THE OLDEST THEROCEPHALIANS (THERAPSIDA, EUTHERIODONTIA) AND THE EARLY DIVERSIFICATION OF THERAPSIDA

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Abstract: The oldest records of mammal-like therapsids in Laurasia are from the Ocher Complex of Russia and the Xidagou Formation of China, whereas in Gondwana they are restricted to the *Eodicynodon* Assemblage Zone, Beaufort Group of the South African Karoo. This fauna, which is relatively depauperate when compared with younger assemblage zones from the Karoo, shows an amazing diversity of therapsids including: dinocephalians (already represented by the carnivorous anteosaurids and the herbivorous tapinocephalids), anomodonts (including dicynodonts), gorgonopsians, and therocephalians. The last group is represented by two specimens in this assemblage zone. This paper presents a full description of these therocephalians, which are assigned to the scylacosaurid species *Glanosuchus macrops* and *Ictidosaurus angusticeps*. We also discuss diversity trends of therocephalians and explore some hypotheses implicated by the diverse oldest record of therapsids, represented by five of the six major lineages of the group.

Key words: Therocephalia, Scylacosauridae, *Eodicynodon* Assemblage Zone, Karoo Basin, South Africa, Middle Permian.

THE rocks of the Beaufort Group (Karoo Supergroup) of South Africa preserve a rich diversity of fossils which provide an uninterrupted record of continental tetrapod biodiversity from the Middle Permian to the Middle Triassic (Rubidge 2005). Because of this diversity and abundance, an eight-fold tetrapod biostratigraphic subdivision of the rocks of the Beaufort Group in the Karoo sedimentary succession has been established (Rubidge *et al.* 1995). A remarkable aspect is that a rich diversity of therapsids is present in the oldest rocks of the lowermost Beaufort Group (Abrahamskraal Formation), with five of the six therapsid groups recorded from the Karoo already represented in this geological unit.

The oldest biozone of the Beaufort Group is the *Eodicynodon* Assemblage Zone (AZ), which, on biostratigraphic evidence, has been correlated with the oldest therapsid faunas of the Ocher Complex of Russia and the Xidagou Formation of China (Li and Cheng 1995; Battail 2000; Kemp 2005; Rubidge 2005; but see Lucas 2006 for a different opinion about the age of the Chinese fauna). From this assemblage zone are recorded the basal dicynodonts *Eodicynodon oosthuizeni* and '*E.*' *oelofseni* [Barry 1974; Cluver and King 1983; Rubidge 1990*a*; Rubidge *et al.* 1994 (Modesto *et al.* 2003 concluded that *E. oelofseni* was not the sister taxon of *E. oosthuizeni* and will

have to be assigned to a new genus)], the basal anomodont *Patranomodon nyaphulii* (Rubidge and Hopson 1996), the dinocephalians *Tapinocaninus pamelae* (Rubidge 1991; Govender *et al.* 2002) and *Australosyodon nyaphuli* (Rubidge 1994), two fragmentary skulls of gorgonopsians, and the remains of therocephalians (Rubidge *et al.* 1983; Rubidge 1995). The provenance of this oldest terrestrial fauna of the Karoo was initially attributed to levels of the Ecca Group (e.g. Barry 1974; Cluver and King 1983; Rubidge *et al.* 1983), but later it was recognized as being at the base of the Beaufort Group (Rubidge 1990*b*).

The first report of a therocephalian in the lowermost assemblage zone of the Beaufort Group was the description of a partial skull from Prince Albert, which was assigned to the family Pristerognathidae (Rubidge *et al.* 1983). Later, Rubidge (1995) listed the therocephalian genera *Glanosuchus* and *Alopecodon* as part of the fauna of the *Eodicynodon* AZ. As therocephalians are not known from either the Ocher Complex of Russia or the Xidagou Formation of China, these two specimens are the oldest therocephalians represented in the fossil record. Considering that only a brief description of one of these specimens has been published (Rubidge *et al.* 1983), this paper presents a full account of these important therocephalian

specimens and addresses their taxonomic identity. We also explore therocephalian diversity through time and discuss some implications of the record of eutheriodonts among the oldest therapsid fauna known.

Institutional abbreviations. NMQR, National Museum, Bloemfontein; SAM, Iziko South African Museum, Cape Town.

Anatomical abbreviations. cp, coronoid process; D, dentary; F, frontal; J, jugal; lp, lower postcanines; Mx, maxilla; N, nasal; or, orbit; Pf, prefrontal; Pm, premaxilla; Pof, postfrontal; ptb; pterygoid boss; ptr, pterygoid ridge; ptt; pterygoid teeth; rla, reflected lamina of the angular; rup, roots upper postcanines; Sa, surangular; Sm, septomaxilla; Sp, splenial.

GEOLOGICAL SETTING

The therocephalian specimens examined here were collected from the *Eodicynodon* AZ (Rubidge 1995). The specimens were discovered in pedogenic calcareous nodular layers within siltstone successions below the first maroon mudrock of the Abrahamskraal Formation. These rocks are considered to have been deposited in a subaerial delta plain depositional environment (Rubidge 1995; Rubidge *et al.* 2000).

The age of the *Eodicynodon* Assemblage Zone is not well established, although there is a growing consensus that it is Middle Permian (Battail 2000; Lucas 2002, 2004, 2006; Catuneanu *et al.* 2005; Rubidge 2005). Considering the geologic time scale proposed by the International Commission of Stratigraphy (Gradstein and Ogg 2004), we follow Catuneanu *et al.* (2005) and Rubidge (2005) who assign a Wordian age to this assemblage zone.

MATERIAL AND METHODS

The specimens NM QR2908 (Text-fig. 1) and NM QR2910 (Text-figs 2–3) were prepared mechanically with an airscribe. Computerized axial tomography (CAT) scanning was undertaken on NM QR2910 (Text-fig. 3) along the sagittal and coronal axes of the specimen. The purpose of CAT scanning was to determine whether the precanine immediately in front of both upper canines represents the tip of erupting canines (e.g. van den Heever 1980). Comparative morphological analysis of these specimens with other early therocephalians was mainly based on the extensive study undertaken by van den Heever (1987).

Recent phylogenetic analyses (Abdala 2007; Botha *et al.* 2007) indicate that Therocephalia is not monophyletic but also includes Cynodontia. Our use of therocephalians in the text thus refers to a paraphyletic assemblage.

SYSTEMATIC PALAEONTOLOGY

THERAPSIDA Broom, 1905
THERIODONTIA Owen, 1876
SCYLACOSAURIDAE Broom, 1903*a*

Specimens examined. NM QR2908, consisting of the preorbital portion and part of the interorbital region of a skull; NM QR2910, a partial skull, which lacks most of the orbital and temporal regions.

