A second varanopseid skull from the Upper Permian of South Africa: implications for Late Permian ‘pelycosaur’ evolution

SEAN MODESTO, CHRISTIAN A. SIDOR, BRUCE S. RUBIDGE AND JOHANN WELMAN

LETHAIA

Late Permian terrestrial faunas of South Africa and Russia are dominated taxonomically and ecologically by therapsid synapsids. On the basis of a single specimen from the Upper Permian of South Africa, the varanopseid *Elliotsmithia longiceps* is the sole basal synapsid (‘pelycosaur’) known from Gondwana. Recent fieldwork in the Upper Permian of South Africa has produced a second varanopseid specimen that is referable to *Elliotsmithia*. Data from both this specimen and the holotype suggest that *Elliotsmithia* forms a clade with *Mycterosaurus* from the Lower Permian of North America and *Mesenosaurus* from the Upper Permian of Eastern Europe. That postulate is supported by the three most parsimonious trees discovered in a new analysis of varanopseid phylogeny. However, the available data cannot resolve the interrelationships of these three genera. The new phylogenetic results contrast with earlier work identifying *Elliotsmithia* as the basal member of a clade that includes the North American taxa *Aerosaurus*, *Varanops*, and *Varanodon*. The new trees reduce the stratigraphic debt required by the latter scenario, and the one with the least stratigraphic debt identifies *Elliotsmithia* and *Mesenosaurus* as sister taxa. Two new taxa are erected, *Mycterosaurinae* and *Varanodontinae*, for the two varanopseid subclades.

Basal synapsids (‘pelycosaurs’ of traditional usage) were the most conspicuous and most numerous land vertebrates of Late Carboniferous and Early Permian faunas, yet they were extremely rare members of the succeeding therapsid-dominated faunas of Late Permian times (Reisz 1986). Specimens of varanopseid and caseid ‘pelycosaurs’ have been collected with those of early therapsids from Upper Permian localities near Mezen, Russia (Ivakhnenko et al. 1997). Reports of a similarly mixed fauna of basal and therapsid synapsids from North America (e.g. Olson 1962) have in recent years been considered to be incorrect (e.g. Laurin & Reisz 1996), with those materials that were recognized originally as therapsids now attributable to caseids and sphenacodontids (Sidor & Hopson 1995). In the southern hemisphere, only a single ‘pelycosaurian’ specimen is known: the holotype of the varanopseid *Elliotsmithia longiceps*, from the Upper Permian of Western Cape Province, South Africa. Described by Broom (1937, p. 301) as an ‘early synapsid’, *Elliotsmithia* was considered a varanopseid by most authors (e.g. Romer & Price 1940; Haughton & Brink 1954) with the exception of Reisz (1986), who regarded it as Pelycosauria Incertae Sedis. Recent restudies of the holotype have reaffirmed its varanopseid identity (Dilkes & Reisz 1996; Reisz et al. 1998). *Elliotsmithia* is one of only two Tatarian (latest Permian) varanopseids known, the other being *Mesenosaurus romeri* from Russia. All other varanopseids are known from older deposits in North America.

Studies on varanopseids have appeared sporadically over the past few decades (e.g. Olson 1965; Langston & Reisz 1981; Berman & Reisz 1982; Dilkes & Reisz 1996; Reisz et al. 1997), and it was only recently that a comprehensive investigation of varanopseid phylogeny was published (Reisz et al. 1998). In that study, *Elliotsmithia longiceps* was identified as the basal member a clade that included *Aerosaurus wellesi*, *Varanops brevirostris*, and *Varanodon agilis*, a grouping that was the sister group of a smaller clade formed...
by *Mesenosaurus romeri* and *Mycterosaurus longiceps*. *Aerosaurus*, *Varanops*, *Varanodon*, and *Mycterosaurus* are all known only from North America. Accordingly, the Reisz *et al.* (1998) tree implies that *Elliotsmithia* and *Mesenosaurus* represent two varanopseid lineages that dispersed out of western Euramerica into the Gondwanan and eastern Euramerican regions of Pangea, respectively, with both surviving into the latest Permian. Given the evidence for a sister-group relationship between *Elliotsmithia* and the clade of *Aerosaurus*, *Varanops*, and *Varanodon* (Reisz *et al.* 1998), this palaeobiogeographical scenario is persuasive. However, because of the early appearance of *Aerosaurus*, this phylogenetic hypothesis necessitates a 30-million-year-long ghost lineage for *Elliotsmithia* (the longest for any basal synapsid), which extends from immediately below the Permo-Carboniferous boundary right up to the onset of the Tatarian (Reisz *et al.* 1998: fig. 4). Interestingly, there appears to be no evidence suggestive of a sister-group relationship between *Elliotsmithia* and its contemporary *Mesenosaurus*. Such an arrangement would support the idea that Late Permian varanopseids are descended from a more recent common ancestor and it would greatly reduce the long ghost lineage of *Elliotsmithia*.

