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# Morphology and evolutionary significance of the atlas-axis complex in varanopid synapsids

NICOLÁS E. CAMPIONE and ROBERT R. REISZ



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The atlas-axis complex has been described in few Palaeozoic taxa, with little effort being placed on examining variation of this structure within a small clade. Most varanopids, members of a clade of gracile synapsid predators, have well preserved atlas-axes permitting detailed descriptions and examination of morphological variation. This study indicates that the size of the transverse processes on the axis and the shape of the axial neural spine vary among members of this clade. In particular, the small mycterosaurine varanopids possess small transverse processes that point posteroventrally, and the axial spine is dorsoventrally short, with a flattened dorsal margin in lateral view. The larger varanodontine varanopids have large transverse processes with a broad base, and a much taller axial spine with a rounded dorsal margin in lateral view. Based on outgroup comparisons, the morphology exhibited by the transverse processes is interpreted as derived in varanodontines, whereas the morphology of the axial spine is derived in mycterosaurines. The axial spine anatomy of Middle Permian South African varanopids is reviewed and our interpretation is consistent with the hypothesis that at least two varanopid taxa are present in South Africa, a region overwhelmingly dominated by therapsid synapsids and parareptiles.

**Key words:** Synapsida, Varanopidae, Mycterosaurinae, Varanodontinae, atlas-axis complex, axial skeleton, Middle Permian, South Africa.

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## Introduction

The multipartite atlas-axis complex of Palaeozoic tetrapods is the skeletal bridge between the skull and the postcranium. This structure allows for not only the movement between these two regions of the animal, but also provides surface areas for the origin and insertion of anterior axial musculature and for tendons that stabilize the cranial region. It is therefore reasonable to expect taxic variation in this complex as a result of differences in cranial and vertebral anatomy, as well as behaviour. Although numerous studies have concentrated on the morphology and variation of the skull of basal tetrapods, a detailed morphology of the atlas-axis complex has been described in relatively few taxa (e.g., Godfrey and Reisz 1991; Sumida et al. 1992; Laurin 1993), and rarely within a comparative framework. Among basal synapsids, atlantal and axial morphology is well known in *Ophiacodon*, *Dimetrodon* (Romer and Price 1940), and *Secodontosaurus* (Reisz et al. 1992). In varanopids, it has been briefly described for some taxa, such as *Varanops brevirostris* and *Elliotsmithia longiceps* (Williston 1911; Reisz et al. 1998; Modesto et al. 2001) and potential variation between varanopid taxa was identified by Maddin et al. (2006). The varanopid atlas-axis complex is

preserved in several species and therefore this clade allows for a detailed comparative study of the atlas-axis, with implications for varanopid systematics and diversity.

Varanopidae include three possible basal species, *Archaeovenator hamiltonensis* Reisz and Dilkes, 2003, *Apsisaurus witteri* Laurin, 1991, and *Pyozia mesenensis* Anderson and Reisz, 2004, although the assignment of the latter to Varanopidae has been questioned (Maddin et al. 2006; Campione and Reisz 2010). Varanopids generally include two main clades, Mycterosaurinae (*Mycterosaurus longiceps* Williston, 1915, *Mesenosaurus romeri* Efremov, 1938, and *Heleosaurus scholtzi* Broom, 1907), and Varanodontinae (*Varanops brevirostris* [Williston, 1911], *Varanodon agilis* Olson, 1965, *Aerosaurus wellesi* Langston and Reisz, 1981, and *Watongia meieri* Olson, 1974), though the monophyly of mycterosaurines has recently been questioned (Reisz et al. 2010). *Elliotsmithia longiceps* Broom, 1937 is also a varanopid but its phylogenetic affinities are currently in flux (see below). Mycterosaurines and varanodontines are generally differentiated by morphological variation in the organization of the skull bones, primarily in the occipital region. In lateral view, the occiput of mycterosaurines forms an almost right angle with the ventral margin of the skull, which results in a tall and oval temporal fenestra (Fig. 1A).

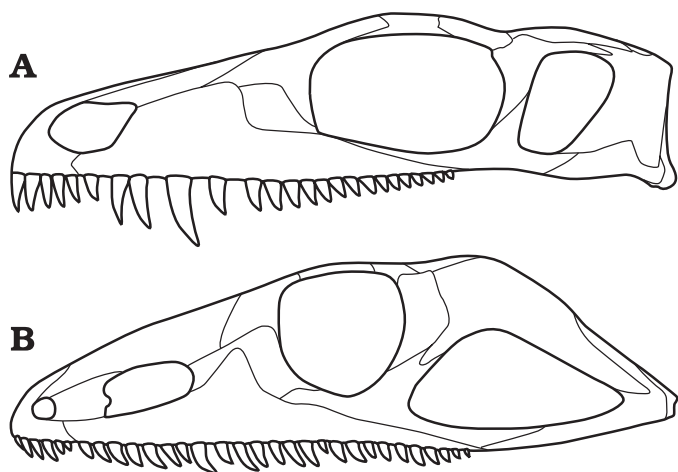


Fig. 1. Outline reconstructions of the skull of varanopids. **A.** *Mesenosaurus romeri* Efremov, 1938 (modified from Reisz and Berman 2001). **B.** *Varanodon agilis* Olson, 1965 (modified from Reisz and Laurin 2004). These taxa show the characteristic differences in the occiput of varanopids. Not to scale.

Varanodontines show an alternate morphology in which the occiput and the ventral margin of the skull form a sharp, acute angle (Fig. 1B). If the atlantal-axial morphology is related to the organization of the tendons, muscles, and ligaments that support the skull, then major cranial variation in occipital organization, as seen in varanopids, should be reflected in the morphology of the atlas-axis. This hypothesis is supported by two closely related sphenacodontids, in which *Dimetrodon* has a tall, massive skull that is associated with a tall axial spine, whereas *Secodontosaurus* has a low, slender skull that is associated with a low axial spine (Reisz et al. 1992).