Diagnosis. Large therocephalians (with maximum skull length around 400 mm) presenting the following combination of characters: snout long and narrow; anterior border of the orbit on transverse midline of the skull; interorbital region narrow; suborbital bar shallow; most of them showing precanines; incisors varying from six to seven uppers and three lowers; five to nine upper postcanines; presence of serrations on the teeth; teeth on pterygoid boss; premaxilla with vomerine process; ventromedial crest on posterior portion of the vomer; choana long; crista choanalis well developed; ventromedian crest on pterygoid; interpterygoid vacuity narrow; basal tubera small; presence of an angle in the posteroventral region of the dentary.

Remarks. Most of the characters mentioned above were proposed by van den Heever (1987) to differentiate Scylacosauridae from the contemporaneous Lycosuchidae. We should mention, however, that some of these features are found in other therocephalians (e.g. scaloposaurids also possess precanines). In addition, serrations on the marginal dentition and the angle of the dentary are only known in Scylacosauridae and Lycosuchidae among therocephalians.

Locality and horizon. The study specimens come from the farm Modderdrift, near Prince Albert, western Cape Province, South Africa (see Rubidge *et al.* 1983, fig. 2). The outcrops on Modderdrift are assigned to the *Eodicynodon* AZ, which is part of the Abrahamskraal Formation, Beaufort Group, Karoo Supergroup; Middle Permian.

Glanosuchus macrops Broom, 1904
Text-figure 1

Description. In comparison with the large skulls that characterize most *Tapinocephalus* AZ therocephalians, NM QR2908 is a relatively small individual. The skull measures 50 mm from the tip of the snout to the interorbital region in dorsal view and the complete skull length is estimated to have been 80 mm. The partially preserved snout is notably distorted on the right side, and the horizontal mandibular rami are preserved in occlusion, such that only two anterior lower postcanines of the right side are
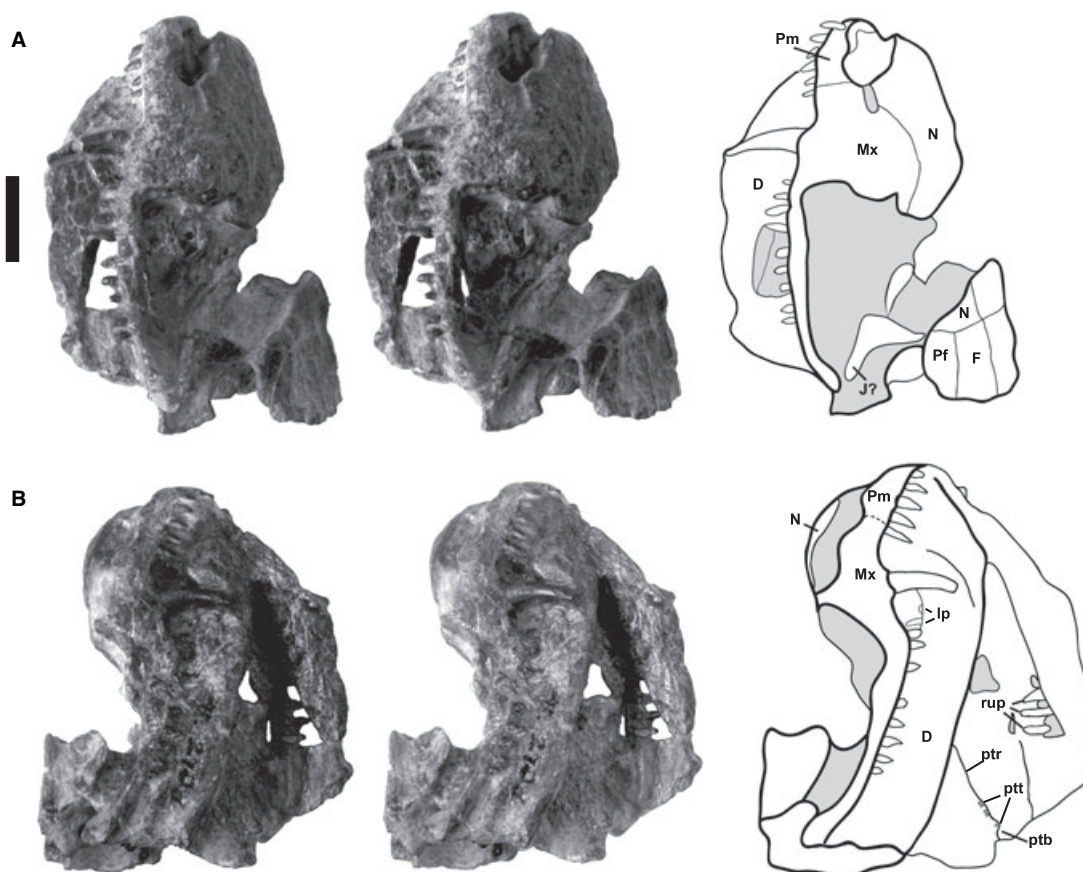
TEXT-FIG. 1. *Glanosuchus macrops*, NM QR2908. Photographs and interpretative drawing in A, left lateral and B, right lateral views. Grey indicates broken bone. Scale bar represents 1 cm.

visible laterally. Only the anteriormost lower postcanines of the left side are visible in medial view. Despite this minor deformation, the complete series of upper dentition are preserved on both sides (Text-fig. 1), and the palate is also partially preserved.

The anterior portion of the nasals is visible in dorsal view but it is not possible to recognize with certainty the nasal process of the premaxilla between these bones. On the left side of the snout the suture between the nasal and the maxilla is visible. An elongated space is present anteriorly between the nasal and the maxilla (Text-fig. 1A) for the facial process of the septomaxilla, which is not preserved. The lateral surface of the maxilla shows a series of shallow pits above the canine. In the interorbital region a clear midline suture is present between the frontals (Text-fig. 1A).

The palate is poorly preserved with the left pterygoid boss showing three teeth. The right boss is not preserved, but at least six pterygoid teeth are observed on the pterygopalatine ridge. These elements are poorly preserved on the left ridge, where it is possible to recognize four teeth (Text-fig. 1B).

The lower jaw has an unfused symphysis, a backward-sloping mentum, and a straight ventral margin (Rubidge *et al.* 1983), but it is not possible to observe the splenial in ventral view.

Upper dentition comprises six incisors, one canine, and nine postcanines on both sides (Text-fig. 1). The incisors are cylindri-

cal, with the first four teeth larger than the last two. Serrations were observed on the distal margin of some incisors. There are no precanines, but a long diastema is present between the last incisor and the large canine. The tip of the canine reaches the ventral margin of the mandible, and serrations are present on the posterior margin of the right canine, but there is no evidence of anterior serrations. A diastema between the canine and the first postcanine is also present. The postcanines, most of which are only partially preserved, are lanceolate cones. Serrations are present on the posterior margin of the first right postcanine, but its anterior margin is poorly preserved, whereas the eighth right postcanine has serrations on both anterior and posterior margins of the tooth.

