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EUNOTOSAURUS AFRICANUS AND THE GONDWANAN ANCESTRY OF ANAPSID REPTILES

by

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ABSTRACT

Phylogenetic analyses confirm that the turtle-like Late Permian reptile *Eunotosaurus africanus* is a parareptile (*sensu* deBraga & Reisz 1996) and identify it as the sister taxon of Procolophonomorpha. The tree topology for anapsid reptiles suggests that a distribution in Gondwanan Pangaea is ancestral for anapsids (*sensu* Gauthier, Kluge & Rowe 1988). Minimum divergence times (MDTs) determined from stratigraphic calibration of anapsid phylogeny suggest that anapsids were diversifying in Early Permian Gondwana as early as the Sakmarian. MDTs also support the idea that a preservational bias was operating on terrestrial vertebrates in Gondwana prior to the onset of continental sedimentation in the Late Permian.

KEYWORDS: Anapsida, *Eunotosaurus*, Gondwana, palaeobiogeography, parareptiles

INTRODUCTION

The Permian reptile *Eunotosaurus africanus* was described over a century ago by Seeley (1892) on the basis of a partial skeleton from a locality near Beaufort West, South Africa. Although he recognised the turtle-like nature of the vertebrae and ribs of his specimen, Seeley (1892) concluded tentatively that *Eunotosaurus* was a close relative of the mesosaurs. Watson (1914), having at his disposal an additional four specimens, suggested that *Eunotosaurus* was a suitable turtle ancestor. Since those early studies, further skeletons of this enigmatic reptile have been collected, although one with a complete skull was recovered only twenty years ago. That specimen allowed Keyser & Gow (1981) to concur with Cox's (1969) assessment that *Eunotosaurus* was a very basal reptile that was related only distantly to turtles. In the most recent appraisal of *Eunotosaurus*, Gow (1997a) argued that it belonged to a group now known formally as Parareptilia (*sensu* deBraga & Reisz 1996). Furthermore, he suggested that *Eunotosaurus* was related most closely to the millerettids among parareptiles. Although Gow (1997a) used cladistic terminology, he did not conduct a phylogenetic analysis and accordingly could not evaluate his hypothesis in a rigorous manner. Such an analysis is crucial, as it would have allowed a more comprehensive assessment of his conclusions by other workers.

The hypothesis that *Eunotosaurus* is a parareptile related most closely to millerettids can be examined by using information from cladistic analyses of early reptiles that are available in the literature. Two recent studies have focused on the interrelationships of parareptiles (Laurin & Reisz 1995; deBraga & Reisz 1996). Data from Gow (1997a) and Gow & de Klerk (1997), the two most recent descriptions of *Eunotosaurus*, can be incorporated into the data matrices of those phylogenetic studies and analyzed using the same phylogenetic programs employed by Laurin & Reisz (1995) and deBraga & Reisz (1996). This procedure was used by Modesto (1999b) for mesosaurs, who identified those early aquatic amniotes as the closest relatives of parareptiles within the clade Anapsida (*sensu* Gauthier *et al.* 1988; see Modesto 1999b for a discussion of the phylogenetic taxonomy of 'Anapsida' and 'Parareptilia'). Bearing in mind that mesosaurs, *Eunotosaurus*, and the latter's possibly closest relatives, millerettids, are all restricted to Gondwana, the resultant phylogenetic tree(s) can be used to examine the hypothesis that these reptiles originated in that region of Pangaea. It seems likely, given the basal phylogenetic positions of these taxa within Anapsida, that they are descended from an anapsid ancestor that dispersed into Gondwanan Pangaea from Euramerica during the Permo-Carboniferous.

MATERIALS AND METHODS

Anatomical descriptions from the literature (Gow 1997a; Gow & de Klerk 1997) were used to code *Eunotosaurus africanus* for the phylogenetic characters utilized by Laurin & Reisz (1995) and deBraga & Reisz (1996). The descriptions published by Gow (1997a) and by Gow & de Klerk (1997) were verified by personal examination of M777, in the collections of the Council for Geosciences, Pretoria and a latex cast of AM 5999, reposited in the Albany Museum, Grahamstown. Specimens PK4328, PK-K7670, PK-K7909, PK-K7910 and PK11954 in the South African Museum, Cape Town were examined during the course of this study. The work of Cox (1969) was used to code for several characters of the appendicular skeleton. Modified data matrices from Laurin & Reisz (1995) and deBraga & Reisz (1996)