A detailed description of the variation in the atlas-axis of varanopids may also contribute to clarifying the phylogenetic affinities of *Elliotsmithia longiceps*, from South Africa. This species was described by Reisz et al. (1998) as a varanodontine, and was re-interpreted as a mycterosaurine by Modesto et al. (2001). Modesto et al. (2001) considered the holotype to be crushed and they based their interpretation on another specimen that they assigned to *E. longiceps*, which showed morphological features common to mycterosaurines. This interpretation was revisited by Reisz and Dilkes (2003), who interpreted the second specimen as a different mycterosaurine taxon, distinct from *E. longiceps*. The authors scored both specimens separately in a phylogenetic analysis and recovered *Elliotsmithia* as more closely related to varanodontines, and the putative second specimen as a mycterosaurine. Recently, *Heleosaurus scholtzi* was re-diagnosed as a mycterosaurine varanopid, and it was suggested that *E. longiceps* might represent a junior synonym of *H. scholtzi* (Botha-Brink and Modesto 2007, 2009; Reisz and Modesto 2007). This interpretation is supported by a phylogenetic analysis (Botha-Brink and Modesto 2009) and a recent stratocladistic analysis (Campione and Reisz 2010), which recovered *E. longiceps* and *H. scholtzi* as sister taxa, nested within Mycterosaurinae. At present, the systematics of South African varanopids remains unresolved.

The most complete description of a varanopid atlas-axis complex is that of the varanodontine *Varanops brevirostris* (Williston 1911; Maddin et al. 2006; Campione and Reisz 2010). Less is known about mycterosaurines, in which the only description is based on a partial axis *Mycterosaurus* (Reisz et al. 1997). Based on known specimens of varanopids, along with new material from the Richards Spur locality in Oklahoma, we present a detailed description of the anatomy and variation in the varanopid atlas-axis complex. This study provides the first complete description of a mycterosaurine atlas-axis and discusses the morphological variation between the two varanopid clades along with possible systematic implications.

**Institutional abbreviations.**—BP, Bernard Price Institute for Palaeontological Research, Johannesburg, South Africa; FMNH, Field Museum of Natural History, Chicago, Illinois, USA; KUVF, Kansas University Vertebrate Paleontology Collection, Lawrence, Kansas, USA; MCZ, Museum of Comparative Zoology, Cambridge, Massachusetts, USA; OMNH, Sam Noble Oklahoma Museum of Natural History, Norman, Oklahoma, USA; PIN, Paleontological Institute of the Russian Academy of Sciences, Moscow, Russia; SAM, Iziko South Africa Museum, Cape Town, South Africa; TM, Transvaal Museum, Pretoria, South Africa; TMM, Texas Memorial Museum, Austin, Texas, USA; UCMP, University of California Museum of Paleontology, Berkeley, California, USA.

## Material and methods

This study is based on observations and measurements taken from several varanopid specimens. Varanodontines include: *Aerosaurus wellsi*, UCMP 40096; *Varanodon agilis*, FMNH UR 986; *Varanops brevirostris*, FMNH UR 2423, TMM 43628-1; and an isolated varanodontine axis, OMNH 73531. Mycterosaurines include: *Heleosaurus scholtzi*, SAM-PK-1070 and SAM-PK-K8305; an isolated indeterminate mycterosaurine axis (identical to that of OMNH 73500), OMNH 53514; a partial atlas-axis complex, associated with a complete undescribed mycterosaurine skull, OMNH 73500; and an isolated indeterminate mycterosaurine axis, OMNH 74628. Other varanopids include: *Archaeovenator hamiltonensis*, KUVF 12483; *Elliotsmithia longiceps*, TM 1483; and BP/1/5678, which is suggested to represent a specimen of either *E. longiceps* or *H. scholtzi*. Outgroup comparisons are made with published descriptions and figures of *Ophiacodon retroversus* (Cope, 1878), and *Cotylorhynchus romeri* Stovall, 1937, as well as *Haptodus garnettensis* Currie, 1977, and the sphenacodontids, *Dimetrodon limbatus* Romer and Price, 1940 and *Secodontosaurus obtusidens* Romer, 1936.

Measurements were taken from each axial spine (Appendix 1). These include: the spine height, taken from the base of the postzygapophyses to the tallest part of the spine; spine length, taken parallel to the vertebral column; the centrum height, taken on the posterior face; and the maximal height of