Ictidosaurus angusticeps Broom, 1903b
Text-figures 2–3

Description. NM QR2910 is the anterior portion of a medium-sized skull measuring 168 mm from the tip of the snout to the posterior portion of the left mandible (Text-fig. 2). The anterior portion of the snout is preserved with the mandible in occlusion, whereas the orbits and temporal region are missing. On
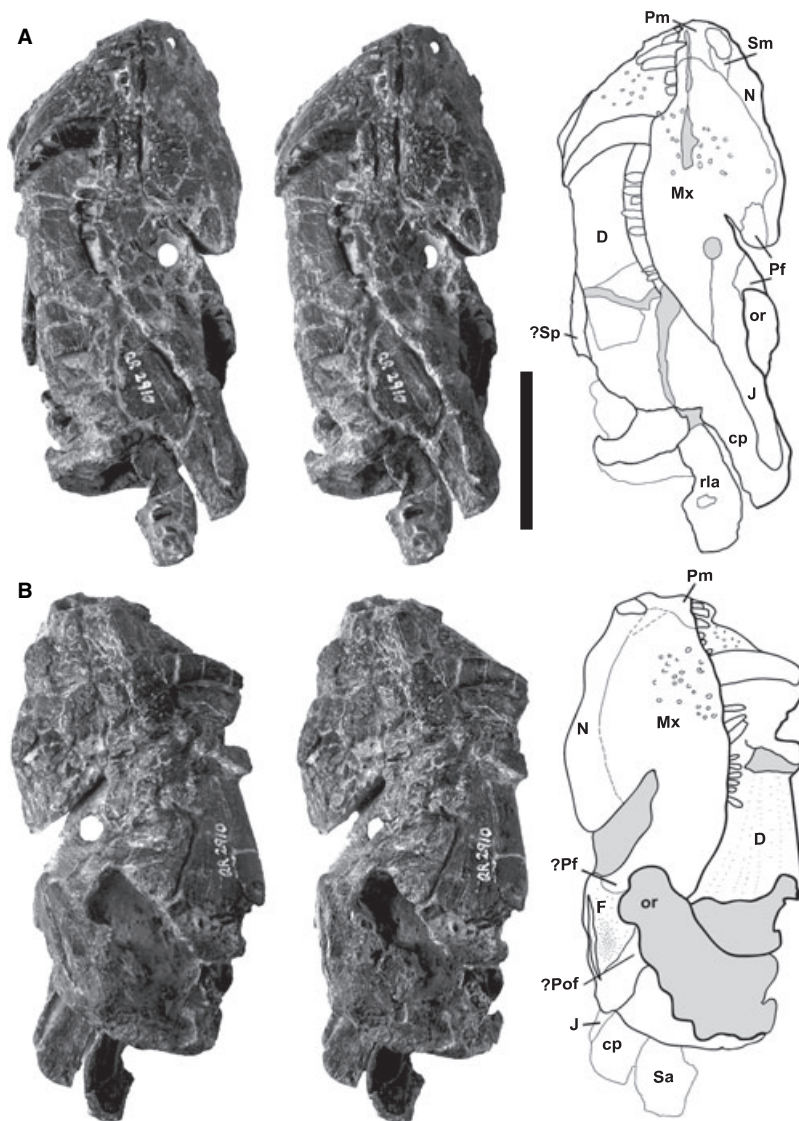
TEXT-FIG. 2. *Ictidosaurus angusticeps*, NM QR2910. Photographs and interpretative drawing in A, left lateral and B, right lateral views. Grey indicates broken bone. Scale bar represents 5 cm.

the left side, part of the zygoma is preserved as well as most of the mandible (Text-fig. 2A). The bone surface is poorly preserved, with many fractures obscuring sutures.

The external naris is ovoid with the long axis directed anteroposteriorly. Both septomaxillae are poorly preserved, with only part of the median transverse shelf and the posterodorsal process between the nasal and the maxilla being visible (Text-fig. 2A). The snout has been laterally flattened, resulting in many fractures and displaced bones. On both sides, the suture between the premaxilla and the maxilla is visible, such that the last two incisors are laterally delimited by the anterior extension of the maxilla (Text-fig. 2). The ventral (alveolar) margin of the maxilla is remarkably convex, and is followed on the posterior end by a slender suborbital bar formed by the anterior portion of the jugal (Text-fig. 2A). Many pits and shallow furrows are present on the lower half of lateral surface of the maxilla; more dorsally the pits are smaller, and are also present on the nasals. A large break dorsally has resulted in the loss of the posterior part

of the snout and the dislocation of the interorbital region (Text-fig. 2). On the left side, the anterior projection of the prefrontal contacts the maxilla and the nasal (Text-fig. 2A).

Two elongate bones, tentatively identified as the frontals, are separated by a long midline gap and are visible on the dorsal surface of the skull roof (Text-fig. 2B). These elements are twisted in relation to the longitudinal axis of the skull and are evidently out of position. The left bone appears to be in contact with the prefrontal. At their posterior ends is a suture followed by a small fragment of bone that we interpret as the postfrontal (Text-fig. 2B).

In the palate all the bones are fractured and displaced, thus complicating interpretation and description. The following description is based on the bones on the right side. The transverse process of the pterygoid is greatly deformed and a suborbital vacuity is present lateral to the pterygoid boss. The ectopterygoid, which forms the lateral border of the vacuity, is displaced but its triangular lateral margin is visible. The ptery-

goid bosses are anteroposteriorly expanded with the long axis directed obliquely to the midline of the skull. The left boss is larger with 16–17 teeth, whereas only ten teeth are visible on the right boss. A possible transverse suture between the pterygoid and the palatine extends to the anteromedial margin of the sub-orbital vacuity. A sharp pterygopalatine crest is present but, as in NM QR2908, there is no evidence of palatal teeth. A long crista choanalis of the palatine extends anteriorly as far as the level of the fifth postcanine.