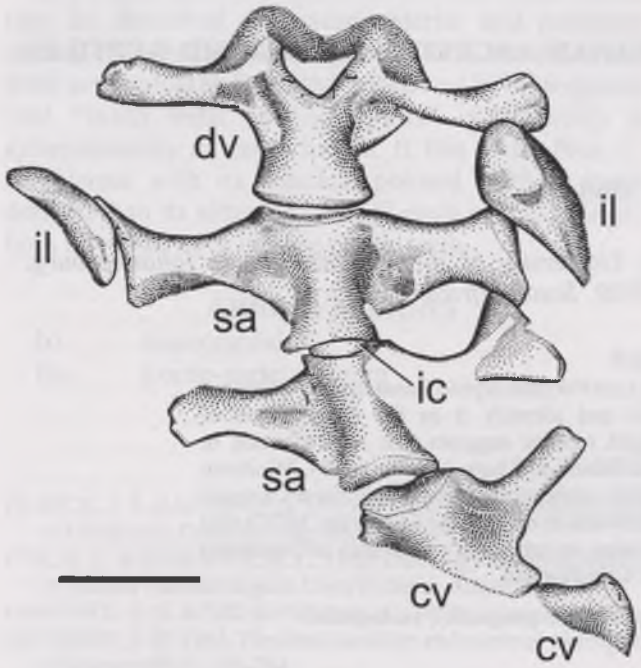


Figure 1. Ventral view of the pelvic region of *Eunotosaurus africanus*, showing the two sacral vertebrae, their ribs, and neighbouring elements. Drawn from a latex cast of AM 5999. Abbreviations: **cv**, caudal vertebra; **dv**, dorsal vertebra; **ic**, intercentrum; **il**, ilium; **sa**, sacral vertebra. Scale bar equals 5 mm.

were constructed in MacClade 3.07 (Maddison & Maddison 1997) and then evaluated (separately) using PAUP 3.1 (Swofford 1993) following the parameters used by those authors. The exact modifications made to both data matrices, including the character codings for *Eunotosaurus*, are outlined in the appendix.

RESULTS

The most recent anatomical descriptions of *Eunotosaurus africanus* (Gow 1997a; Gow & de Klerk 1997) were found to be accurate in all details save two. Gow & de Klerk (1997) concurred with Cox (1969) that only a single sacral vertebra was present, but examination of a latex cast of AM 5999 indicates that two sacral vertebrae are present (Figure 1): what was regarded by Gow & de Klerk (1997) as the first caudal vertebra bears ribs that are expanded distally and differ from the slender rib of the succeeding caudal vertebra and the tapering first caudal ribs of other early reptiles. The left rib of what is interpreted here as being the second sacral vertebra of AM 5999 is even marginally broader distally than either rib of the preceeding one (*i.e.*, the first sacral), although, because of foreshortening in the angle of view, this is not apparent in Figure 1. Gow & de Klerk (1997) deduced that the ribs in question were caudal ribs because their distal ends did not meet those of the (first) sacral. That line of reasoning is difficult to believe because the ribs of the first and second sacral vertebrae of an adult skeleton of the basal parareptile *Milleretta* clearly do not meet laterally in the specimen illustration of Gow (1997b). Furthermore, the outline of the right second sacral rib of AM 5999 is not complete owing to loss of the matrix that preserves the anterior margin of the rib (Figure 1), and what can be determined from the left rib suggests that distally there could have been a narrow contact between the first and second sacral ribs. Such an organization for the sacral ribs is regarded to be a parareptilian apomorphy (Laurin & Reisz 1995). The other emendation is the observation that at least one intercentrum is preserved in AM 5999 (Figure 1), which confirms Cox's (1969) report that intercentra are present in this reptile (*contra* Gow 1997a).