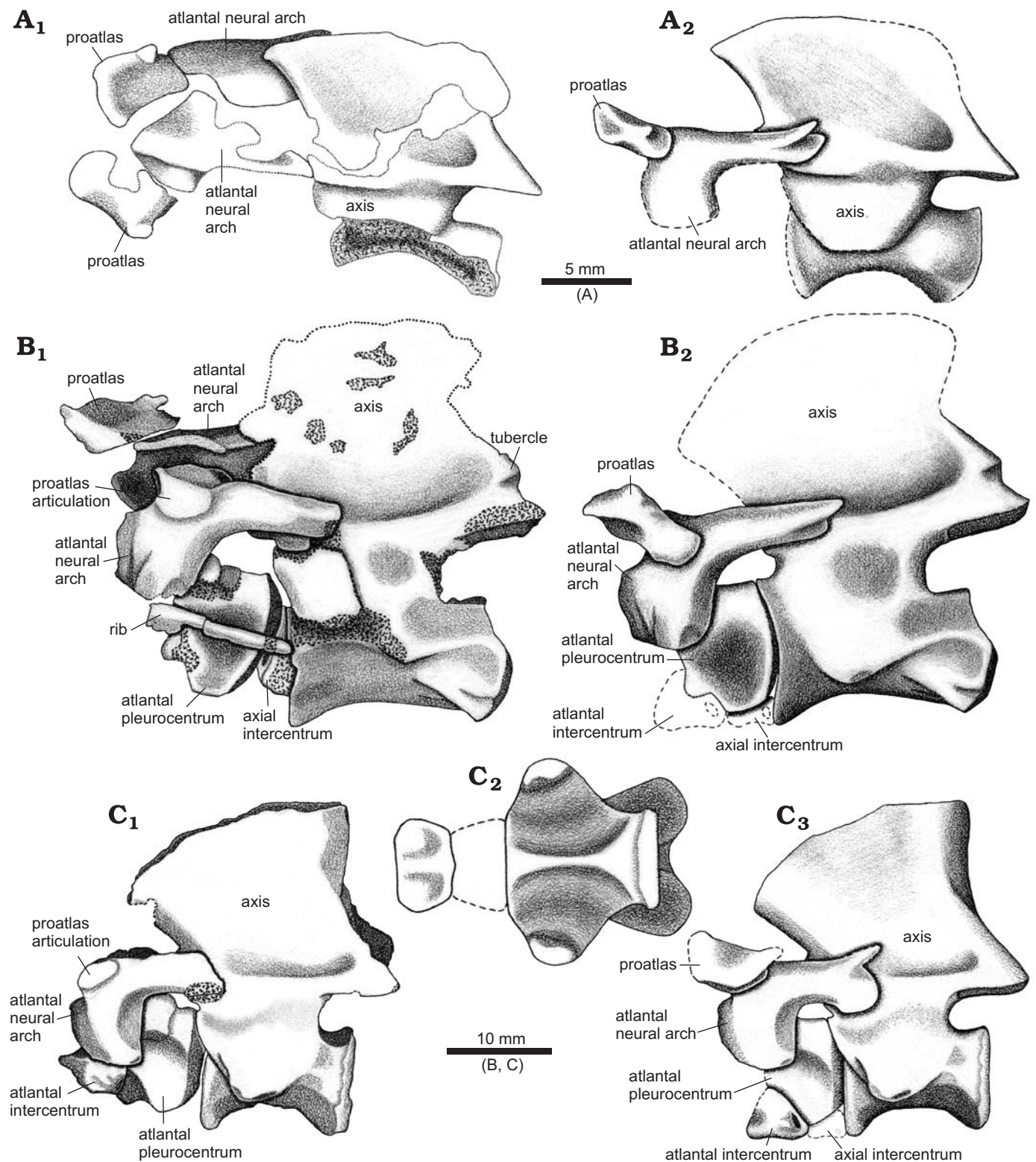


Fig. 2. Atlas-axis complex of varanodontines. **A.** *Aerosaurus welllesi* Langston and Reisz, 1981, Abo/Cutler Formation, Cutler Group, Upper Pennsylvanian–Lower Permian; El Cobre Canyon, Rio Arriba County, New Mexico, UCMP 40096, in right lateral view, drawing (A<sub>1</sub>) and reconstruction (A<sub>2</sub>). **B.** *Varanodon agilis* Olson, 1965, Chickasha Formation, Permian, Blaine County, Oklahoma, FMNH UR 986 in left lateral view, drawing (B<sub>1</sub>) and reconstruction (B<sub>2</sub>). **C.** *Varanops brevirostris* (Williston, 1911), Arroyo Formation, Clear Fork Group, Lower Permian; Indian Creek, Baylor County, Texas, FMNH UR 2423, drawing in left lateral view (C<sub>1</sub>), reconstruction in ventral view (C<sub>2</sub>), and reconstruction in left lateral view (C<sub>3</sub>).

the axial vertebra. For the purpose of this study and because of the isolated nature of most specimens, centrum height is

considered as representative of overall body size. Measurements from specimens were taken with dial callipers and

measurements from illustrations were taken using the software package Image J (Rasband 2007). Bivariate plots and regressions are based on the data presented in Appendix 1. All data were logarithmically transformed (base 10) and plots were constructed using R-project (R-Development-Core-Team 2010).

## Description

The atlas-axis of varanopids comprises eight separate ossifications: paired proatlases, paired atlantal neural arches, the atlantal intercentrum, the atlantal pleurocentrum, the axial intercentrum, and a fully fused unpaired axial neural arch and pleurocentrum. This configuration represents the general plesiomorphic condition for tetrapods (Romer 1956; Sumida et al. 1992).

**Atlas.**—The proatlas articulates with the atlantal prezygapophysis posteriorly and the exoccipital anteriorly. It is rarely preserved in known specimens, and unknown in mycterosaurines. The most complete is present in *Aerosaurus wellesi* (Fig. 2A), which has a small spine that points ventrolaterally. Although the proatlas is generally not preserved, this bone is likely present in varanopids, based on the presence of articulation surfaces along the posterodorsal margin of the exoccipital and the anterodorsal surface of the atlas arch.

The atlantal neural arches of varanopids are similar to those in *Ophiacodon* (Romer and Price 1940). The anterior

portion is tall and robust and bends at a right angle to form a slender posterior process that represents the atlantal postzygapophysis, which articulates with the axis. The posterior process of the atlantal neural arches is more gracile in *Varanodon agilis* and *A. wellesi* than that of *Varanops brevirostris*, especially in the region of the posterior process (Fig. 2). Both *Varanops brevirostris* and *Varanodon agilis* have proatlantal articulation facets. In *A. wellesi*, the articular surface for the proatlas is not visible, but the proatlas is preserved.