Recent prospecting of lowermost terrestrial rocks of the Permo-Triassic Beaufort Group in South Africa has resulted in the collection of a number of amniote fossils (Rubidge *et al.* 1999), including that of a varanopseid. The latter was collected from a locality on the farm Alarmkraal (Cape map co-ordinates: 31°08.097'S, 22°22.696'E) in Carnarvon District, Northern Cape Province. Remains of dinocephalian therapsids and the parareptile *Eunotosaurus africanus* indicate that the Beaufort exposures on Alarmkraal and neighbouring farms are representative of middle-to-upper horizons of the Upper Permian *Tapinocephalus* Assemblage Zone (Rubidge *et al.* 1999). The varanopseid specimen comprises a partial skull and a few associated vertebrae that differ only in minor respects from *Elliotsmithia* as that taxon has been characterized in the recent literature (Dilkes & Reisz 1996; Reisz *et al.* 1998). Although there are minor differences in anatomy between the new specimen and the holotype, they are attributable to individual variation and to previous misinterpretations of a few, yet critical aspects of the latter. Accordingly, we refer the Northern Cape varanopseid specimen to *Elliotsmithia longiceps*. The new specimen preserves more of the skull than does the holotype, thereby furnishing new data on the cranial anatomy of this taxon. More importantly, the new specimen displays none of the plastic distortion exhibited by the holotype. The latter comes from the famous Abrahamskraal locality in the southern part of the Karoo Basin, where the lowermost Beaufort rocks have been subjected to strong folding during the Cape Fold Belt orogeny. In our opinion, deformation of the holotype of *Elliotsmithia longiceps* has led previous workers to misinterpret several aspects of the anatomy of this taxon. A description of the Northern Cape specimen is presented here, followed by a reappraisal of the relationships of *Elliotsmithia* among varanopseids.

**Materials and methods**

The following description of the specimen, reposited in the Bernard Price Institute for Palaeontological Research and catalogued as BP/1/5678, is based on a part and counterpart derived from a natural cleavage through the bones of the left side of the skull, which continues posteriorly to divide the cervical vertebrae into left and right halves (Figs 1, 2). Judging from natural sections through the encasing mudrock, the skull itself is three-dimensional, but it exhibits the same degree of transverse compression seen in the holotype (Dilkes & Reisz 1996; Reisz *et al.* 1998). Taking into consideration the intractable nature of the matrix and the observation that little more than the right cheek and part of the braincase would be revealed by mechanical preparation, we have not cleaned the skull more than has been necessary to expose additional teeth and the subtemporal bar. Another problem is that bone has weathered away from component blocks of both counterparts to various degrees, leaving impressions of the bone surfaces and precluding straightforward mechanical preparation of this side of the skull. Thus, further cleaning of the specimen and examination of the right cheek and braincase will be possible only if the areas represented as impression can be salvaged successfully. The holotype of *Elliotsmithia longiceps*, TM 1483 in the Transvaal Museum, Pretoria was examined and compared in detail to BP/1/5678. We have examined specimens of all other varanopseid genera (see Appendix 2). The following institutional abbreviations are used throughout the text: AMNH, American Museum of Natural History, New York; FMNH, The Field Museum, Chicago; MCZ, Museum of Comparative Zoology, Harvard University; PIN, Paleontological Institute, Moscow; UCMP, University of California Museum of Paleontology, Berkeley.