In the most parsimonious trees of both analyses, *Eunotosaurus africanus* forms a clade with parareptiles that excludes millerettids. In the analysis that uses a modified version of the data matrix of Laurin & Reisz (1995), *Eunotosaurus* forms a sister group with Procolophonia within Parareptilia (Figure 2). This sister-group relationship is relatively robust, requiring 3 extra steps to collapse (*i.e.*, to make *Eunotosaurus* form a sister-group relationship with Parareptilia *sensu* deBraga & Reisz 1996). Three extra steps are also required for *Eunotosaurus* to become the sister taxon of Millerettidae. In the analysis that uses a modified version of the data matrix of deBraga & Reisz (1996), *Eunotosaurus* falls within Parareptilia and forms a clade with Procolophonomorpha (Figure 3); 2 additional steps are required to place *Eunotosaurus* into a sister-group relationship with millerettids, and 3 extra steps to exclude it from Parareptilia. It can be noted here that Procolophonomorpha Romer 1964, as defined phylogenetically by Lee (1995), is the senior synonym of Ankyramorpha deBraga & Reisz 1996.

The two resultant trees are mutually compatible. Although the data matrix of deBraga & Reisz (1996) incorporates three more parareptilian taxa (*Acleistorhinus pteroticus*, Lanthanosuchidae, and *Macroleter poezicus*) than that of Laurin & Reisz (1995), the topology of the tree shown in Figure 3 would be equivalent to that seen in Figure 2 if these taxa are removed. A composite tree of the anapsid phylogenies shown in Figures 2 and 3 is reproduced as a stratocladogram in Figure 4. Ghost lineages and taxa (Norell 1992) have been drafted to establish minimum divergence times (MDTs) for anapsid taxa. The implications of the MDTs are discussed in the following section.

DISCUSSION

The phylogenetic analyses confirm Gow's statement that *Eunotosaurus africanus* is 'a good parareptile' (Gow 1997a: 33). Much more interestingly, it identifies procolophonomorphs rather than millerettids as the closest relatives of *Eunotosaurus* within Parareptilia. The new topology has interesting implications for anapsid evolution. Two issues that will be addressed here include the early biogeography and biostratigraphy of anapsid reptiles. The former issue has received some minor attention in the literature (Milner 1993; Modesto & Rybczynski 2000), whereas the latter has come under scrutiny for Anapsida (*sensu lato*) in concert with

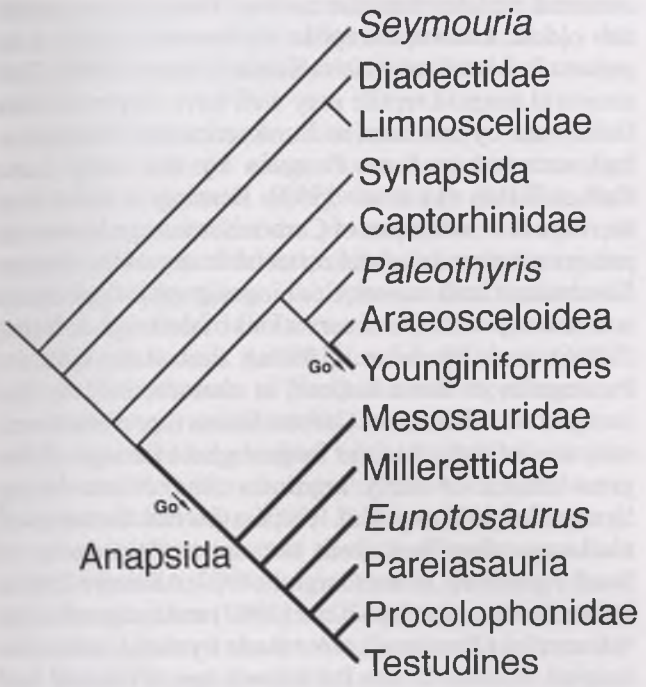


Figure 2. Most parsimonious resolution resulting from a PAUP analysis of a data matrix modified from Laurin & Reisz (1995). Thin branches indicate the taxon is present in Euramerican Pangaea, whereas thick branches signify a distribution in Gondwanan Pangaea. The arrows indicate dispersal events into Gondwana (**Go**) from Euramerica. A Gondwanan distribution is inferred to be ancestral for both Procolophonidae and Pareisauria based on phylogenies for these groups provided by Lee (1995, 1997). The palaeobiogeographical analysis here suggests that a Gondwanan distribution is ancestral for anapsids, but this tree does not include some Euramerican taxa seen in the succeeding figure.

recent phylogenetic work (Laurin & Reisz 1995; deBraga & Reisz 1996).