The atlantal intercentrum is preserved only in *Varanops brevirostris* (FMNH UR 2423; Fig. 2C). It is crescentic in posterior view and wedge-shaped in lateral view. A small process on the posterior ventrolateral surface of the atlantal intercentrum marks the parapophysis for the atlantal rib. The atlantal pleurocentrum in all varanopids is sub-triangular in lateral view, with a flattened dorsal surface that forms the floor of the spinal canal. In *Varanops* it is bevelled anteriorly and posteriorly for reception of the atlantal and axial intercentra respectively (Fig. 3A). In an undescribed mycterosaurine from the Richards Spur locality (OMNH 73500), the axial intercentrum is fused to the atlantal pleurocentrum, and no suture line is visible, except in posterior view (Fig. 3B). The fusion of these elements does not appear to occur in *Elliotsmithia* (Reisz et al. 1998), or in the much larger *Varanops* (Fig. 3A). A distinct excavation is present on the lateral surfaces of the atlantal pleurocentrum in *Varanops* (Figs. 2C<sub>3</sub> and 3A<sub>1</sub>), similar to the deep excavations at the bases of the neural arches in more posterior vertebrae. Lateral excavations on the atlantal pleurocentrum are thus far unique to *Varanops*; however, other varanodontines do not preserve this region in detail. Excavations are not present in mycterosaurines (Fig. 3B<sub>2</sub>) or in other basal synapsids. The posterior margin of the bone is convex in lateral view; but is deeply concave with a notochordal pit in posterior view; a notochordal pit is also visible in anterior view, above the articulation surface for the atlantal intercentrum. Contrary to Williston (1911), the atlantal intercentrum contacts the axial intercentrum, and hence the atlantal pleurocentrum does not contribute to the ventral margin of the vertebral column. This condition is similar to the plesiomorphic condition in tetrapods, and differs from the condition seen in Sphenacodontia and early therapsids, in which the atlantal pleurocentrum extends to the ventral margin of the column (Reisz and Dilkes 1992). The atlantal pleurocentrum retains the basal synapsid plesiomorphic condition (Romer and Price 1940) and is not fused to the axis pleurocentrum in either varanopid clade.

**Axis.**—The axial intercentrum (Fig. 3) is similar in varanodontines (e.g., *Varanops brevirostris*, TMM 43628-1) and in mycterosaurines (OMNH 73208). They differ only in that the axial intercentrum is fused with the pleurocentrum in mycterosaurines and remains separate in varanodontines. In general, the axial intercentrum is triangular in lateral view, and although smaller than the atlantal intercentrum, it is also crescentic.

The axial pleurocentrum and axial neural arch (henceforth referred to as the axis) are indistinguishably fused to

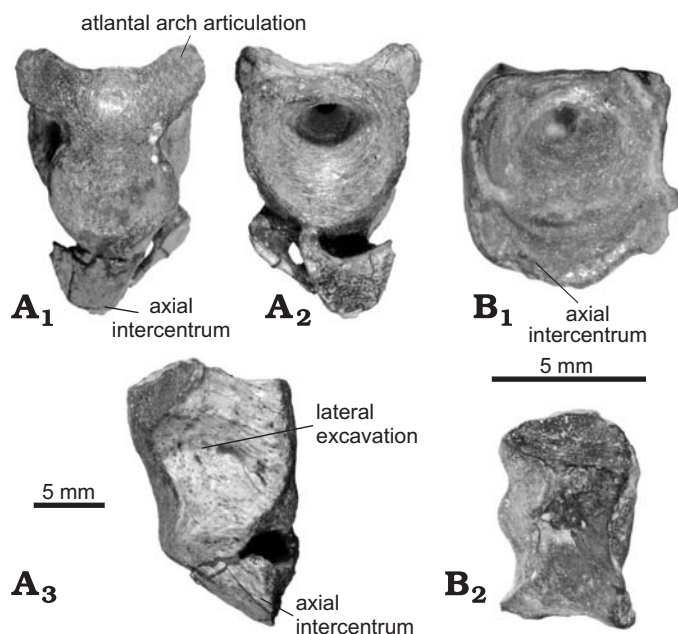


Fig. 3. Atlantal pleurocentrum and axial intercentrum of varanopids. **A.** The varanodontine *Varanops brevirostris* Campione and Reisz, 2010, Vale Formation, Clear Fork Group, Lower Permian, Mud Hill locality, Taylor County, Texas, TMM 43628-1, in anterior (A<sub>1</sub>), posterior (A<sub>2</sub>), and right lateral (A<sub>3</sub>) views. **B.** An undescribed mycterosaurine, Lower Permian, Richards Spur Locality, Comanche County, Oklahoma, OMNH 73500, in posterior (B<sub>1</sub>) and left lateral (B<sub>2</sub>) views.



