More specifically, the likelihood is that the intermediate grades occurred in an as yet unsampled environment that was particularly conducive to the evolution of the novel biological organization of therapsids. The model also predicts that there was an environmental trigger for the rapid Mid-Permian radiation of the group, that was also related to the associated decline to extinction of the pelycosaurs.

The palaeogeography, timing and palaeoecology of the replacement of pelycosaurs by therapsids

It is therefore necessary to place the origin and early radiation of therapsids in a palaeogeographic and palaeoecological context.

Palaeogeography and timing (Fig. 3)

There has been a recent shift to the use of the Chinese marine stages in place of the Russian for the global stratigraphic scale of the Upper Permian (Gradstein *et al.*, 2004). However this has not been universally accepted yet as it creates an apparent anomaly in the correlation between the Russian and South African therapsid faunas (M.J. Benton, pers. comm.) Therefore, pending resolution of the issue, the Russian stage names have been retained in the present work.

The known worldwide pattern of distribution of tetrapods through the Permian has been reviewed by a number of authors (Parrish *et al.*, 1986; Behrensmeyer *et al.*, 1992; Milner, 1993; Berman *et al.*, 1997). Three geographical areas are of prime relevance (Figs 3 and 4).

North America

Pelycosaurs first appeared in North America and Europe during the Upper Carboniferous Westphalian, about 300 Ma (Reisz, 1972), and the taxon dominated terrestrial faunas of the Lower Permian, with six families and over 25 genera described (Romer & Price, 1940; Reisz, 1986). The youngest members of the radiation occur in the San Angelo, Flowerpot, and Chickasha Formations of southern USA, where diversity declines to three families, the sphenacodontid *Dimetrodon*, the herbivorous caseids, and the carnivorous varanopids. These later formations have also yielded a number of poorly preserved, fragmentary specimens that Olson & Beerbower (1953) and Olson (1962, 1974) described as members of several groups of Therapsida, leading them to believe that pelycosaurs and therapsids co-existed for a time here. Furthermore it was believed that they dated from the Guadalupian stage and were therefore of Mid-Permian age. However both the identification and the timing of these remains have been challenged. Parrish *et al.* (1986) and King (1988) regarded the specimens as indeterminate. Sidor & Hopson (1995) interpreted Olson's supposed San Angelo and Flowerpot therapsids explicitly as pelycosaurs, mostly caseids and possibly *Dimetrodon*, whilst Reisz & Laurin (2001) reinterpreted *Watongia*, Olson's (1974) supposed Chickasha Formation gorgonopsian therapsid, as a large-bodied varanopid pelycosaur.

Meanwhile, irrespective of their faunas, the Guadalupian age of the San Angelo, Flowerpot, and Wichita Formations has been questioned by Lucas (2002, 2004) who argued that they actually date from the preceding Leonardian stage, and are therefore of Early Permian age.

Russia

The second relevant fossil-bearing localities occur in the cis-Uralian region of Russia. This area lying west of the Ural Mountains has a complex sequence of tetrapod-bearing strata that only recently has begun to be understood in detail (Golubev, 2000; Modesto & Rybczynski, 2000; Ivakhnenko, 2005; Tverdokhlebov *et al.*, 2005). The earliest tetrapods occur in the Inta Assemblage, which is dated as Ufimian, and correlates approximately with the start of the Guadalupian, and is therefore of Mid-Permian age. It contains a variety of amphibians and reptiles related to western European and North American taxa, but no synapsids, neither pelycosaur nor therapsid.

The tetrapod fauna of the succeeding Russian stage, the early Kazanian, is represented by tantalizingly fragmentary material of indeterminate identification, found in the Copper Sandstones of Bashkortostan. Isolated femora have been considered to belong to therapsids by Efremov (1954), and at least one as a caseid by Olson (1962), but the specimens are not adequate to document reliably the earliest appearance of synapsids of either group in the Russian sequence (Modesto & Rybczynski, 2000).