In a recent consideration of Palaeozoic tetrapod biogeography, Milner (1993) recognized a 'Mesosaurid Province' comprising the mesosaurs of Lower Permian South America and southern Africa. Milner's (1993) 'Mesosaurid Province' marks the earliest manifestation of endemism among anapsid reptiles ('parareptiles' of Gauthier *et al.* 1988). Following the systematic work of Ivakhnenko (1987), Milner (1993) regarded pareiasaurs and nyctiphruretids as having a cosmopolitan distribution in the Late Permian, and considered the contemporaneous lanthanosuchids and nycteroleterids as endemic groups of Euramerican Pangaea (although he viewed the latter two as anamniote taxa). Interestingly, Milner (1993) did not consider millerettids and *Eunotosaurus*, nor did he discuss the implications of their Gondwanan distributions for the idea of homogeneity among Late Permian amniote faunas.

Milner's (1993) biogeographic conclusions require some reconsideration in the wake of recent systematic work on anapsids. In contrast to Ivakhnenko's (1987) views, Lee (1995) regarded the Russian taxon *Nyctiphruretus ineptus* as the sole valid nyctiphruretid and identified the Gondwanan 'nyctiphruretids' (*Owenetta*, *Barasaurus*) of Ivakhnenko (1987) as basal procolophonoids. Nycteroleterids, comprising *Nycteroleter* and *Macroleter*, form a Russian clade, and thus represent, like the lanthanosuchids, a parareptilian group that was restricted to Euramerica (Lee 1995). More recently, Lee (1997) published a phylogeny for pareiasaurs in which the most basal members (*Bradysaurus*, *Embrithosaurus*) are Gondwanan taxa. Optimization of Gondwanan and Euramerican distributions of pareiasaurs onto Lee's phylogeny suggests strongly that pareiasaurs diversified initially in Gondwana and that northern Pangaea was colonised by more recently derived taxa on at least two separate occasions (Modesto & Rybczynski 2000). Other recent studies reveal the existence of a clade of early parareptiles, Acleistorhinidae, that was restricted to Early Permian North America (deBraga & Reisz 1996; Modesto 1999a). Collectively these revisions of

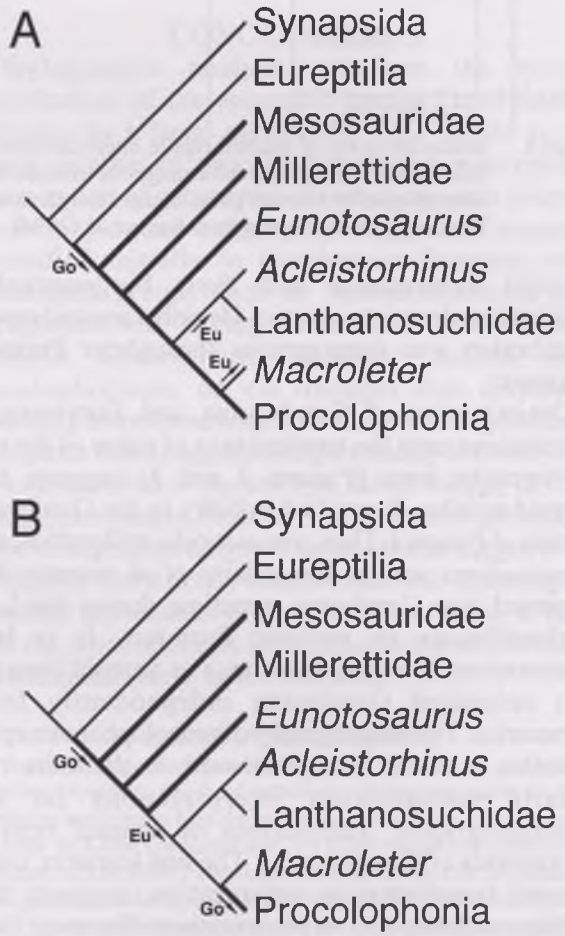


Figure 3. Most parsimonious resolution (MPR) resulting from a PAUP analysis of a data matrix modified from deBraga & Reisz (1996). Acleistorhinidae, Lanthanosuchidae and *Macroleter* are anapsid taxa in addition to those seen in the preceding figure. Procolophonia includes the terminal taxa Pareiasauria, Procolophonidae, and Testudines of the preceding figure. A, The MPR with distributions optimized using delayed transformation. B, The MPR optimized using accelerated transformation. As in the previous figure, thin and thick branches signify distributions in Euramerica and Gondwana, respectively. The arrows indicate dispersal events into Gondwana (**Go**) from Euramerica or into Euramerica (**Eu**) from Gondwana. The ancestral Gondwanan distribution inferred for Procolophonia is discussed in the text.