The mandible is preserved in occlusion, and although the left dentary is complete, it has many fractures (Text-fig. 2A). The dentary manifests a straight ventral margin and a defined angle of the dentary, which is positioned at the level of the middle of the orbit. The dorsal dentigerous margin of the dentary is high anteriorly, especially in the region of the canine. Posteriorly, the dorsal margin of the dentary descends ventrally in the area of the postcanine teeth and then ascends dorsally to form the coronoid process (Text-fig. 2A). The latter process is very high but shortened anteroposteriorly. Many pits, slightly smaller than those of the maxilla, are present in the anterior portion of the mandible. The left splenial is *in situ*, covering the dentary medially, and is confluent with the symphysis line in ventral view (van den Heever 1994). The right splenial has been displaced over the left horizontal ramus. The Meckelian canal, represented by two shallow furrows separated by a thin ridge, is present on the anterior border of the right dentary. On the left side the postdentary bones have also been displaced. A posteriorly positioned bone following the angle of the dentary is interpreted as the posterior portion of the splenial, which was displaced backwards out of the Meckelian canal (Text-fig. 2A). Below the coronoid process there is a strip of bone representing the surangular and the most dorsal portion of the reflected lamina of the angular. The posterior portion of the surangular, exposed in medial view (Text-fig. 2B), exhibits a tall and smooth surface that is directed posteriorly and ventrally.

The upper dentition comprises six incisors, one precanine, a large canine, and nine postcanines on either side. The incisors are cylindrical and serrations are present on three of the teeth. The third and fourth incisors are the largest, although those of the left side are notably larger than those on the right. The fifth and sixth incisors appear to be smaller, but are incompletely preserved. On both sides the precanine is preserved only as a small distal tip emerging immediately in front of the canine. The canine is long and extends to the level of the ventral margin of the mandible (Text-fig. 2A). It is slightly more posteriorly curved than the canine of NM QR2908 and show serrations on the posterior margin. A diastema is present between the canine and the first postcanine. All postcanines comprise a single cone that is laterally convex. The third left postcanine, which is in the process of eruption, has marked serrations on its anterior and posterior margins.

DISCUSSION

For a long time the majority of large therocephalians known from the *Tapinocephalus* and *Pristerognathus* AZs (both = *Tapinocephalus* Zone of older literature) were included in the family Pristerognathidae (e.g. Boonstra 1954*a*, 1969; Haughton and Brink 1954; Romer 1956; Watson and Romer 1956; Rubidge *et al.* 1983; Hopson and Barghusen 1986). In an extensive taxonomic revision of early therocephalians, van den Heever (1987) recognized two valid families, the Lycosuchidae and the Scylacosauridae, and specified the priority of the latter name over the extensively used Pristerognathidae. Features observed in NM QR2908 and NM QR2910, such as the presence of more than five incisors, numerous upper postcanines and the presence of teeth on the pterygoid boss, indicate that these specimens are members of the Scylacosauridae. In addition, other characters typical of scylacosaurids, such as a long snout, the presence of the crista choanalis, and the absence of teeth on the transverse process of the pterygoid, are also observed in NM QR2910.

The taxonomic revision of early therocephalians undertaken by van den Heever (1987) involved first-hand study of all the relevant material and resulted in a noteworthy reduction of recognized taxa. Thus, the 53 previously recognized species were reduced to eight valid species (a taxonomic reduction of 85 per cent). As demonstrated by van den Heever (1987), a large number of the named species were based on inadequate and poorly preserved type specimens from which it is impossible to recognise diagnostic features. From that revision, six valid species of Scylacosauridae, *Alopecodon priscus*, *Glanosuchus macrops*, *Ictidosaurus angusticeps*, *Pardosuchus whaitsi*, *Pristerognathus polyodon* and *Scylacosaurus sclateri*; and two of Lycosuchidae, *Lycosuchus vanderrieti* and *L. keyseri* sp. nov., were recognized. However, *L. keyseri* was never formally named and the only specimen included in the species was later referred to as lycosuchid skull (van den Heever 1994). Other species that seem to be clearly different and not included here in any family are *Simorhinella baini*, characterized by an extremely short and massive snout (Mendrez 1975, fig. 3), *Crapartinella croucheri*, the only therocephalian (and indeed eutheriodont) with vomerine teeth (Mendrez 1975, fig. 4), and *Blattoidealestes gracilis*, representing the oldest record of multicusped postcanines among theriodonts (Boonstra 1954*b*). These species are each represented by a single specimen from the *Tapinocephalus* AZ (Boonstra 1954*b*; Mendrez 1975).

Features used for the taxonomic distinction of scylacosaurid species by van den Heever (1987) were the number of incisors and precanines. The presence of six incisors, the absence of precanines, and the small skull size of NM QR2908 indicate that it is a juvenile *Glanosuchus macrops*. This species is the most abundant basal therocephalian, being represented by at least 29 specimens (van den Heever 1987) and, therefore, represents one of the best known scylacosaurids (van den Heever 1994). The only

difference in the dentition between NM QR2908 and NM QR2910 is the presence of one precanine in the latter, a feature confirmed through CAT scan (Text-fig. 3), and thus NM QR2910 can be assigned to *Ictidosaurus angusticeps* (van den Heever 1987). The two specimens recognized by van den Heever (1987) as members of this species (the holotype SAM-PK-630 and SAM-PK-11957) comprise only weathered anterior portions of the snout with the anterior part of the mandible in occlusion. For that reason, contrary to the condition in *G. macrops*, the cranial anatomy of *I. angusticeps* is practically unknown, and NMQR 2910, although poorly preserved, can be regarded as the best representative cranial material of the latter species.

Therocephalian diversification

Therocephalia is a remarkably heterogeneous taxon, considered as the monophyletic sister group of cynodonts by most recent therapsid workers (e.g. Hopson and Barghusen 1986; Sidor and Hopson 1998; Rubidge and Sidor 2001; Sidor 2003). Recent phylogenetic analyses by Botha *et al.* (2007) and Abdala (2007), however, suggest that therocephalians are paraphyletic, and that the whaitsiid

Theriognathus is the sister taxon of cynodonts, as previously proposed by Kemp (1972).

The oldest records of therocephalians are the two scylacosaurids from the *Eodicynodon* AZ of the Karoo Basin described here. Among Russian faunas, the oldest known therocephalian is also a scylacosaurid, *Porosteognathus efremovi*, from the Isheevo assemblage, which is usually considered younger than the *Eodicynodon* AZ (Battail 2000; Battail and Surkov 2000; Golubev 2005).