**Description**

As the anatomy of *Elliotsmithia* has been redescribed in detail in two recent publications (Dilkes & Reisz...
1996; Reisz et al. 1998), this study concerns only new anatomical information and emendation of previous work that is afforded by the new specimen. With the exception of the upper dentition, the skull of BP/1/5678 is missing almost the entire snout (Figs 1, 2). The sharp, recurved teeth are indistinguishable from those preserved in the holotype. Cutting edges are present on the trailing edges of all well-preserved teeth. The largest maxillary tooth is conspicuously caniniform and is positioned anteriorly in the tooth row, as in the basal varanopseid *Mycterosaurus* (Berman & Reisz 1982). Serrations are present on its cutting edge and on those of well-preserved postcaniniform teeth in both upper and lower dentitions (Fig. 3), but appear

Fig. 1. Photograph and outline drawing of the left side of the skull and cervical vertebrae 1–3 of *Elliotsmithia longiceps*, referred specimen BP/1/5678. Solid lines and grey infill represent preserved bones and their impressions, dashed lines represent restored bone margins, and dotted lines indicate overlying matrix. Unidentified fragments are not labelled. See Appendix 1 for abbreviations. Scale bar = 1 cm.
to be absent from the premaxillary and the anterior-most dentary teeth. Although the presence of serrations was described as indeterminate in *Elliotsmithia* (Reisz et al. 1998), additional cleaning of the holotypic dentition reveals the presence of serrations on the trailing edges of five out of the nine teeth that are present, the remaining four being too damaged by weathering. Among varanopseids, serrations are present on the marginal teeth in *Mesenosaurus* and *Mycterosaurus*. Ivakhnenko & Kurzanov (1979) reported that serrated teeth are present only on the trailing edges of the teeth of *Mesenosaurus*, but personal examination reveals that serrations are present also on the mesial margins. Examination of the holotype of *Mycterosaurus longiceps*, FMNH-UC 692, and a referred specimen, AMNH 7002, reveals the presence of serrations on the better preserved marginal teeth. Serrations are absent in *Aerosaurus* and *Varanodon*, in which teeth are well preserved, and are indeterminate in *Varanops*.

Only the antorbital region remains of the snout. Here the dorsal flange of the maxilla is as deep as in
other varanopseids, but there is no suggestion of the exact form the process would have taken more anteriorly, and whether it contacted the nasal or possessed an external maxillary buttress. The ventral process of the prefrontal is only narrowly separated from the maxilla by a small posterovertrally-angled finger of bone representing the lacrimal. The relation-

ship of the antorbital bones is identical to that seen in both *Mycterosaurus* and *Mesenosaurus*. Reisz *et al.* (1998) ascribe the primitive condition to *Elliotsmithia* (where the prefrontal is separated widely from the maxilla by the lacrimal). Due to crushing, the bones of the left antorbital region of the holotype are separated somewhat, but otherwise they compare closely in arrangement and morphology to those of BP/1/5678 (Fig. 4): posteriorly, the lacrimal is dorsoventrally slender and the prefrontal extends further ventrally than illustrated by Reisz *et al.* (1998).

The posterior skull table of BP/1/5678 is preserved mostly as impression, but what is visible agrees with previous descriptions of *Elliotsmithia*. However, the morphology of the bones forming the posterior cheek, which are little disturbed from their natural relations, differs markedly from the form proposed in recent studies (Dilkes & Reisz 1996; Reisz *et al.* 1998), prompting the following emendation. Most importantly, the temporal fenestra resembles more the reniform opening of *Mycterosaurus* (Berman & Reisz 1982) than the broadly triangular one ascribed to *Elliotsmithia* first by Broom (1937) and more recently by Reisz *et al.* (1998). The narrow outline of the temporal opening in BP/1/5678 is due largely to the fan-like ventral portion of the squamosal, which is almost identical to that of *Mycterosaurus* (Fig. 5A). Descriptions of a broadly triangular opening for

---

**Fig. 3.** Marginal teeth of *Elliotsmithia longiceps*, illustrating the serrated cutting edges. □A. Second last left maxillary tooth of BP/1/5678. □B. Posteriormost left maxillary tooth of the holotype, TM 1438. Anterior is to the left. Scale bar = 1 mm.

**Fig. 4.** Right lateral view of the skull roof, quadrate, and mandible of TM 1438, holotype of *Elliotsmithia longiceps*. See Appendix 1 for abbreviations. Scale bar = 1 cm.
Elliotsmithia appear to be in error, and may have been influenced by the damaged and distorted left temporal region. Examination of the right side, which differs only slightly from that seen in BP/1/5678, indicates that up to 4 mm was lost from the anteroventral corner of the left squamosal, thereby narrowing the bone and giving the impression that the temporal opening is expanded posteroventrally. The squamosal’s posterior margin in BP/1/5678 is angled approximately 70° to a line drawn across the ventral edge of the posterior cheek. This is slightly more vertical than the posterior margin of the squamosal in Mycterosaurus, which ranges 63°–65° as measured from the holotype FMNH-UC 692. Interestingly, the posterior margins of both squamosals in the holotype of Elliotsmithia are angled at approximately 55° (Fig. 5C). Given the intimate association of the posterior margin of the quadrate with that of the squamosal, it can also be concluded that the posterior margin of the quadrate of Elliotsmithia did not exhibit the extreme anterior lean attributed to it by Reisz et al. (1998).