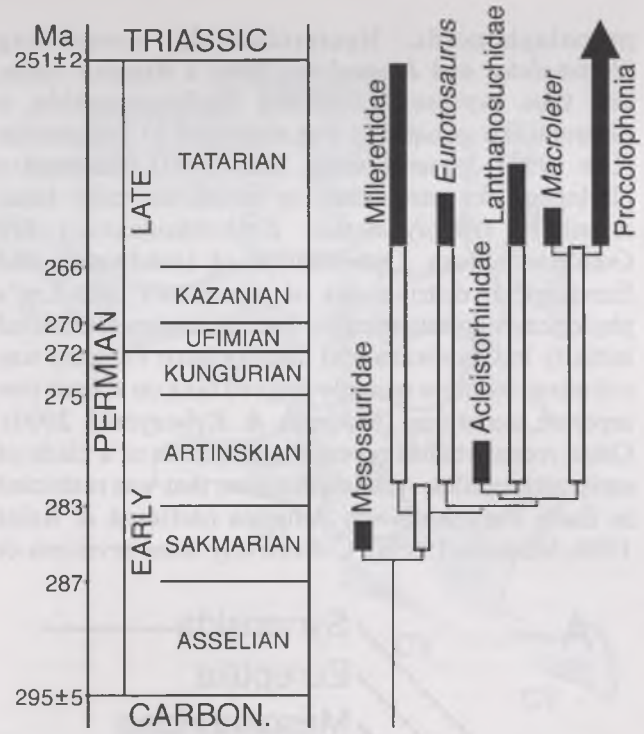


Figure 4. Stratocladogram of anapsid reptile interrelationships. Solid bars indicate stratigraphic ranges for terminal taxa, whereas open bars denote ghost lineages and ghost taxa. The time scale is adapted from Ross *et al.* (1994).

anapsid systematics and their biogeographic implications draw into question ideas that anapsid reptile distribution was homogenous throughout Permian Pangaea.

Optimization of Gondwanan and Euramerican distributions onto the terminal taxa of either of the two phylogenetic trees (Figures 2 and 3) suggests that anapsid reptiles diversified initially in the Gondwana portion of Pangaea. Thus, mesosaurids, millerettids, and *Eunotosaurus* are the descendants of an ancestor that dispersed into Gondwana sometime during the Late Carboniferous or earliest Permian. It is less parsimonious to regard these taxa as anapsid lineages that colonised Gondwana independently from Euramerica. The biogeography of procolophonomorphs, however, is not as straightforward, as there are two equally parsimonious interpretations for the palaeogeographic distributions of anapsid reptiles crownwards of *Eunotosaurus*. The first scenario, using delayed transformation optimization, suggests that lanthanosuchoids and nyctiphruretians dispersed from Gondwana to colonise Euramerica separately (Figure 3A); pareiasaurs and procolophonoids evolved in Gondwana because their recent common ancestor had arisen there. The second scenario, using accelerated transformation, suggests that the ancestral procolophonomorph dispersed from Gondwana into Euramerica, whereupon lanthanosuchoids, nyctiphruretians, and the ancestral procolophonian appeared, with the last then emigrating back into the former area from the latter, subsequently giving rise to procolophonoids and pareiasaurs (Figure 3B).