Only Lycosuchidae and Scylacosauridae are represented in the overlying *Tapinocephalus* AZ of the Karoo Basin, where the first major pulse of therocephalian diversification occurs (Table 1). This diversity is abruptly reduced in the following *Pristerognathus* AZ, in what seems to be a transitional fauna for therocephalians. This assemblage zone has produced remains of the last representative of the Scylacosauridae in the Karoo and the first record of the problematic Scaloposauria (= basal Baurioidea of Hopson and Barghusen 1986). The Russian taxon *Hexacynodon*, recorded among the fauna of the end-Permian *Archosaurus rossicus* Assemblage (Table 2), was considered recently as a scylacosaurid (Battail and Surkov 2000) but van den Heever (1994) demonstrated that the taxon is not a member of this family. *Hofmeyria* and representatives of Scaloposauria are recorded in the
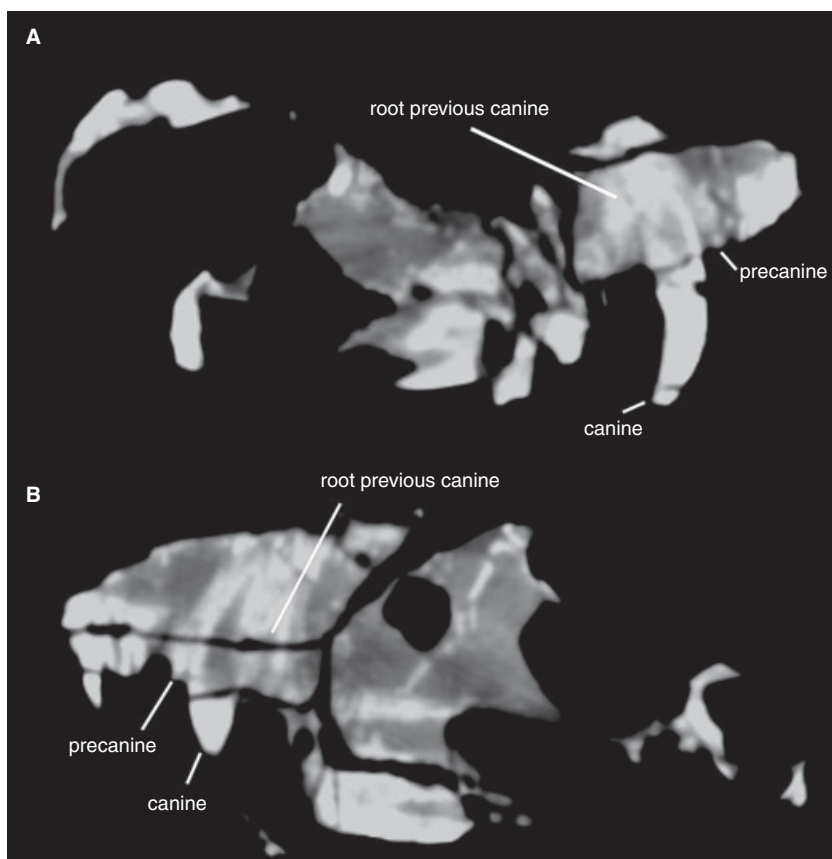
TEXT-FIG. 3. *Ictidosaurus angusticeps*, NM QR2910. CAT scans showing parasagittal sections of A, right side and B, left side of the snout.

TABLE 1. Therocephalian taxa in the Permian–Triassic assemblage zones (AZ) of the Karoo Basin. Taxonomic list modified after Rubidge *et al.* (1995).

TRIASSIC
Cynognathus AZ (Olenekian–Anisian)
    1. *Bauria cynops*
    2. *Microgomphodon oligocynus*[6]
Lystrosaurus AZ (Induan)
    1. *Ericiolacerta parva*
    2. *Ictidosuchoides longiceps*[5] S
    3. *Moschorhinus kitchingi*
    4. *Olivierosuchus parringtoni*
    5. *Regisaurus jacobi*
    6. *Scaloposaurus constrictus* S
    7. *Tetracynodon darti* S
    8. *Zorillodontops gracilis* S
PERMIAN
Dicynodon AZ (Changhsingian)
    1. *Akidnognathus parvus*
    2. *Cerdops burgheri*
    3. *Homodontosaurus kitchingi*[4] S
    4. *Ictidosuchoides longiceps*[3] S
    5. *Ictidosuchops intermedius* S
    6. *Lycideops longiceps*
    7. *Moschorhinus kitchingi*
    8. *Nanictidops kitchingi* S
    9. *Promoschorhynchus platyrhinus*
    10. *Scaloporhinus angulorugatus* S
    11. *Scaloposuchus rubidgei* S
    12. *Tetracynodon tenuis* S
    13. *Theriognathus microps*
Cistecephalus AZ (Wuchiapingian)
    1. *Akidnognathus parvus*
    2. *Euchambersia mirabilis*
    3. *Hofmeyria atavus*
    4. *Ictidosuchoides longiceps* S
    5. *Ictidosuchops intermedius*[2] S
    6. *Mirotenthes digitipes*
Tropidostoma AZ (Wuchiapingian)
    1. *Choerosaurus dejageri* S
    2. *Hofmeyria atavus*
    3. *Ictidostoma hemburyi*[1] S
    4. *Ictidosuchoides longiceps* S
    5. *Ictidosuchops intermedius* S
    6. *Ictidosuchus primaevus* S
Pristerognathus AZ (Capitanian)
    1. *Ictidosuchoides longiceps* S
    2. *Pristerognathus polyodon*
Tapinocephalus AZ (Capitanian)
    1. *Alopecodon priscus*
    2. *Blattoidealestes gracilis*
    3. *Crapartinella croucheri*
    4. *Glanosuchus macrops*
    5. *Ictidosaurus angusticeps*
    6. *Lycosuchus vanderrieti*
    7. *Pardosuchus whaitsi*
    8. *Pristerognathus polyodon*

TABLE 1. Continued.

    9. *Scylacosaurus sclateri*
    10. *Simorhinella baini*
Eodicynodon AZ (Wordian)
    1. *Glanosuchus macrops*
    2. *Ictidosaurus angusticeps*

[1]One of the localities quoted by Kitching (1977) with individuals of this taxon have exposures of levels corresponding to the *Cistecephalus* and *Dicynodon* AZs; [2]Kitching (1977) did not report this species in the *Cistecephalus* AZ; [3]Kitching (1977) did not report this species in the *Dicynodon* AZ; [4]some localities quoted by Kitching (1977) with individuals of this species have exposures of levels corresponding to the *Cistecephalus* and *Dicynodon* AZs; [5]location in the *Lystrosaurus* AZ after Smith and Botha (2005) and Botha and Smith (2006); [6]this species probably includes *Sesamodon browni* and *Herpetogale marsupialis* (Abdala, pers. obs.); S, basal Scaloposauria (i.e. Ictidosuchoidea; Brink 1965): most of the representatives of the group need taxonomic revision; therefore, their status as a valid taxon is uncertain. Age stages for assemblage zones after Rubidge (2005).

successive *Tropidostoma* and *Cistecephalus* AZs of the Karoo (Nicholas 2007), whereas the bizarre *Euchambersia* is also represented in the latter zone. A second major pulse of diversity occurs in the *Dicynodon* AZ, although it is difficult to give a precise number of taxa represented as seven of the 13 therocephalian recorded from this AZ are members of the Scaloposauria (Table 1), a group that is in need of taxonomic revision. At least three lineages of therocephalians are represented in *Dicynodon* AZ times (Hopson and Barghusen 1986): (1) Euchambersiidae, including *Moschorhinus* from South Africa and *Annatherapsidus* from Russia; (2) Whaitsiidae, represented by *Theriognathus*, which is abundant in the Karoo and is also present in the Kawinga Formation of Tanzania (Abdala and Allinson 2006), and by the Russian *Moschowhaitsia*; and (3) basal representatives of Baurioidea (i.e. Scaloposauria). Faunas from the end of the Permian in Russia include only one representative of Scaloposauria recorded in the Vyazniki Assemblage, whereas this group is particularly abundant in the fauna of the Kotelnich Subassemblage (Table 2), which is more likely correlated with the *Pristerognathus* AZ of South Africa (Golubev 2005).