The next horizon preserved in the sequence is Kazanian and probably early Tatarian, and is represented by two rather different faunal assemblages (Golubev, 2000; Ivakhnenko, 2003a). The Mezen Assemblage occurs on the western coast of what at the time was the East European Sea (Ivakhnenko, 2005). The fauna includes both pelycosaurs and therapsids, the former represented by the caseid *Ennatosaurus* and the varanopid *Mesenosaurus* (Reisz & Berman, 2001), and the latter by *Biarmosuchus* and two taxa of small, herbivorous therapsids of unclear relationships, niaftasuchids and nikkasaurids. The approximately contemporaneous Ocher Assemblage lies on the eastern shore of the East European Sea. The synapsid fauna was lacking in pelycosaurs but had a considerably richer therapsid component. *Biarmosuchus* was present, but in addition there were large herbivores in the form of estemmenosuchids. Additional carnivores were represented by the anteosaurid dinocephalians *Archaeosyodon* and *Chthhamaloporus*, and the probable basal gorgonopsian *Kamagorgon*. Anomodontians were represented by the small, herbivorous *Otsheria*. A much less rich fauna of about the same age is found at Belebey, which Tverdokhlebov *et al.* (2005) regarded as late Kazanian. *Estemmenosuchus* is the only therapsid recorded from here.

The final stage to consider in the development of the therapsid fauna in Russia is the Isheevo Assemblage, which is dated as the later part of the early Tatarian (Golubev, 2000; Ivakhnenko, 2003a). It is noticeable that both biarmosuchians and estemmenosuchids are absent, and in their place there is a rich dinocephalian element consisting of the herbivorous tapinocephalid *Ulemosaurus* and carnivorous anteosaurids such as *Titanophoneus* and *Syodon*. Basal anomodontians are represented by *Ulemica*. A new taxon, the Therocephalia has also made an appearance in the form of *Porostereognathus*.

South Africa

The third area of interest is South Africa, where a number of basal therapsids have been found in the lowermost part of the Beaufort Formation, which is the *Eodicynodon* Assemblage Zone (Rubidge, 1995). It has not yet been precisely correlated with the Russian continental strata, but the degree of similarity between the two faunas is such as to indicate a likely Early Tatarian age; Ivakhnenko (2005) compared it to the Mezen and Ocher Assemblages. The *Eodicynodon* Assemblage Zone fauna consists of the dicynodont anomodontian *Eodicynodon*, the tapinocephalid dinocephalian *Tapinocaninus* (Rubidge, 1991), the anteosaurid dinocephalian *Australosyodon* (Rubidge, 1994), the basal anomodontian *Patranomodon* (Modesto et al. 1999), a poorly preserved pristerognathid therocephalian (Rubidge *et al.*, 1983), and fragmentary remains of possible gorgonopsians. Above the *Eodicynodon* Assemblage Zone lies the *Tapinocephalus* Assemblage Zone. Here dinocephalians, both anteosaurids and tapinocephalids, are abundant and biarmosuchians present, as indeed are all the other main Upper Permian therapsid taxa except for cynodonts. More unexpectedly, two specimens of the varanopid pelycosaur *Elliotsmithia* have been described (Modesto *et al.*, 2001), indicating an overlap, albeit of extremely limited extent, between pelycosaurs and therapsids in Gondwana, as well as in Russia.

Other geographical regions

At present, no other geographical regions of the world add significant information about the pattern of replacement of pelycosaurs by therapsids. Therapsids contemporary with those of Russia and South Africa are known from the Xidagou Formation in Gansu Province of China (Li *et al.*, 1996; Li & Cheng, 1997; Lucas, 2001), a basal anteosaurid dinocephalian, *Sinophoneus*, and a biarmosuchian, *Biseridens*.

Langer (2000) has described isolated dinocephalian teeth from the Paraná Basin in southernmost Brazil, which he believes are Late Kazanian to Early Tatarian in age.

Possibly the youngest pelycosaurs so far discovered have recently been described from Uruguay (Pineiro *et al.*, 2003). They consist only of fragmentary postcranial remains identified as a varanopid, and a possible vertebra of the sphenacodontid *Dimetrodon*. At present, the dating of the Buena Vista Formation in which they occur is no more precise than Late Permian to possibly Early Triassic.