The primary dichotomy in reptilian evolution, the division into anapsid and eureptilian lineages, must have occurred no later than the earliest Westphalian, when the oldest known eureptile *Hylonomus lyelli* was present in what it now Nova Scotia (Carroll 1963). The ancestral anapsid reptile may well have dispersed into Gondwana by this time, as Euramerica and Gondwana had accreted to form Pangaea by the early Late Carboniferous (Li *et al.* 1993). Bearing in mind that there are few sediments of Carboniferous age known to preserve tetrapod skeletal material in any of the former Gondwanan land masses, this biogeographic hypothesis is consonant with the observations of deBraga & Reisz (1996) and Modesto (1999a) that Anapsida (= Parareptilia of those authors) is characterized by the conspicuous absence of Carboniferous representatives, and, accordingly, has the longest ghost lineage of the great clades of early amniotes (the others being Synapsida and Eureptilia). It is possible that the tetrapod trackways described from the upper Palaeozoic of South America (Cei and Gargiulo 1977; Aramayo 1993), reconsidered in part by Milner (1993) and assigned to his 'Mesosaurid Province', were made by early, unknown anapsid reptiles. Given the knowledge of manual and pedal morphology of mesosaurs that has been drawn from several excellent specimens (Modesto 1996, 1999b), it is unlikely that any of the known South American trackways represent terrestrial excursions of those aquatic reptiles.

Within Anapsida itself, the stratigraphic ranges of the constituent members are suggestive of an extensive, unrecorded tenancy in Gondwana for anapsid reptiles (Figure 4). Mesosaurs, restricted to the Sakmarian of southern Africa and eastern South America (Oelofsen & Araújo 1987), are the oldest known anapsid reptiles. The next oldest anapsids in Gondwana are *Eunotosaurus*, millerettids, pareiasaurs, and procolophonoids (Gow & Rubidge 1997), which appear in the *Tapinocephalus* Assemblage Zone of the Beaufort Group in South Africa (Smith & Keyser 1995). This terrestrial vertebrate biozone is either latest Kazanian or earliest Tatarian in age, so that there is a substantial temporal gap between the time that mesosaurs disappear and when parareptiles make their first appearance in Gondwana. It is in this interval during the Early Permian that the acleistorhinids are present in western Euramerica. Using Acleistorhinidae as the first appearance datum for Parareptilia, minimum divergence times suggest that at least four lineages of Late Permian parareptiles can trace their origins as far back as the Artinskian (Figure 4). Accordingly, the presence of two endemic Gondwanan lineages, Millerettidae and *Eunotosaurus*, can be extended well into the Early Permian. The extensive ghost lineages of these two taxa, together with information from the biogeographical analysis, suggest that millerettids and *Eunotosaurus* must have been present in Gondwana prior to Beaufort times, yet we have no record of these reptiles until well into the *Tapinocephalus* Assemblage Zone. Thus, the phylogeny and the biostratigraphy of anapsid reptiles provide support for the hypothesis that a preservational bias acted on terrestrial vertebrates in Early Permian and earliest Late Permian Gondwana.

This preservational bias was not alleviated until the onset of continental sedimentation represented by the Beaufort Group in South Africa (Modesto & Rubidge 2000).

Identification of *Eunotosaurus* as the procolophonomorph sister taxon suggests strongly, again using minimum divergence times (MDTs), that there were at least four parareptilian lineages in existence from the late Artinskian onwards during the Early Permian. Given the known distributions of parareptilian taxa, MDTs can be used to predict the presence of various parareptiles for given strata and regions. The absence of Early Permian specimens of *Eunotosaurus*, millerettids and other terrestrial vertebrates can be ascribed to the dearth of suitable continental deposits during this time in Gondwana (Modesto & Rubidge 2000). It is less straightforward, however, to account for the absence of lanthanosuchids in uppermost Lower Permian deposits. In Europe there appears to have been a hiatus in continental sedimentation between the Asselian (earliest Permian) and the Ufimian (earliest Late Permian), which accounts for the absence of lanthanosuchids in the Lower Permian of western Russia. Their absence in Lower Permian North American deposits might be taphonomic, or it may reflect a true restriction of lanthanosuchids to Eastern Euramerica. *Lanthanosuchus watsoni*, the first described species, has long been regarded as an aquatic form (*e.g.*, Watson 1954), although this assessment was based solely on its remarkably temnospondyl-like skull. If lanthanosuchids did indeed inhabit the freshwater systems of Permian Eastern Euramerica, this habitat preference could explain why there is no evidence of them in Lower Permian rocks of North America, especially in light of Milner's (1993) observation that aquatic Permian tetrapods appear to have been strongly characterized by endemism. Following his description of two additional taxa, Ivakhnenko (1980) disputed the idea that lanthanosuchids were aquatic and proposed instead that they were Permian analogues of species of the extant genus *Phrynosoma*, the horned lizards of North America. If that idea is correct, then it is possible that future collecting efforts in uppermost Lower Permian deposits of North America will yield lanthanosuchids.