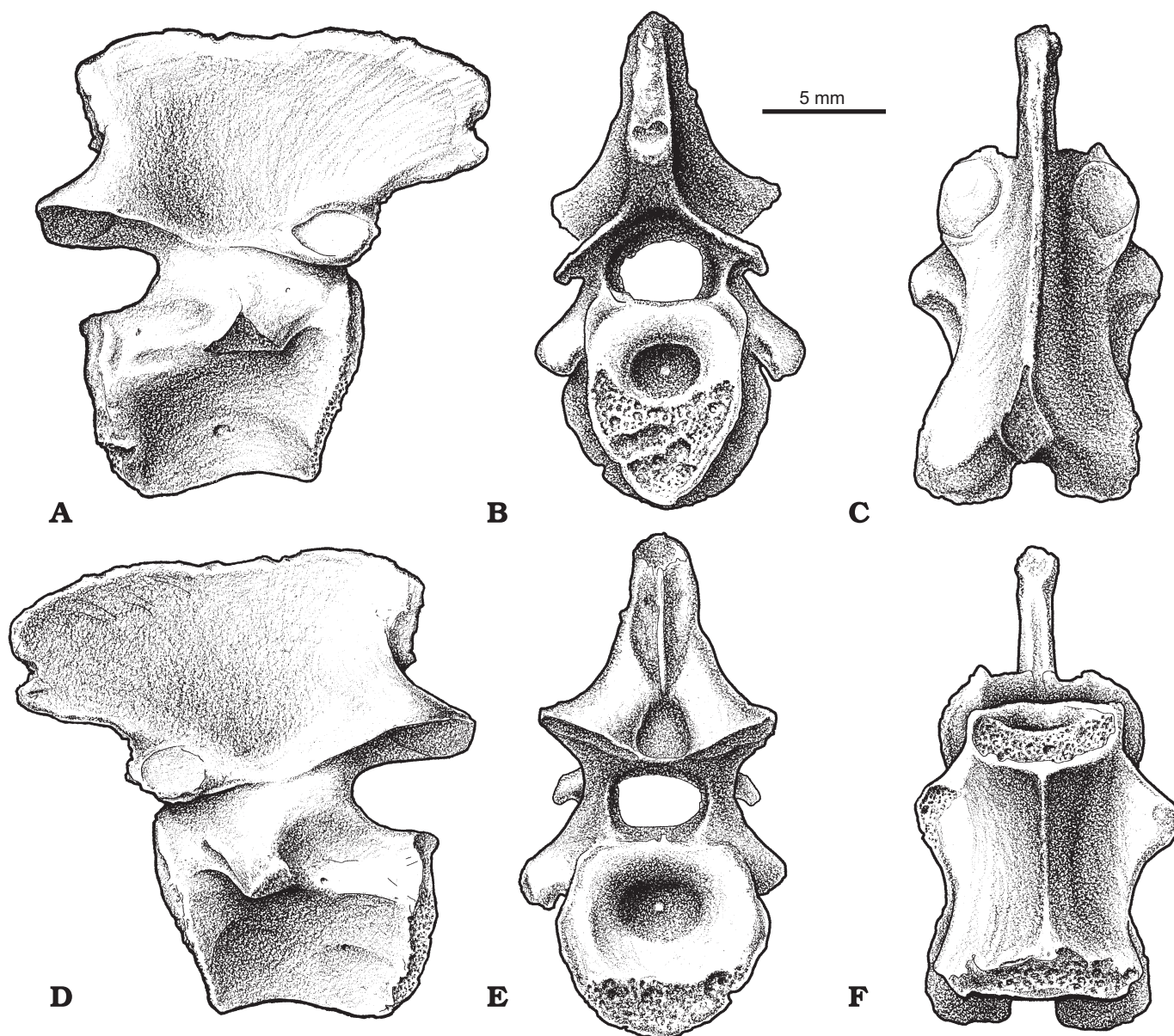


Fig. 4. Axis of an indeterminate mycterosaurine from Richards Spur, Oklahoma, USA, Lower Permian, OMNH 53514, identical to the undescribed mycterosaurine skull, OMNH 73500. This specimen has an anteroposteriorly elongate spine and a flat dorsal margin in lateral view. Specimen in right lateral (A) anterior (B), dorsal (C), left lateral (D), posterior (E), and ventral (F) views.

each other. The axis is the best-represented element of the atlas-axis complex in varanopids. It is preserved in most taxa, and its anatomy is therefore easily compared. The axial centrum is similar in all varanopids and in basal synapsids. It is strongly amphicoelus and notochordal, ventrally convex in lateral view, and it possesses a well-developed medial keel along the ventral margin. Varanodontines possess an anteroposteriorly robust transverse process that projects laterally and ventrally (Fig. 2). In the mycterosaurine specimens (OMNH 53514 and 73500; Fig. 4), in *Elliotsmithia longiceps* (TM 1483; Reisz et al. 1998), and in *Archaeovenator hamiltonensis* (KUVP 12483; Fig. 5A), the transverse processes are small and circular in cross-sectional outline, and they project laterally and posteroventrally. Dorsal to the trans-

verse processes the axis possesses an anteroposteriorly directed ridge that connects the pre and postzygapophyses. This ridge is more pronounced in varanodontine specimens than in mycterosaurines. The ridge is not pronounced in the holotype of *Elliotsmithia*, though this region is not well preserved.

The main source of variation among varanopids is in the morphology of the axial neural spine. In *Varanops* and *Varanodon* the axial spine is tall. Though not well preserved in *Varanodon*, the axial spine of *Varanops* has a strongly convex dorsal margin in lateral view (Fig. 2C<sub>1</sub>), similar to *Ophiacodon* (Romer and Price 1940) and *Haptodus garnettensis* (Laurin 1993). In lateral view, the posterior margin is approximately vertical, and the anterior edge of the spine

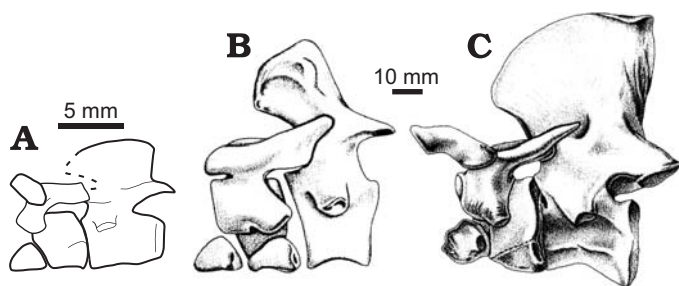


Fig. 5. Atlas-axis complexes of varanopid outgroups used in recent phylogenetic analyses (Botha-Brink and Modesto 2009; Campione and Reisz 2010). **A.** Atlas-axis complex of *Archaeovenator hamiltonensis* Reisz and Dilkes, 2003, Virgilian Series, Upper Pennsylvanian, Hamilton Quarry, Greenwood County, Kansas (modified from Reisz and Dilkes 2003). **B.** *Cotylorhynchus romeri* Stovall, 1937, Hennessey Formation, Permian, Logan County, Oklahoma (after Stovall et al. 1966). **C.** *Ophiacodon retroversus* Romer and Price, 1940, Admiral Formation, Wichita Group, Lower Permian, Wichita County, Texas (after Romer and Price 1940).

forms an approximately 45° angle between the dorsal margin and the longitudinal axis of the vertebra (Fig. 2C). In *Varanodon agilis* (Fig. 2B<sub>1</sub>), a small tubercle extends posterodorsally from the postzygapophyseal buttress. A similar feature occurs in some specimens of *Dimetrodon* (MCZ 1335 and 5573) and in *Sphenacodon* (Case and Williston 1913). In the mycterosaurine specimens (PIN 1580/1, OMNH 53514, 73208, 74628; Fig. 4) the spine is dorsoventrally short, with a flattened dorsal margin in lateral view, and it appears to project further anteriorly from the anterior margin of the centrum than it does in varanodontines. The length of the spine in the mycterosaurine specimens is almost equivalent to the height of the entire axial vertebra, whereas in varanodontines the length is a third of the height. Similarly, the length of the spine is almost double its height in mycterosaurines, and approximately equal in length in varanodontines (Appendix 1).