Palaeoecological circumstances

General

The palaeoclimatology and palaeoecology of the Permian have been subjected to extensive analysis on the basis of palaeobiotic and geochemical data, and computer modelling, with the consequence that the environmental conditions surrounding the extinction of the pelycosaurs and the origin and early radiation of the therapsids are fairly clear. There is no evidence at all, neither geochemical nor biotic, of any drastic, or sudden environmental perturbation between the period of the pelycosaur radiation in the Early Permian and the commencement of the therapsid radiation early in the Mid-Permian. However, there were some possibly significant ongoing trends. The best-known one is a gradual rise in global temperatures, and an accompanying increase in seasonality. Royer *et al.* (2004) calculated that during the Permo-Carboniferous glaciation mean global temperature was about 2 °C below today's value. By the start of the Mid-Permian it was about 3 °C above. Meanwhile, the disappearance of coal deposits and the increase in evaporites and red beds indicate increasing seasonal aridity in many areas. A second trend concerned the atmospheric oxygen level. This had peaked at 300 Ma at a level of about 35%, and was declining. Nevertheless, at the time of the first appearance of the therapsids in the fossil record, about 267 Ma, it was still some 27% compared with the present day value of 21% (Berner, 1999; Berner *et al.*, 2000). There was an accompanying change in the level of CO_2, which had reached a minimum at 300 Ma, was rising, and is estimated to have measured approximately 1000 p.p.m. by 267 Ma, three times the current level (Royer, 2001; Royer *et al.*, 2004).

Lower Permian (Fig. 4a)

All the Upper Carboniferous and Early Permian pelycosaurs known come from within about 10° either side of the palaeoequator of Pangaea (Parrish *et al.*, 1986; Milner, 1993; Berman *et al.*, 1997). During the Upper Carboniferous, the presence of coal measures in this zone indicates hot, continuously humid conditions, with widespread freshwater swamps. The plant life was dominated by spore-bearing pteridophytes and lycopsids, although seed-bearing plants, conifers and cordaites in particular, were already increasing in prominence (Behrensmeyer *et al.*, 1992; Berman *et al.*, 1997). During the succeeding Lower Permian, conditions continued to change as the Asselian glaciation of southern Gondwana retreated, and the now almost completely assembled supercontinent of Pangaea drifted northwards. There was a decline of coal measure formation, an increase in evaporite deposits, and the laying down of the huge expanses of red beds in the southern parts of North America. These all indicate a generally drier, seasonally arid environment, an interpretation supported by the increasing dominance of seed-bearing taxa of plants with xerophytic adaptations. Rees *et al.* (2002) have reconstructed the global Lower Permian climate (Fig. 4a) on the basis of the fossil plant record and climate-sensitive deposits. The age of their reconstruction is Sakmarian, which is equivalent to the Wolfcampian–Leonardian of the North American continental record (Izart *et al.*, 2003). To either side of the equatorial mountain range that bisected Pangaea there was a narrow climatic zone described as the Tropical Everwet Biome, the closest modern analogy to which is tropical rainforest. It was bounded both north and south by an equally narrow band of Tropical Summer Wet Biome, analogous to present day tropical deciduous forest and savanna. This zone was in turn bounded by Hot Desert Biome, which extended to about 30°N and 30°S, and was continued as a narrow band of mid-latitude desert in the southern hemisphere. The desert extended from the east to the west coast of Pangaea, and so completely isolated the temperate biomes from the tropical regions.

The known Lower Permian pelycosaurs were restricted to the equatorial Everwet Biome, where they constituted the dominant taxon of large-bodied terrestrial tetrapods. They were accompanied by a variety of fish, small aquatic and terrestrially adapted amphibians, and basal amniotes. The only other large bodied terrestrial taxa present were the herbivorous diadectids, the amphibian *Eryops*, and the limnoscelids which were probably semi-aquatic, crocodile-like animals. Olson (1966, 1971) was the first to appreciate, from the relatively large number of terrestrial carnivores compared with terrestrial herbivores in the fauna, that during the Upper Carboniferous and Lower Permian, the pelycosaur-dominated terrestrial ecosystem must still have had its trophic base dependent on the freshwater biota of aquatic plants, fish and piscivorous tetrapods. Subsequent reviewers have agreed with this interpretation (e.g. Behrensmeyer *et al.*, 1992; Milner, 1993; Sennikov, 1996).