The Permian/Triassic extinction event greatly reduced the diversity of therapsids. The real impact of the extinction event on therocephalian diversity is downplayed by the fact that most of therocephalians recorded in the faunas above and below the Permian/Triassic boundary are members of the Scaloposauria. Seven taxa, most of which are of small to medium size, are represented in the Lower Triassic *Lystrosaurus* AZ. Three of them, *Moschorhinus*, *Ictidosuchoides* and *Tetracynodon*, are the only therocephalians that crossed the P/T boundary (Smith and Botha 2005; Botha and Smith 2006). It is important to note that

the last genus is represented by only three small specimens, one from the Late Permian (Broom and Robinson 1948) and two from the Early Triassic (Sigogneau 1963; Damiani *et al.* 2004). These specimens are juveniles, which make it difficult to establish an unequivocal taxonomic identity for them. Early Triassic therocephalians are also known from Antarctica, where they are represented by the advanced baurioid *Ericiolacerta*, the very small *Pedaeosaurus* (differs from *Ericiolacerta* in the presence of a pineal foramen), and also the small, probable scaloposaurid, *Rhigosaurus* (Colbert and Kitching 1981). From the Jiucaiyuan Formation in north-western China there is *Urumchia*, a therocephalian that is closely related to the South African *Regisaurus* (Sun 1989; Sun *et al.* 1992). A possible scaloposaurid, *Yikezhaogia*, is known from the Lower Ermaying Formation in Mongolia (Li 1984). Finally, remains of a scaloposaurid were recovered from a borehole in the Russian locality of Sredyaya Makarikha, which corresponds to the Vetlugian Supergorizont (Table 2).

Ultimately, therocephalian diversity in the upper Beaufort Group of the Karoo Basin is reduced to the herbivorous Bauriidae, which is probably represented by two taxa in the *Cynognathus* AZ (FA personal data; see Table 1). This group is also known from the Omingonde fauna of Namibia (Keyser 1973), which is coeval with the *Cynognathus* AZ (Abdala *et al.* 2005). Representatives of this family are also known from the Middle Triassic of Russia (see Table 2) and the Lower and Middle Triassic of China (e.g. *Traversodontoides*: Sun 1989; Sun *et al.* 1992). After this decline at the beginning of the Middle Triassic, therocephalians became extinct in the Ladinian.

The early evolution and diversification of therapsids

The oldest record of therapsids in the *Eodicynodon* AZ is already represented by a fairly diverse fauna with members of dinocephalians, basal anomodonts, dicynodonts, gorgonopsians, and therocephalians (Rubidge 1995; Kemp 2005; Table 3). A high degree of diversity is also present in the oldest therapsid faunas from Russia. Disregarding the Roadian record of indeterminable therapsids (Modesto and Rybczynski 2000), the Wordian faunas from Russia comprise at least 16 different species of therapsids (Table 3), which include dinocephalians (represented by both carnivorous Anteosauridae and herbivorous Estemmenosuchidae), the anomodont *Otsheria*, and the biarmosuchian *Biarmosuchus* (Battail 2000; Modesto and Rybczynski 2000; Golubev 2005). Additional therapsid groups are represented in these early Russian faunas (e.g. *Phthinosuchus*, *Phthinosaurus*, Niaftasuchidae) but their phylogenetic placement is problematic (Kemp 2005).

TABLE 2. Therocephalian taxa in the Permian–Triassic Russian faunas. Faunal zonation follows Golubev (2000, 2005) and Sennikov and Golubev (2006).

MIDDLE TRIASSIC
Eryosuchus Assemblage (Donguzian Substage;
  Anisian–Lower Ladinian)
  1. *Dongusaurus schepetovi*
  2. *Nothogomphodon danilovi*
LOWER TRIASSIC
Vetlugian Stage (Induan–Lower Olenekian)
  1. *Scalopognathus multituberculatus*
PERMIAN
Archosaurus rossicus Assemblage Zone (= Vyazniki Assemblage;
  uppermost Changhsingian)
  1. *Malasaurus germanus* S
  2. *Hexacynodon purlinensis*
  3. *Moschowhaitsia vjuschkovi*
  4. Whaitsiidae indet.
Scutosaurus karpinskii Assemblage Zone (Sokolki Subassemblage;
  Changhsingian)
  1. *Anatherapsidus petri*
  2. *Chthonosaurus velocidens*
Proelginia permiana Assemblage Zone (Ilyinskoe Subassemblage;
  Lower and Upper Wuchiapingian)
  1. *Scylacosuchus orenburgensis*
Deltavjatia vjatkensis Assemblage Zone (Kotelnich
  Subassemblage; Lower Wuchiapingian)
  1. *Chlynovia serridentatus* S
  2. *Karenites ornamentatus* S
  3. *Kotelcephalon viatkensis*
  4. *Perplexisaurus foveatus* S
  5. *Scalopodon tenuisfrons* S
  6. *Scalopodontes kotelnichi* S
  7. *Viatkosuchus sumini*
Ulemosaurus svijagensis Assemblage Zone (Isheevo
  Subassemblage; Malaya Kinel Subassemblage; Upper
  Wordian–Capitanian)
  1. *Porosteognathus efremovi*

S denotes basal Scaloposauria (i.e. Ictidosuchoidea; Brink 1965): most of the representatives of the group need taxonomic revision; therefore, their status as a valid taxon is uncertain. Age stages for the assemblages after Golubev (2005) and Sennikov and Golubev (2006).