The anterodorsal process of the squamosal appears to be the same shape as that of the holotype of Mycterosaurus (pers. obs.). Reisz et al. (1998) described this process as being relatively long in the holotype of Elliotsmithia, an observation with which we concur. In BP/1/5678, the distal tip of this process is directed into the interior of the skull and, as a consequence, is not fully exposed. In FMNH-UC 692, the holotype of Mycterosaurus, the same condition pertains to the left squamosal, whereas this region in the right element is obscured by damage. Accordingly, in both BP/1/5678 and in Mycterosaurus the anterodorsal process of the squamosal could have reached the relative length seen in the holotype of Elliotsmithia. The squamosal of BP/1/5678 possesses a posterodorsal extension that gives the dorsal part of the bone an anvil-like appearance in lateral aspect. This process is present in the holotype (Reisz et al. 1998: fig. 1) and Mesenosaurus (Ivakhnenko et al. 1997; pers. obs.). The presence of this process is indeterminate in Mycterosaurus because both squamosals are preserved as impression in the only specimen (FMNH-UC 692) that preserves these elements (and this region is also damaged on the right: pers. obs.). The posterodorsal process in BP/1/5678 is bounded ventrally by a narrow occipital flange of the squamosal. The latter feature appears to have been flattened by crushing and is difficult to demarcate from the lateral surface in both squamosals; a very narrow part of the occipital flange is present posterodorsally on the left element, although this was not illustrated by Reisz et al. (1998: fig. 1). Lastly, the braincase is not visible and so we cannot confirm whether the paroccipital process resembles that seen in the holotype; Reisz et al. (1998) regarded a long, slender paroccipital process to be an autapomorphy of Elliotsmithia.

The left lower jaw is complete, of which the posterior half agrees in general morphology with that seen in the holotype. As in all other varanopseids, the anterior part of the jaw is remarkably slender. Interestingly, the dentary teeth opposing the caniniform region are slightly enlarged in comparison with preceding and succeeding teeth, a feature that may represent an additional autapomorphy of Elliotsmithia. The atlantal neural arch, axis, and third cervical vertebra are indistinguishable from those of the holotype. The posterior margin of the axial neural spine is aligned roughly vertically, rather than displaying the 40° anterodorsal slope reported for the holotypic axis by Reisz et al. (1998). Examination of the holotype suggests that the left postzygapophyseal buttress of the axis was misidentified as the posterior margin by previous workers, and that the neural spine continues a little farther posteriorly than illustrated by Reisz et al. (1998: fig. 2). The dorsal and posterior margins are damaged by overpreparation (the anterior portion of the axial neural spine continues on the
block preserving the skull) and their edges are difficult to distinguish from the supporting matrix (Fig. 6); indeed, comparison with the axes of other varanopseids suggests that the height of the neural spine has been reduced by approximately 20%. Another factor that appears to have misled Reisz et al. (1998: fig. 2) in attributing a strong lean to the axial neural spine is that they regarded the intercentrum of BP/1/5678 as the posteroventral portion of the axial pleurocentrum, a misinterpretation that contributes to the illusion that the axial spine leans conspicuously forward. The ventral margin of the axial centrum in the holotype, however, is obscured completely by one of the hyoid elements. If one draws a line through the anterior and posterior zygapophyses of the holotypic axis, and regards this as representing the horizontal plane of the vertebra, then what remains of the base of the neural spine suggests that the posterior margin was aligned subvertically.

Finally, there is a small fragment lying just anterodorsal to the axial neural spine. It could represent one of the osteoderms that are associated with the postaxial cervical vertebrae in the holotype, or it may be simply an indeterminate bone fragment. In the holotype, osteoderms appear to increase in numbers immediately posterior to the axis. The observation that only the lower two-thirds of the third cervical vertebra are present and the remaining cervicals are missing in BP/1/5678 could account for the lack of osteoderms. Moreover, taphonomic loss and the fact that the cervical region of BP/1/5678 is visible only in sagittal section may each play a role.