Accounting for the absence of nyctiphruretians and procolophonians in North American deposits of Early Permian age is complicated by the ambiguous nature of the biogeographic scenarios that can be drawn from the available phylogeny (Figure 4). If representatives of either procolophonomorph group were present in Euramerica during the late Early Permian, either their remains have gone unrecognised or they remain uncollected. On the other hand, Early Permian nyctiphruretians and procolophonians may have been upland forms, and because Lower Permian localities preserving such tetrapods appear to be rare (Olson & Vaughn 1970; deBraga & Reisz 1996; Modesto 1999a), it is possible that these two taxa have not been preserved amongst known late Early Permian faunas of Euramerica. Further work on vertebrates from the Chickasha, San Angelo and Flower Pot formations of south-central North America, strata regarded as lowermost Upper Permian by previous workers but better regarded as uppermost Lower Permian (Modesto *et al.*, unpublished), may provide important clues for establishing the geographic origins of nyctiphruretian and procolophonian parareptiles.

CONCLUSIONS

Phylogenetic analyses confirm the recent identification of the enigmatic reptile *Eunotosaurus africanus* as a basal parareptile. This reptile is the closest relative of procolophonomorph parareptiles. Optimization of geographic distributions onto anapsid reptile phylogeny suggests strongly that anapsids diversified initially in Gondwanan Pangaea, with descendant groups such as lanthanosuchoids and nyctiphruretians having descended from either a common Euramerican ancestor shared with procolophonians, or via lineages that dispersed separately from Gondwana into Euramerica. Minimum divergence times suggest a longer tenancy in Gondwana for anapsids than is implied by a direct reading of their stratigraphic ranges. Similarly, phylogenetic calibration of the stratigraphic ranges of anapsids also supports the hypothesis that a preservational bias was operating on terrestrial vertebrates in Permian Gondwana, at least until the onset of terrestrial sedimentation at the end of the Kazanian (early Late Permian).

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APPENDIX

Eunotosaurus africanus was coded for the data matrix of Laurin & Reisz (1995) as follows, with uncertain character states separated by a virgule ('/'), from 1 to 124: ?1001 ????? 01111 1101/2? ?1110 12100 20210 2012? ???? 0 1???1 000?1/2 1???? ????? 011?? ?0??? 0??0? 1???? 1011? ?00?? 11000 1100? 0010? 00002 00100 0000. Furthermore, two characters in the data matrix of Laurin & Reisz (1995) were modified, following the reasons outlined by Modesto (1999b): captorhinids were recoded as '0' for character 51, and character 54 was 'deleted' (by recoding all taxa for that character as '?' in MacClade). New information permitted the rescoring of two characters for Mesosauridae (Modesto 1999b): mesosaurs were recoded as '1' and '2' for characters 17 and 55, respectively. The two additional characters of Modesto (1999b, app. 1) were added to the data matrix of Laurin & Reisz (1995), with *Eunotosaurus* coded as '1' for character 125 and '?' for character 126.

Eunotosaurus africanus was coded for the data matrix of deBraga & Reisz (1995) as follows, using the organisation of the above paragraph: ???0? ?00?? 00000 ?010? 01101 ????0 ????? 00010 011?? 1???? 00000 1?101. Furthermore, character 6 of deBraga & Reisz (1996), concerning the angle of the frontal-nasal suture, was 'deleted' (again, by recoding all states as '?' in MacClade) because it cannot be subdivided into discrete character states (Modesto 1999a).

The two additional characters used in Modesto (1999a) were added to the data matrix of deBraga & Reisz (1996). The first character, which concerns the posterior margin of the skull roof (embayed bilaterally, 0; with a single, median embayment, 1; straight, 2), is recoded from Modesto (1999b), and should appear as follows when added as character 61 to the data matrix of deBraga & Reisz (1996): 0-1-1-1-1-1-1/2-0-1. The second, concerning the nature of the epipophysis (present, 0; absent, 1), is recoded from Lee (1995), and should appear as follows when added as character 62 to the data matrix of deBraga & Reisz (1996): 0-1-1-?-?-?-1-0-?. *Eunotosaurus* is represented by the last character state in these two sets of codings.