The Xidagou fauna from China has yielded remains of two dinocephalians, *Stenocybus* and *Sinophoneus*, with the latter assigned to the Anteosauridae (Li 2001), and the problematic *Biseridens*, which has been assigned to both Eotitanosuchia and Anomodontia (Li and Cheng 1997; Battail 2000; Li 2001). Of these earliest therapsid records, the South African fauna is indeed remarkably heterogeneous. The *Eodicynodon* AZ is usually considered to be one of the oldest faunas with therapsids because of the presence of primitive anomodonts and dinocephalians (Lucas 2006). The record of theriodonts (gorgonopsians and therocephalians) and dicynodonts in the South

African fauna, which are absent from the Russian and Chinese assemblages, allows for an alternative interpretation of the *Eodicynodon* AZ as being somewhat younger than the Russian and Chinese faunas. This seems to be reinforced by the record of caseid 'pelycosaurs' in the Mezen assemblage of Russia (Golubev 2000, 2005). In addition, varanopid 'pelycosaurs' are abundant in the Mezen assemblage (Golubev 2000, 2005), but this group has also been recovered from the *Tapinocephalus* AZ of South Africa (Modesto *et al.* 2001; Botha-Brink and Modesto 2007).

The Chinese fauna shows more similarity with the Russian assemblage because of the presence of dissorophids and bolosaurids, and they are probably of similar age (Li 2001). If this interpretation is correct (see also Golubev 2005), then *Patranomodon* and *Australosyodon* of the *Eodicynodon* AZ would be hold-overs, as in the case of *Anomocephalus*, the most basal anomodont (Modesto and Rubidge 2000; Fröbisch 2007) known from the *Tapinocephalus* AZ (Text-fig. 4).

Considering the early record of therapsids from a phylogenetic perspective (Rubidge and Sidor 2001), members of Therapsida, Eutherapsida, Neotherapsida, Theriodontia, and Eutheriodontia are already present in the oldest therapsid faunas (Text-fig. 4). In addition, groups such as dinocephalians (that suddenly became extinct in the Capitanian) and anomodonts (whose members, particularly dicynodonts, later comprise the most diverse Permian therapsids) are already in a first pulse of diversification at the end of Roadian–Wordian. The character of the Roadian land-vertebrate faunas from North America (e.g. from the Chickasha and San Angelo formations; Reisz and Laurin 2001, 2002; Lucas 2002, 2004, 2006) is remarkably different with respect to that of the oldest faunas from South Africa, Russia and China. One of the major differences is the lack of therapsids in the North American faunas. The only putative record of this group in North America is the problematic taxon *Tetraceratops* from Early Permian deposits of Texas, which is regarded as the oldest known therapsid by Laurin and Reisz (1996), but not by others (Sidor and Hopson 1998; Conrad and Sidor 2001; Rubidge and Sidor 2001). The lack of a definitive therapsid record in Roadian and older faunas and the first appearance of this group at the end of the Roadian-Wordian with an already remarkable diversity can be interpreted as evidence supporting a gap in the fossil record (Lucas 2004), or at least in the record of therapsids, when an important segment of the initial evolution of this group occurred.

The explosive origin and early diversification of therapsids in the fossil record has similarities with patterns such as those of metazoans in the Cambrian, early tetrapods in the Late Devonian, and modern birds and placental mammals after the end of the Cretaceous (Cooper and

TABLE 3. Roadian–Wordian therapsids.

South Africa
  Tapinocaninus pamelae
  Australosyodon nyaphuli
  Patranomodon nyaphulii
  Eodicynodon oosthuizeni
  '*Eodicynodon*' *oelofseni*
  Glanosuchus macrops
  Ictidosaurus angusticeps
  Gorgonopsia
Russia
  Mezen Assemblage
    Niaftasuchus zekkeli
    Nikkasaurus tatarinovi
    Reiszia gubini
    Reiszia tippula
    '*Biarmosuchus*' *tagax*
  Ocher Assemblage
    Estemmenosuchus uralensis
    Estemmenosuchus mirabilis
    Molybdopygus arcanus
    Archaeosyodon praeventor
    Eotitanosuchus olsoni
    Biarmosuchus tener
    Otsheria netzvetajevi
    Parabradysaurus udmurticus
    Microsyodon orlovi
    Phtinosaurus borissiaki
    Kamagorgon ulanovi
China
  Stenocybus acidentatus
  Sinophoneus yumenensis
  Biseridens qilianicus

Fortey 1998; Ruta *et al.* 2006; Wible *et al.* 2007). Some of these patterns were explained in different terms by the phylogenetic fuse model (Cooper and Fortey 1998; Bininda-Emonds *et al.* 2007). However, the inability of molecular data to establish the diverging time of therapsids is a major drawback as this limits interpretation of the origin and early radiation of therapsids to only the fossil record and the interpreted cladistic relationships. Two possible interpretations for the early record of therapsids can be explored regarding most of the proposed phylogenetic hypotheses of therapsid evolution (contrast for example Hopson and Barghusen 1986; Kemp 1988; Rowe 1988; Sidor and Hopson 1998; Rubidge and Sidor 2001). If *Tetraceratops* is indeed a basal therapsid, approximately 30 Ma separates the oldest records of sphenacodontids (the sister group of therapsids) and therapsids. This 30-Ma interval can be interpreted as the phylogenetic 'long fuse' (Kemp 2006, p. 1239), followed by the explosion of diversity at the end of Roadian–Wordian (occurring within only 5–6 myr; Text-fig. 4, grey bar A). This outbreak of diversity at the end of the Roadian–
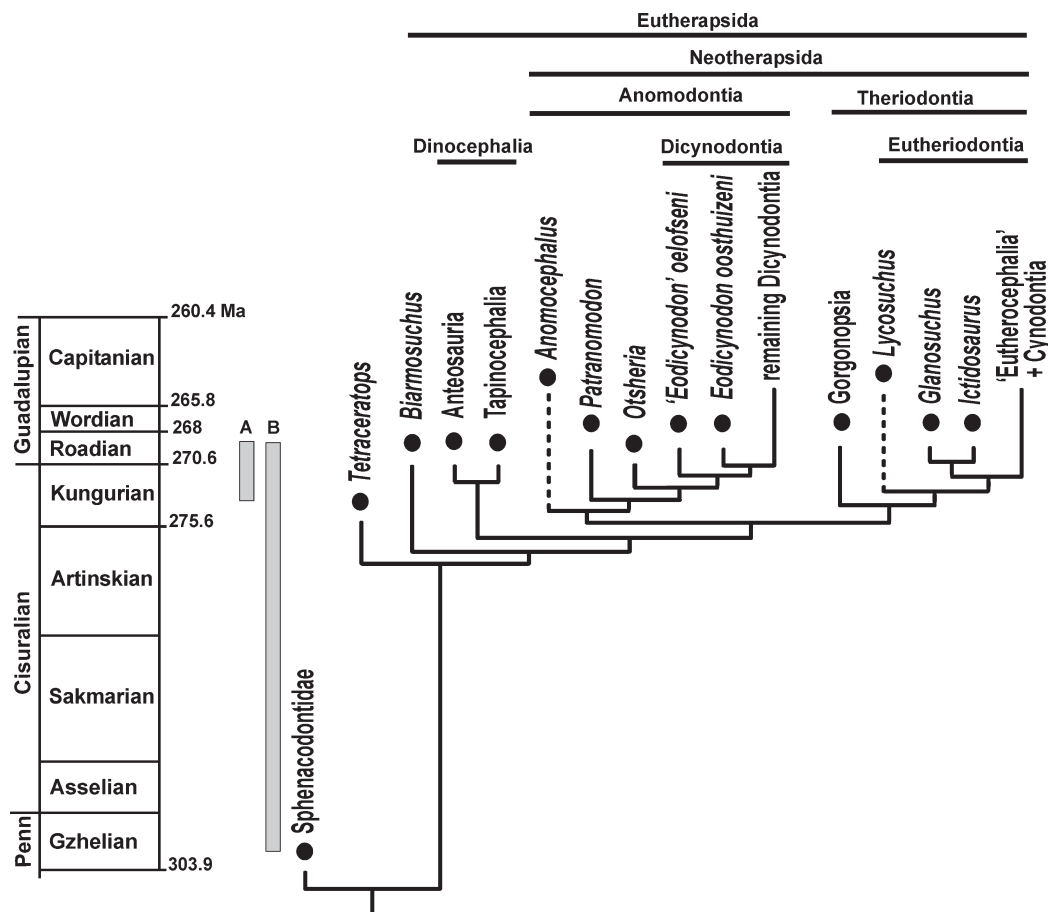
TEXT-FIG. 4. Cladogram showing therapsid relationships and earliest records of the groups (filled circles). These records correspond to the therapsids recovered from the *Eodicynodon* AZ, South Africa; the Mezen and Ocher assemblages, Russia; and the Xidagou fauna, China. Dashed lines in the branches of *Lycosuchus* and *Anomocephalus* indicate that the taxa are not recorded in the Wordian, but their basal placement in the phylogeny of Eutheriodontia and Anomodontia, respectively, suggests that they should be present at that age. *Biarmosuchus* is the oldest (and the only Wordian) representative of the Biarmosuchia. Phylogenetic relationships of the taxa follow Rubidge and Sidor (2001) except for Anomodontia, which follows Modesto and Rubidge (2000) and Modesto *et al.* (2003), and the paraphyly of 'Therocephalia', which follows Abdala (2007). Grey bars indicate temporal gap without record of therapsids including (A) and excluding (B) *Tetraceratops* as a basal therapsid (see text). Time scale from Gradstein and Ogg (2004).