**Discussion**

BP/1/5678 is only the second specimen of a non-therapsid synapsid (‘pelycosaur’) to be recovered from the former Gondwanan landmasses. Although confirming the presence of the two autapomorphies identified for _Elliotsmithia longiceps_ by Reisz et al. (1998) is currently impossible, the preserved portions of BP/1/5678 are essentially identical to the holotype TM 1438, such that the former can be assigned to that taxon as a referred specimen. The minor difference in the angle of the posterior margin of the squamosal may be attributable to the larger size of the holotypic skull, which is approximately 10% larger than the Northern Cape specimen. Although it is visible only in section, the Northern Cape varanopseid specimen is otherwise well preserved and the temporal region exhibits none of the distortion and little of the damage evident in the left side of the holotype. BP/1/5678 therefore permits a reinterpretation of some aspects of the holotype’s morphology and the evolutionary implications that have been drawn from the most recent study of the genus (Reisz et al. 1998).

_Elliotsmithia_ was identified recently as the basal most member of a clade that included _Aerosaurus, Varanops_, and _Varanodon_ (Reisz et al. 1998). This clade was diagnosed by four synapomorphies (numbers follow the scheme of Reisz et al. 1998): (8) the anterodorsal process of the squamosal was present and formed the dorsal border of the lateral temporal fenestra; (9) the lateral temporal fenestra has a posteroventral expansion resulting in a triangular outline for the fenestra; (15-2) a squamosal occipital shelf is absent; and (27) the quadrate occipital edge exhibits a strong anterior slope approaching 45°. _Elliotsmithia_ was described by Reisz et al. (1998) as having a narrow occipital flange of the squamosal. In their data matrix, however, this taxon was coded incorrectly as lacking this flange (character 15). Thus, the clade is diagnosed only by characters 8, 9, and 27.

Character 8 of Reisz et al. (1998) is problematic because it partly duplicates information in another character: one of the apomorphies uniting _Aerosaurus, Varanops_, and _Varanodon_ was the presence of an anterodorsal squamosal-jugal contact that excludes the postorbital from the lateral temporal fenestra (character 24). Accordingly, either characters 8 and 24 should be combined to form a multistate character (Maddison 1993), or character 8 should be discarded from the analysis. _Elliotsmithia_ was interpreted originally as having a ventrally narrow squamosal, thereby imparting a triangular outline to the lateral temporal fenestra (character 9). Re-examination of the more complete right holotypic squamosal (Fig. 5B) reveals that this is not correct and that _Elliotsmithia_
should be coded as plesiomorphic for character 9. Finally, character 27 is also problematic. The derived state for this character was defined as a quadrate having an ‘occipital edge with strong anterior slope approaching 45 degrees’ (Reisz et al. 1998: 611). The plesiomorphic state was defined simply as the posterior margin of the quadrate being vertical or nearly so. Therefore, only the derived state of the character has been quantified. Moreover, it should be noted that the angles can be judged only by using the posterior margin of the squamosal as a proxy for that of the quadrate, because the latter is hidden in lateral view by the former; this is considered acceptable as the posterior margins of the two bones are closely coupled in basal synapsids. The posterior margins of the squamosals in *Elliotsmithia* (from the holotype, left and right elements) and for *Mycterosaurus* are roughly 55° and 63°/65°, respectively. In *Varanopus* this figure is about 40° (pers. obs. of MCZ 1926), in *Aerosaurus* (UCMP 40096) it is about 34°, and in *Varanodon* (holotype) it is about 40° and 42°. Thus, the measures in the last three taxa span a range of 34° to 42°, which we regard as the apomorphic condition for the character. Those for BP/1/5678 and *Mycterosaurus* span a range of 63° to 70°. The latter range overlaps that of 63° to 73° for the lean of the posterior margin of the squamosal of three species of *Ophiacodon* as determined from skull reconstructions in Reisz (1986: fig. 36). Accordingly, the plesiomorphic condition for character 27 of Reisz et al. (1998) could be redefined as ‘quadrate occipital edge with an anterior slope of 63° to 73°’. The angle of 55° for the posterior margin of the squamosal in the holotype of *Elliotsmithia* thereby presents something of a problem as it falls between the apomorphic and plesiomorphic ranges. Because there is only a difference of 8° between the measure for the holotype of *Elliotsmithia* and the lower bound of the plesiomorphic range (63°), as opposed to a difference of 13° between it and the upper bound of the apomorphic range (42°), we can redefine the plesiomorphic condition for character 27 as ‘quadrate occipital edge with an anterior slope of 55° to 73°’. Thus, under this character state definition, there is no evidence uniting *Elliotsmithia* with the clade of *Aerosaurus*, *Varanopus*, and *Varanodon*.