## Discussion

The overall morphology of the varanopid atlas-axis complex conforms to the plesiomorphic condition in tetrapods (Romer 1956; Sumida et al. 1992). However, there appears to be important, though subtle, morphological variation in this complex within Varanopidae, primarily in the shape of the axial spine. This variation makes it possible to suggest possible taxonomic affinities for certain specimens and allows us to comment on possible implications regarding the systematics, diversity, and relationships of varanopids.

Polarization of the axial characters is based on comparisons with a basal varanopid (a close relative of both varanopid clades), *Archaeovenator hamiltonensis*, and with the chosen outgroups to varanopids, *Ophiacodon retroversus* and *Cotylorhynchus romeri*, based on recent phylogenetic analyses (Botha-Brink and Modesto 2009; Campione and Reisz 2010).

The transverse processes of the axis in mycterosaurines are small and point posteroventrally (Fig. 4). In contrast, the transverse processes in varanodontines are large, with a broad base and point ventrally (Fig. 2). When compared to *Archaeovenator hamiltonensis*, *Ophiacodon retroversus*, and *Cotylorhynchus romeri* (Fig. 5), the mycterosaurine condition resembles most closely that of the outgroup taxa. This suggests that a large and broad transverse process on the axis represents a possible synapomorphy between *Aerosaurus wellsi*, *Varanodon agilis*, and *Varanops brevirostris*. In *Elliotsmithia longiceps*, the transverse processes are small, like the outgroup condition and unlike varanodontines. Since small transverse processes are plesiomorphic, this morphology does not support or refute any of the possible phylogenetic hypotheses pertaining to *Elliotsmithia longiceps*.

The axial spine in all varanopids is a broad, medioventrally flattened structure that served as attachment site for the ligaments and muscles that supported the skull. The skulls of mycterosaurines and varanodontines vary significantly, especially in the organization of the occipital region (Fig. 1). In varanodontines the occiput is angled anteriorly and the majority of the squamosal is limited to the lateral aspect of the skull. In contrast, mycterosaurines have a vertically oriented occiput with a large exposure of the squamosal in occipital view. These differences suggest that the musculature between the skull and the axis is different in these clades, and therefore it is expected that this be reflected in the axis spine morphology. This expectation is confirmed in Sphenacodontidae, in which differences in the cranial architecture of *Dimetrodon* and *Secodontosaurus* are reflected in the morphology of their axial spines (Reisz et al. 1992). Given the differences in cranial morphology in varanopids, however, it is surprising that the differences in the axial spine are subtle and not as extreme as in sphenacodontids.

Although differences in axial morphology are subtle between varanodontines and mycterosaurines, a bivariate and residual plot comparing spine height (Fig. 6A, C) and spine length (Fig. 6B, D) to centrum height (size proxy) demonstrates that height is the main distinguishing factor between the two varanopid clades. Unfortunately, statistical significance cannot be evaluated due to small sample size. Variation in the length of the axial spine shows overlap between mycterosaurines and varanodontines and appears random; however, this plot is based on a smaller sample than the spine height comparison. In general however, a dorsoventrally tall and dorsally rounded spine in lateral view characterizes the varanodontine condition, exemplified by *Varanops*, whereas a dorsoventrally shorter spine with a flattened dorsal margin in lateral view characterizes mycterosaurine specimens. *Archaeovenator hamiltonensis* (Fig. 5A) and virtually all other basal synapsids examined here exhibit a tall axial spine (approximately double the height of the axial centrum; Figs. 5, 6), and several (such as *A. hamiltonensis* and *Ophiacodon retroversus*) have a dorsally convex spine in lateral view. The morphology of the sphenacodontids, *O. retroversus*, and *A. hamiltonensis* suggests that a dorsoventrally shortened