Wordian strongly suggests that rapid evolution (i.e. character acquisition) occurred in therapsids at the end of the Kungurian and in the Roadian.

We have a more uncertain interpretation if *Tetraceratops* were not a therapsid. A 35-Ma interval separates sphenacodontids from the Wordian therapsid groups (Text-fig. 4, grey bar B), and in this context it is possible to assume that different lineages of therapsids arose during that interval with no known fossil record. Because the earliest therapsids were relatively large animals, the absence of ancestral therapsids (and of any representative of therapsid groups first recorded in the Wordian) during this 35-Ma interval cannot be explained by small and fragile-boned organisms, as was suggested by Cooper and Fortey (1998) for cases of Mesozoic representatives of modern birds and placental mammals (but see Fara and

Benton 2000 and Fountaine *et al.* 2005). A possible explanation could be the lack of recognizable therapsid autapomorphies in the skeletons of older forms (Cooper and Fortey 1998), or the lack of preservation of adequate environments where therapsids may have lived (Kemp 2006).

We should mention that while there is a 35-Ma-long fuse period between the first sphenacodontid and the first therapsid, Sidor and Hopson (1998) have pointed out that the accumulation of therapsid apomorphies did not necessarily occur over the entire 35 Ma, but may have happened in a shorter period. As previously mentioned, the early diversification of therapsids leaves room for two interpretations: (1) a rapid process of apomorphy accumulation in the main therapsid lineages, or (2) the less conclusive possibility of a gradual acquisition of apomor-

phies in different therapsid lineages during a time interval of 35 Ma or less. A decision might be possible if therapsid fossils were found among the already known Early Permian faunas, or if new therapsid-bearing rocks older than Late Roadian were discovered. In a phylogenetic context, the initial outbreak of diversity in therapsids could be mitigated if the sister-group relationship between Dinocephalia and Anomodontia were correct (King 1988) because this would decrease the number of main therapsid lineages represented at the end of Roadian–Wordian. The initial evolutionary pattern of therapsids could also change if this group were shown to be paraphyletic, as recently suggested by Ivakhnenko (2002). However, this hypothesis is strongly contradicted by cladistic analyses (Sidor and Hopson 1998; Rubidge and Sidor 2001).

A gradual evolution model has been generally assumed to be the best to explain synapsid phylogeny and its fossil record (Kemp 1985; Hopson 1994; Sidor and Hopson 1998). However, when confronted with the explosive diversification of most of the Permian therapsid lineages, it does not seem to be accurate. The apparently 'simultaneous' origin of these dissimilar groups of therapsids is an artefact of an incomplete fossil record or of imprecision of the time scale. One of the possibilities explored here, however, suggests that the early evolution of therapsid diversity resulted from the acquisition of many characters over a relatively short period of time. Taking into account the phylogeny of Sidor and Hopson (1998), which is the most extensive in relation to the groups of interest in this study, at least 29 unambiguous synapomorphies were acquired by monophyletic groups appearing at the end of Roadian–Wordian following the spine of their cladogram (i.e. Eutherapsida, Node 7, Theriodontia and Eutheriodontia; see Sidor and Hopson 1998, fig. 2), plus another 21 unambiguous synapomorphies taking into account each main lineage first recorded in that age (i.e. Biarmosuchia, Eotitanosuchia, Dinocephalia, Anomodontia, Gorgonopsia, and Therocephalia). These 50 synapomorphies, acquired in 5–6 myr, following the 'long fuse model', can be compared with the 36 unambiguous synapomorphies of therapsids supposedly accumulated, if we follow the hypothesis of the accumulation of synapomorphies in the maximum possible time, over a 30-myr period (Sidor and Hopson 1998). The second interpretation presented is largely based on negative evidence: the main lineages of therapsids were evolving gradually during 35 myr but fossils have yet to be discovered. In summary, nearly all the therapsid diversity (Biarmosuchia, Dinocephalia, Anomodontia, Gorgonopsia, and basal Therocephalia) is suddenly recorded at the end of Roadian–Wordian. The only main lineages absent, 'Eutherocephalia' and Cynodontia, will be first represented at the end of the Capitanian and beginning of the Lopingian, when part of the original therapsid diversity was already diminished by the sudden extinction of dinocephalians in the Capitanian.

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