Our study, however, suggests that there is a close relationship between *Elliotsmithia* and the clade of *Mycterosaurus* and *Mesenosaurus*. Notably, all three taxa possess the same derived morphology of the antorbital region, where the prefrontal is expanded ventrally at the expense of the lacrimal. In addition, they all share the presence of serrations on the marginal teeth. *Elliotsmithia* and *Mesenosaurus* also possess a posterodorsal process on the squamosal (indeterminate in *Mycterosaurus*). Given the absence of support for grouping *Elliotsmithia* with the other varanopseids, the possibility that *Elliotsmithia* is related closely to *Mesenosaurus* and *Mycterosaurus* merits serious consideration. In order to test this hypothesis, we conducted a phylogenetic analysis of the Varanopseidae using a modified version of the data matrix of Reisz et al. (1998). We have introduced two new characters and made several coding changes to their matrix. These additions and modifications are outlined in Appendix 2.

The results of the cladistic analysis indicate that *Elliotsmithia* forms a clade with *Mesenosaurus* and *Mycterosaurus* (Fig. 7). The present study and the phylogenetic analysis of Reisz et al. (1998) both recognize two major varanopseid subclades, which are officially named here in order to simplify the following discussion. The first new taxon name is *Mycterosaurinae*, which we define as a stem-based group that includes *Mycterosaurus longiceps* and all varanopseids related more closely to it than to *Varanodon agilis*. The second new taxon name is *Varanodontinae*, which we define as a stem-based group that includes *Varanodon agilis* and all varanopseids related more closely to it than to *Mycterosaurus longiceps*. Thus, *Elliotsmithia longiceps* is recognized in the present study as a mycterosaurine, but in the Reisz et al. (1998) phylogeny it would be considered a basal varanodontine.

---

Fig. 7. Strict consensus of the three most parsimonious trees from a PAUP analysis of varanopseid phylogeny. The three trees differ only in the interrelationships of mycterosaurines. From a branch-and-bound analysis of a modified version (see Appendix 2) of the data matrix in Reisz et al. (1998), Statistics: tree length = 40, consistency index (excluding uninformative characters) = 0.87, retention index = 0.91, rescaled consistency index = 0.79. The position of *Elliotsmithia* within *Mycterosaurinae* is relatively robust, requiring three additional steps to transfer it to *Varanodontinae*. Clades relevant to the discussion are numbered: 1, Synapsida; 2, Varanopseidae; 3, Mycterosaurinae, new taxon; 4, Varanodontinae, new taxon.
Although the interrelationships among mycterosaurines cannot be resolved with available data, Mycterosaurinae is relatively robust. Three extra steps are required to place Elliotsmithia within Varanodontinae as its most basal member. One major consequence of the new phylogeny is that it greatly reduces the remarkably long ghost lineage of Elliotsmithia necessitated by the Reisz et al. (1998) tree. A second consequence is that there is little support for the double dispersal scenario implied by Reisz et al. (1998), where Mesenosaurus and Elliotsmithia were interpreted as two distantly related varanopseid lineages thought to have dispersed independently from western Euramerica to eastern Euramerica and Gondwana, respectively. Instead, our results suggest that one major varanopseid subgroup, Varanodontinae, may have been restricted entirely to western Euramerica during the Permian, whereas the other varanopseid subgroup, Mycterosaurinae, is known to have members (Mesenosaurus, Elliotsmithia) that dispersed into the other regions of Pangaea.

The unresolved relationships among Mycterosaurus, Mesenosaurus, and Elliotsmithia preclude a detailed consideration of the biogeography of the Late Permian varanopseids. If Mesenosaurus forms a sister-group relationship with Mycterosaurus, optimization of their geographic distributions would be suggestive of two primary dispersal events (either two separate dispersals out of western Euramerica to account for Mesenosaurus in eastern Euramerica and Elliotsmithia in Gondwana, or, in a slightly more complicated but equally parsimonious scenario, an initial dispersal out of western North America by the ancestral mycterosaurine followed by the return of Mycterosaurus to western Euramerica). If Elliotsmithia and Mesenosaurus are sister taxa, optimization of varanopseid distributions would suggest that their most recent common ancestor could have left western Euramerica...
as late as the middle Kazanian, followed by speciation resulting in the appearance at the end of the Kazanian or earliest Tatarian of *Mesenosaurus* and *Elliotsmithia* in eastern Euramerica and Gondwana, respectively. Furthermore, a sister-group relationship between *Elliotsmithia* and *Mesenosaurus* results in the least stratigraphic debt (*sensu* Fisher 1992) of the three possible tree topologies for mycterosaurines (Fig. 8A).