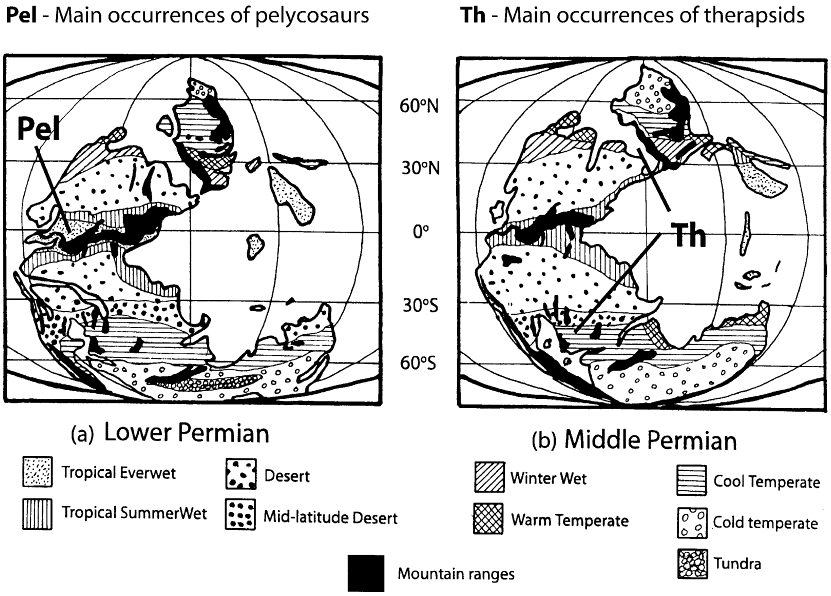

Fig. 4 Palaeoclimatic reconstructions for (a) Lower Permian (Sakmarian Stage); (b) Middle Permian (Wordian Stage), showing the biomes and the major occurrences of pelycosaur and therapsid synapsids. (Redrawn after Rees *et al.*, 2002).

Middle Permian (Fig. 4b)

The trends in climate change continued into the Middle Permian. Rees *et al.* (2002) have also reconstructed the palaeoclimate for the Wordian stage (Fig. 4b), which is equivalent to the Kazanian of Russia (Gorsky *et al.*, 2003; Izart *et al.*, 2003) and therefore approximates to the date of the appearance of the therapsids. By this time, the Tropical Everwet Biome of the equatorial region of Pangaea had disappeared, replaced by expansion of Tropical Summer Wet Biome, while the northern and southern hot Desert Biomes extended beyond latitude 30°. It is particularly significant that the northern Tropical Summer Wet Biome had apparently made contact with the northern temperate areas, via a narrow coastal strip running along the eastern coast of Pangaea. In contrast, according to this reconstruction, no such contact existed in the southern hemisphere, where Desert Biome still intervened. However, Visser (1995) analysed in detail the Middle Permian palaeoenvironment of Southern Africa. He described a warm, moist and seasonal region, which would be equivalent to Rees *et al.* (2002) Summer Wet Biome, extending from about the limit of his study area at 30°S to Cool Temperate Biome starting about 60°S, and which was most humid on the eastern side of the continent. On this evidence, it is probable that Summer Wet Biome was directly continuous with temperate biomes along the eastern margin of Pangaea in the southern, as well as in the northern hemisphere.

This conclusion is strongly supported by the degree of taxonomic similarity between the Middle Permian faunas of Russia and South Africa. There must have been a potential dispersal route, which realistically could only have been via the more humid eastern side of Pangaea as suggested, although as yet no tetrapod fauna of Mid-Permian age has been found in this area. Sidor *et al.* (2005) have recently described a younger tetrapod fauna from the North African Upper Permian, which appears to lie just within the Summer Wet Biome. The possibility of gorgonopsian material has been mentioned (Steyer *et al.*, 2005) although not as yet confirmed. If therapsids are indeed present, they would corroborate the hypothesis discussed later that the Summer Wet Biome was a viable habitat for therapsids, and connected their northern and southern temperate habitats.