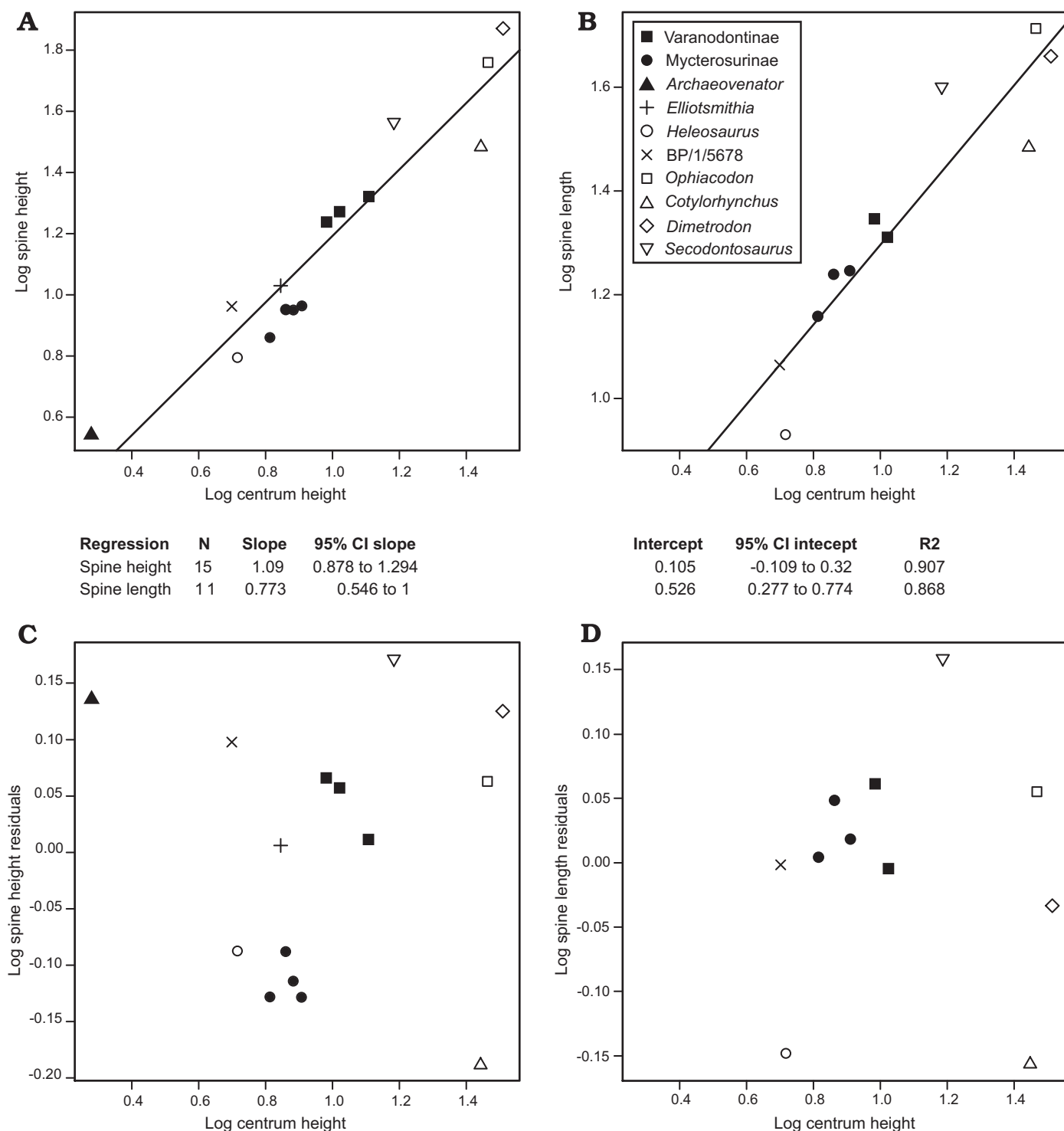


Fig. 6. Bivariate plots and regression analyses of the atlas-axis complex in varanopids and other non-therapsid synapsids. **A.** Spine height relative to centrum height. **B.** Spine length relative to centrum height. **C.** Residual plot of spine height. **D.** Residual plot of spine length. The regressions results and statistics are presented in the table below A and B.

spine, present in mycterosaurines, represents the derived condition and that varanodontines retain the plesiomorphic state. It should be noted that the morphology of *Cotylorhynchus romeri* (Figs. 5B, 6C) conflicts with the morphology present in the other outgroup taxa. The axial spine in this taxon is dorsoventrally short relative to the centrum. This pe-

culiar morphology, when compared to other basal synapsids and tetrapods (Fig. 6C; Sumida et al. 1992), is likely autapomorphic for caseids, possibly due to their relatively small skulls. *Cotylorhynchus romeri* is therefore not an appropriate taxon for assessing polarity in varanopid axial spine morphology.



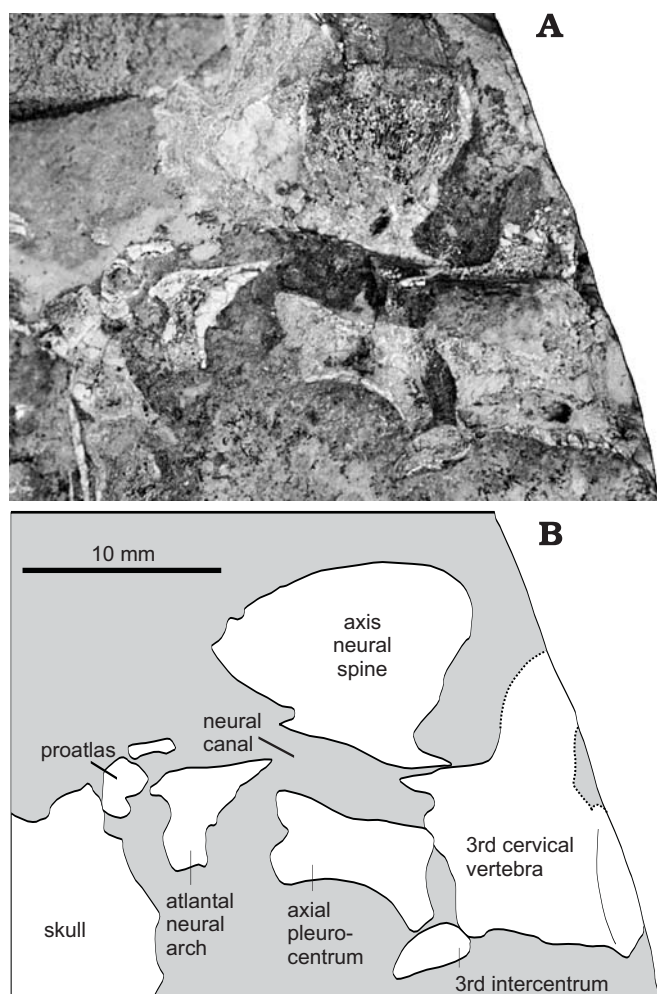


Fig. 7. Photograph (A) and outline drawing (B) of the axis of BP/1/5678, a putative specimen of *Elliot-Smithia longiceps* Broom, 1937, *Tapinocephalus* Assemblage Zone, Abrahamskraal Formation, Middle Permian, Western Cape Province, South Africa (Modesto et al. 2001) or *Heleosaurus scholtzi* Broom, 1907, *Tapinocephalus* Assemblage Zone, Abrahamskraal Formation, Middle Permian (Botha-Brink and Modesto 2009).