We expect that future redescriptions of the numerous materials of both *Mycterosaurus* and *Mesenosaurus* will provide much needed anatomical data that in turn will allow for a more comprehensive understanding of the interrelationships of mycterosaurines. The South African materials, however, are the least well-represented and preserved varanopseids. The discovery of further specimens will be of pivotal importance to discussions of the role of the South African varanopseids in the evolutionary history of these remarkably long-lived basal synapsids.

Finally, we note that there is only one other pelycosaur-grade synapsid known to be contemporaneous with *Elliotsmithia* and *Mesenosaurus*, and that is the caseid *Ennatosaurus tecton*. Its closest relatives are known from deposits in central North America that are widely considered to be lowermost Upper Permian, a position based on the alleged presence of early therapsid material from the same beds (*e.g.*, Olson 1962, 1974). We consider that stratigraphic assignment to be highly suspect, now that these ‘eotherapsid’ remains are recognized as those of caseid and sphenacodontid basal synapsids (Sidor & Hopson 1995). Accordingly, the North American terrestrial horizons regarded previously to be lowermost Upper Permian (the Chickasha Formation of Oklahoma and the San Angelo and Flowerpot formations of Texas) should be regarded henceforth, conservatively, as uppermost Lower Permian. This leaves *Elliotsmithia*, *Mesenosaurus*, and *Ennatosaurus* credibly as the only basal synapsids of Late Permian times, when terrestrial environments were dominated by their more mammal-like relatives, the therapsids.

**Acknowledgements.** – Our fieldwork was funded by National Geographic Society grant 6387-98. We are indebted to Johan Lubbe, Henry Erasmus, and Bertus Steenkamp of Carnarvon for their hospitality and kindness in the field. We acknowledge the assistance of Charlton Dube, Joel Mohoi, Johann Neveling, John Nyaphuli, and Alain Renaut in the collection of the specimen. J. Francis Thackeray, Transvaal Museum, arranged the loan of the *Elliotsmithia* holotype and Eugene Gaffney, American Museum of Natural History, facilitated the loan of additional varanopseid material. Robert Reisz and Michael Ivakhnenko allowed us to examine specimens in their care and also provided recent Russian literature. Thanks to Anthony Alexandre for his technical finesse on the outline drawings in figures 1 and 2. The first author thanks Olivier Rieppel, John Bolt, and John Flynn for assistance during his 1999 visit to the Field Museum, made possible by a Field Museum Visiting Scholarship Program Award. Additional support was provided by the National Research Foundation of South Africa.

**References**


Reisz, R.R. 1986: *Pelycosauroidea*, *Ennatosaurus* and *Elliotsmithia* holotype and Eugene Gaffney, American Museum of Natural History, facilitated the loan of additional varanopseid material. Robert Reisz and Michael Ivakhnenko allowed us to examine specimens in their care and also provided recent Russian literature. Thanks to Anthony Alexandre for his technical finesse on the outline drawings in figures 1 and 2. The first author thanks Olivier Rieppel, John Bolt, and John Flynn for assistance during his 1999 visit to the Field Museum, made possible by a...
Appendix 1: Abbreviations

an, angular; at na, atlantal neural arch; ax, axis; axi, axial intercentrum; ax ns, axial neural spine; ax pc, axial pleurocentrum; can, caniniform tooth; co, coronoid; cr, cervical rib; cv, postaxial cervical vertebra; cv ns, postaxial neural spine; cv pc, postaxial pleurocentrum; f, foramen; fi, intercentrum; j, jugal; la, lacrimal; ltf, lateral temporal fenestra; mx, maxilla; os, dermal ossicle(s); p, parietal; pf, postfrontal; pin, pineal foramen; pm, premaxillary (tooth); po, postorbital; prf, prefrontal; q, quadrate; qj, quadratojugal; r, cervical rib, sa, surangular; scl, sclerotic ossicles; sq, squamosal.

Appendix 2: Phylogenetics

For our re-analysis of varanopseid interrelationships, the data matrix of Reisz et al. (1998: appendix 1) was first recreated in MacClade 3.07 (Maddison & Maddison 1997) and then modified and augmented as detailed in this section. The matrix was then imported into PAUP* 4 (Swofford 2000) and subjected to a branch-and-bound search using DELTRAN optimization. 