The Russian early therapsids occur between latitudes 30° and 40°N (Parrish *et al.*, 1986), apparently within Rees *et al.* (2002) Winter Wet Biome. Their detailed palaeoenvironment has been considered by several authors, most recently Ivakhnenko (2003a, 2005) and Tverdokhlebov *et al.* (2005). Both the Mezen assemblage on the western side and the Ocher assemblage on the eastern side of the Kazanian Sea occupied extensive coastal marshlands. Ivakhnenko (2003a) pointed out that, although usually considered arid conditions because of the presence of red beds, conditions may have been hot but seasonally humid. A wide variety of nonsynapsid tetrapods were also present in the Russian assemblages (Sennikov, 1996; Golubev, 2000; Ivakhnenko, 2005; Tverdokhlebov *et al.*, 2005). These include many amphibians, both aquatic and relatively terrestrially adapted, and several groups of small-bodied amniotes. However, unlike the situation in the Early Permian, synapsids were now the only medium- to large-bodied terrestrial tetrapods present. The increased preponderance of the fully terrestrial therapsid herbivores amongst them indicates that for the first time the terrestrial ecosystem had evolved a primarily dry land rather than freshwater trophic base, and that the rise of the therapsids was an integral part of this fundamentally important development, much as proposed by Olson (1966).

The Middle Permian South African therapsids of the *Eodicynodon* Assemblage Zone are found around the latitude 60°S, where they occupied the Cold Temperate Biome of Rees *et al.* (2002), described as 'cool to temperate, wet' by Visser (1995). Little is yet known of their associated non-therapsid biota.

The Middle Permian therapsids from China occur at approximately latitude 30°N on the North China block, but little is yet known of the paleoecology of the Xigadou Formation.

The possibly Mid-Permian aged dinocephalians of the Paraná Basin of Brazil occupied a region described by Cúneo (1996) as temperate forest fringing an epicontinental sea, with a marked dry season.

A palaeobiological hypothesis

Principles

An hypothesis purporting to account for a palaeobiological phenomenon requires the empirical evidence and its immediate interpretation that has been presented in detail above, namely: the systematics of the relevant groups; the inferred evolutionary changes in characters and their biological significance in the transition from pelycosaur-grade to therapsid-grade; the stratigraphical and palaeogeographical occurrences; the palaeoclimatological and palaeoenvironmental conditions through the Early Permian. The hypothesis also requires a number of framework concepts derived from evolutionary theory more generally.

The validity of using a paraphyletic taxon in the palaeobiological analysis

One of the most significant aspects of the rise of the therapsids is their complete replacement of the pelycosaurs as the dominant, large-bodied, terrestrial tetrapods. It has been objected by some authors that a paraphyletic group such as 'Pelycosauria' cannot be considered to be an evolutionary unit for analysis because its definition is necessarily arbitrary (e.g. Patterson & Smith, 1987; Smith, 1994). Others, such as Sepkoski (1996) and Kemp (1999) argued that if the constituent species of a paraphyletic group are sufficiently similar phenotypically to one another, and distinct from those of another group, then the paraphyletic taxon can legitimately be viewed as a proxy for a group of species with similar biological attributes. The very large number of character differences between all known pelycosaurs, on the one hand, and all known therapsids, on the other (Table 1), adequately supports this requirement. Replacement of the pelycosaurs by the therapsids is in effect shorthand for a species-level evolutionary event, detectable in the fossil record as the extinction of species of the one kind, and their replacement in the habitat by species of the other kind.

The causes of taxon replacement

Benton (1987) suggested criteria by which two extreme possible causes of the replacement of one taxon by another of comparable ecological role might be recognized. Competitive replacement necessarily involves a period of temporal overlap between the two competing taxa, so there would be a double-wedge pattern as the diversity of the earlier group declined in inverse proportion to the increase in the later group. There would be no indication of a large environmental change, but an evolutionary novelty, acting as a key innovation responsible for the competitive superiority of the later group, might be identifiable. In contrast, opportunistic replacement would be marked by a rapid decline in diversity of the earlier group followed rather than accompanied by the increase in diversity of the later group, and indications of the environmental perturbation that had caused the decline of the earlier group would be expected in the geological record. As also discussed by Benton (1987, 1996), this dichotomy is a gross oversimplification because of the likely interaction between the two phenomena, and he proposed a series of alternative models in which the two processes, competition and opportunism, played variable roles. Even this ignores the likely confounding role played by interactions with species of other taxa in the community.