**Systematic implications.**—The main systematic and phylogenetic debate in varanopids centres on the diversity of South African specimens and the phylogenetic position of *Elliot-Smithia longiceps* (Dilkes and Reisz 1996; Reisz et al. 1998; Modesto et al. 2001; Reisz and Dilkes 2003; Maddin et al. 2006; Reisz and Modesto 2007; Botha-Brink and Modesto 2009; Campione and Reisz 2010). This debate arises from different interpretations of cranial morphology in the holotype material of *E. longiceps*, and the possibility that there are more than one species of varanopid co-existing in the late Middle Permian of South Africa. The discovery of new morphological variation in the axial skeleton of varanopids allows for further discussion regarding this debate.

The morphology of the atlas-axis in *Elliot-Smithia longiceps* (TM 1483) has been described on two separate occasions (Reisz et al. 1998; Modesto et al. 2001). The height of the spine is relatively tall compared to the centrum height, and appears to resemble most closely that of varanodontines

than mycterosaurines (Fig. 6A, C). The margins of the axis and centrum are poorly preserved in TM 1483 and therefore measurements are to be considered minima. The anterior sloping of the posterior margin of the spine is unique to *E. longiceps*, and although the sloping is not as pronounced as originally described (Reisz et al. 1998; Modesto et al. 2001), the lack of distortion in the succeeding cervical vertebrae suggests that the anterior tilt is not an artefact of preservation.

A putative second specimen of *Elliot-Smithia longiceps* (BP/1/5678), as described by Modesto et al. (2001), or *Heleosaurus scholtzi* as described by Botha-Brink and Modesto (2009), also preserves an axial vertebra. This vertebra was recently prepared completely (Fig. 7). Although the cranial morphology of BP/1/5678 is consistent with mycterosaurine characters (such as the shape of the lateral temporal fenestra), the axial spine is markedly different from other mycterosaurine specimens, and most closely resembles that of varanodontines and the plesiomorphic condition (Fig. 6C). In comparison, *Heleosaurus scholtzi* (SAM-PK-K8305; Carroll 1976), also from South Africa, most closely resembles the morphology of other mycterosaurines (Fig. 6C). Therefore, based on the morphology of the axis, our interpretation supports the hypothesis of Reisz and Dilkes (2003) that there are at least two distinct varanopids from South Africa during the middle Permian.

This study provides strong evidence for morphological variation in the atlas-axis of varanopids, and although larger samples are still required, the available evidence does not support the hypothesis that the South African varanopids could be synonymised into a single species (contra Botha-Brink and Modesto 2007, 2009; Reisz and Modesto 2007). Rather, variation in the axis spine suggests that there are at least two recognisable varanopid taxa in the middle Permian of South Africa. If this interpretation were valid, South Africa would be the second region to have more than one varanopid species. Currently, three distinct varanopid taxa are recognized from the Richards Spur Locality in Oklahoma (Evans et al. 2009). *Elliot-Smithia longiceps* may represent a third axial spine morphology, however, due to its incomplete nature an unequivocal assessment of its phylogenetic affinities cannot be made at this time. Nevertheless, it is evident that understanding the systematics of South African varanopids will be key to understanding the evolution of both Mycterosaurinae and Varanodontinae.

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# Appendix 1

Measurements (in mm) taken from axes of mycterosaurines, varanodontines, and their outgroups.

|                  | Taxa  | Spine length | Spine height | Centrum height | Total height |
|------------------|---|--------------|--------------|----------------|--------------|
| Mycterosaurinae  | Mycterosaurinae indet. (OMNH 53514)                   | 17.6         | 9.2          | 8.1            | 19.7         |
|                  | Mycterosaurinae indet. (OMNH 74628)                   | 14.4         | 7.3          | 6.5            | 16.7         |
|                  | Mycterosaurinae indet. (OMNH 73500)                   | 17.4         | 9            | 7.3            | 18.1         |
|                  | <i>Mycterosaurus longiceps</i> (FMNH UR 381)          | –            | 8.9          | 7.6            | –            |
|                  | <i>Heleosaurus scholtzi</i> (SAM-PK-K8305)            | 8.5          | 6.3          | 5.2            | 11.5         |
| Varanodontinae   | <i>Varanops brevirostris</i> (FMNH UR 2423)           | 20.5         | 18.7         | 10.5           | 32.5         |
|                  | Varanodontinae indet. (OMNH 73531)                    | 22.2         | 17.3         | 9.6            | 30           |
|                  | <i>Varanodon agilis</i> (FMNH UR 986)                 | –            | 21           | 12.9           | 39.1         |
| Other varanopids | <i>Elliotsmithia longiceps</i> (TM 1483)              | –            | 10.7         | 7              | 16.8         |
|                  | BP/1/5678   | 11.6         | 9.2          | 5              | 17.7         |
|                  | <i>Archaeovenator hamiltonensis</i> (KUVF 12483)      | –            | 3.5          | 1.9            | 7.8          |
| Outgroup         | <i>Ophiacodon retroversus</i> (Romer and Price 1940)  | 51.7         | 57.5         | 29.2           | 91.3         |
|                  | <i>Cotylorhynchus romeri</i> (Stovall et al. 1966)    | 30.5         | 30.6         | 27.8           | 75           |
|                  | <i>Dimetrodon limbatus</i> (Reisz et al. 1992)        | 45.7         | 74.3         | 32.4           | 111.3        |
|                  | <i>Secodontosaurus obtusidens</i> (Reisz et al. 1992) | 39.8         | 36.5         | 15.3           | 58.6         |