Elliotsmithia is recoded as ‘?’ for characters 2, 20, and 21 because they concern areas of the skeleton that are not preserved in the two known specimens. Elliotsmithia is scored as ‘0’ for characters 9 and 27 and ‘1’ for characters 7 and 15. Following suggestions by Maddison (1993) for missing characters in the outgroup, character 3 should be redefined as a multistate character. However, although the character concerns a form of continuous data and despite the fact that the character states were quantified by Reisz et al. (1998), closer inspection reveals that the breakdown of lateral temporal fenestra (LTF) height among basal synapsids is more complex than suggested by the distribution of character states in the data matrix of Reisz et al. (1998). Using skull reconstructions from the literature, for example, the LTF of ophiacodontids ranges roughly 39% to 44% of postorbital skull height (Reisz 1986); that of the basal caseasaur Eothyris falls within that range. The same figures for caseids are 52% to 54%; falling into the latter range are those for Dimetrodon and Varanodon (Reisz, unpublished). The figure for the basal caseasaur Oedaleoceph is approximately 60%. LTF height in Muyerosaurus and Aerosaurus are each approximately 70% postorbital skull height (Berman & Reisz 1982; Langston & Reisz 1981). Already a continuum is forming with regard to LTF height in synapsids. A further problem concerns the source for determining LTF height. For example, if the reconstruction of Romer & Price (1940) is used for Varanops, the LTF height is about 65% skull height, but if the skull reconstruction of Reisz (1986) is used, then this figure drops to 59%. Clearly, it is extremely difficult to distinguish among the relative sizes of synapsid temporal openings. It would seem best to reformat the nature of the LTF as a straightforward absent/present character (but see the following paragraph).

Character 8, which concerns the anterior extent of the anterodorsal process of the squamosal, is partially reiterated by character 24, which concerns whether there is contact between the anterodorsal process of the squamosal and the postorbital process of the jugal. Both characters involve the degree to which the temporal bones contribute to the LTF in synapsid ingroup taxa, especially with regard to the sutural pattern among the postorbital, jugal, and squamosal bones. A problem with character 8 is that it does not apply to the ultimate outgroup (Sauropsida), which should have been coded as ‘?’. However, as discussed by Maddison (1993), this is not a case of missing data. Moreover, the length of the anterodorsal process concerns a form of continuous data, but then the question arises as to how to quantify the length of the process. Again, the differences in some skull reconstructions for some taxa, and the total lack of reconstructions for others greatly complicates such an endeavour. Considering that character 8 is strongly related to character 24 it seems justifiable to combine these characters with character 3 into a multistate character. With this in mind, characters 8 and 24 are deleted (all states recoded as ‘?’ for these characters in MacClade 3.07) and character 3 is redefined as follows: LTF absent (0); LTF present with contribution from postorbital (1); LTF present with postorbital excluded from margin by jugal and squamosal (2). The row of character states for this character should read, from top (Caseasauria) to bottom (Sauropsida) in correspondence with the data matrix of Reisz et al. (1998): 1-1-1-1-1-2-2-2-2-2-0.

Because Sauropsida is the ultimate outgroup and should be scored as plesiomorphic for all characters, taxa with state ‘0’ are scored as ‘1’ and those scored as ‘1’ are now ‘0’ for characters 13 and 26.

Two characters were added to the matrix of Reisz et al. (1998). Varanopseid specimens examined to code for these characters in addition to those mentioned in the main text include FMNH-UC 160 for Muyerosaurus longiceps, FMNH-UC 644, FMNH-UC 2423 and MCZ 1926 for Varanops brevirostris, FMNH-UR 986 for Varanodon agilis, and UCMP 40096 for Aerosaurus wellesi.

The first new character deals with the presence of serrations and is defined as follows: Serrations absent from marginal teeth (0); serrations present on trailing margins of teeth (1). The row of character-state codings for this character should read, from top to bottom, when added as ‘character 32’ to the matrix of Reisz et al. (1998): 0-0-1-1-1-0-0-0-0-0-0.

The second new character concerns the presence of a posterodorsal process of the squamosal and is defined as follows: Posterodorsal process of the squamosal absent (0); or present (1). The row of character states for this character should read, from top to bottom, when added as ‘character 33’ to the matrix of Reisz et al. (1998): 0-0-?1-1-0-0-0-0.