Competition in palaeobiological theory is particularly problematic because, as normally understood, it is a species-level and therefore an ecological time-scale process. Therefore competitive replacement ought to be too rapid to be visible in the fossil record. As a corollary, if a double-wedge pattern is indeed evident at the temporal resolution of the fossil record, at best 10^4–10^5 years, and often of the order of 10^6 years as in the present case, it implies that the replacement took such a long time from start to completion that the selective advantage of the species of one taxon over those of the other must have been exceedingly small. Not only does this render it implausible that every individual species-to-species competitive situation was resolved in favour of a member of the same taxon, but also implies that random events analogous to genetic drift would often have overridden such tiny differential competitive advantages. Rozensweig & McCord (1991) addressed this issue with their more realistic concept of incumbent replacement, in which the new, competitively advantaged taxon is present, but can only replace the original taxon on a species by species basis as the latter's species become extinct due to environmental causes. The timing of the replacement is therefore controlled by the rate of extinction of the currently incumbent taxon. Sepkoski (1996) also attempted to rescue species-level interaction as an explanation for taxon replacement at the scale recorded in the fossil record. He proposed a model, owing not a little to island biogeography theory, based on the logistic curve of a taxon's diversity as it increases towards the maximum, equilibrium value. If, for whatever reason, two interacting taxa differ in their inherent rates of increase in species diversity, their actual diversities at a particular time, and their potential equilibrium diversities in the habitat, then, by assuming suitable values for these parameters, various patterns of clade replacement seen in the fossil record can be modelled.

A further epistemological problem of competition as an explanation is identification of the nature of the putative competitive advantage. Many authors have claimed to identify a key adaptation as the specific reason why members of one taxon gained a competitive advantage over the members of another taxon. However, as long as there are multiple differences between the functionally integrated organisms of the two respective taxa, no one attribute can be shown to have been paramount over all the other attributes in causing differential diversity change.

Thus plausible elucidation of the likely cause of a case of taxon replacement requires knowledge not only of the time course of the replacement, but also of the overall biological nature of the taxa, and the details of the abiotic and biotic environmental setting during which the event occurred. The present case is one of the few where these requirements are to a reasonable extent met.

The causes of long-term evolutionary trends

There have been few recent reviews of the theoretical causes of evolutionary trends (McShea, 1998). The normal default assumption is that an evolutionary trend in morphology at the scale revealed by the fossil record is caused by organism-level natural selection. However, Kemp (1982, 1999), proposed that in some long-term cases, including the trend leading to mammals, a process of species selection might have been the driving force. If a carnivore species with a relatively higher metabolic rate and a smaller population density has, for whatever reason, a higher probability of speciating, then this could lead to a sequence over time of carnivorous species with increasingly elevated metabolic rate. In the present case, this would help to account for the apparent restriction to exclusively carnivorous animals of the lineage from sphenacodontid to ancestral therapsid.

The hypothesis (Fig. 5)

Phase 1

The six families of pelycosaurs occurring at the start of the Early Permian consisted of mostly medium- to large-bodied terrestrial tetrapods adapted for the hot, continuously humid Everwet Biome of the narrow equatorial region of Pangaea. They were part of a community that was extensively dependent on freshwater productivity. Their low activity level, ectothermic temperature physiology, and poor water conservation abilities prevented them from expanding their habitat into the adjacent, seasonally dry, savanna-like, Tropical Summer Wet Biome.

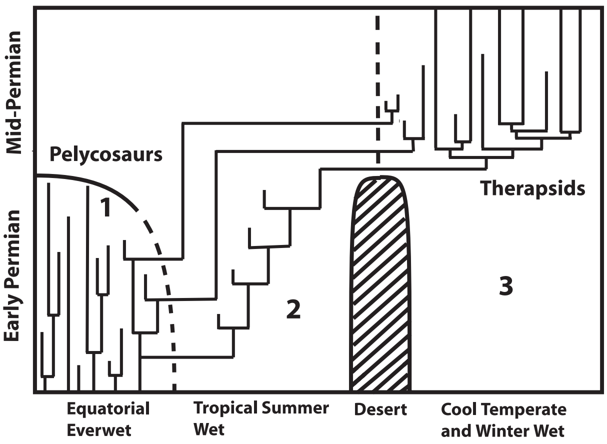

Fig. 5 Schematic illustration of the palaeobiological hypothesis of the origin and early radiation of therapsids. 1–3 are the three phases explained in the text.

Phase 2

During the course of the Early Permian, a unique combination of environmental and biological circumstances resulted in the evolution of the ancestral therapsid from a lineage of sphenacodontid pelycosaurs. The first was the ecological opportunity offered by the immediately adjacent Tropical Summer Wet Biome to any organism capable of existing free of standing bodies of freshwater, of tolerating high ambient temperature fluctuation, and therefore of surviving during the dry season. The second was the high atmospheric oxygen level, which facilitated adequate gas exchange for the start of the evolution of the higher aerobic metabolic rate necessary for enhanced homeostatic regulation. The third was the nature of the carnivorous ancestral sphenacodontid, whose particular combination of functional and structural characters endowed it with the potential to commence the acquisition of all the characters needed for a higher energy mode of life, by the correlated progression process. The outcome of these conditions was the evolution of a lineage of medium-sized carnivores in the Summer Wet Biome. Here, over time, species evolved with increasingly raised aerobic metabolic rates, the fundamental ecological purpose of which was to regulate body temperature and water content increasingly effectively in the seasonal climate. Increment by increment, modifications evolved to the mechanism of collection and assimilation of food, to the ventilatory capacity, to the circulatory anatomy, to the activity level and agility of the gait, and to the sensory and central nervous systems needed for overall control. The lineage continued to consist of exclusively carnivorous animals, and they were competitively excluded from expanding back into the Everwet Biome by the continued presence there of the incumbent sphenacodontid pelycosaurs, which were long adapted to these conditions.

Two other kinds of pelycosaurs also expanded their habitat into the Summerwet Biome, the herbivorous caseids and the carnivorous varanopids. However, in their case they achieved it with no detectable morphological changes, but presumably by evolving physiological tolerance of the seasonality rather than regulatory abilities: aestivation was probably part of their strategy.

Meanwhile, due to the gradually rising global temperatures and seasonal aridity, the equatorial Everwet Biome had been reducing in area and ceased to exist by the end of the Early Permian, resulting in the decline and extinction of the rest of the pelycosaur radiation, independently of direct interaction with therapsids.

Phase 3

The rapid increase in diversity and variety of therapsids recorded at the start of the Mid-Permian also depended on the coincidence of a new ecological opportunity with organisms capable of taking advantage of it. The therapsids, still consisting of carnivores, had achieved sufficiently elevated metabolic rate, activity level, and regulatory abilities to allow them potentially to occupy the cooler, temperate biomes. It was at this time that the changing Permian climate resulted in a contact between the Summer Wet Biome, within which therapsids had been evolving hitherto, and the temperate biomes in which they are first found as fossils. In the northern hemisphere, they expanded their range via the east coast of Pangaea, where they are found in the Winter Wet Biome. In the southern hemisphere, their range similarly expanded, and they have been found in the Cool Temperate Biome.

Once in their newly expanded, temperate ranges, the therapsids radiated rapidly, because of the opportunities now available for a variety of ecotypes, and because it required relatively minor evolutionary changes, so constraints imposed by a correlated progression of many characters no longer applied.

A few pelycosaurs also entered into these temperate regions. The temporal overlap in the fossil record between the two respective groups for several more million years indicates a case of incumbent replacement. In the cooler, more variable conditions, pelycosaur species were closer to the limits of their environmental range, and therefore more prone to extinction than the therapsids with their sophisticated regulatory abilities. Extinction of the caseids allowed further diversification of a variety of large-bodied and small-bodied herbivores, while the final disappearance of the varanopids opened the way for a further increase in carnivorous therapsid groups.

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