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OBSERVATIONS ON THE STRUCTURE OF THE EARLY PERMIAN REPTILE *STEREOSTERNUM TUMIDUM* COPE

by

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ABSTRACT

New information on the mesosaur *Stereosternum tumidum* is derived from a nearly complete skeleton and other material. Two autapomorphies are identified for *Stereosternum*: (1) presence of an 'odontoid' axial process, formed probably by co-ossification of the atlantal pleurocentrum to that of the axis, and (2) the presence of a posterior supraneural process on the neural arch of dorsal vertebrae. Temporal fenestration appears to be absent in *Stereosternum*, marginal teeth are determined to be subcircular rather than oval in cross section and in this respect resemble those of *Mesosaurus*, and there is no sign of fracture planes in the caudal vertebrae that could be indicative of caudal autotomy. A phylogenetic analysis, based on a slightly modified data matrix from the literature, identifies Mesosauridae as the sister group of Parareptilia within the reptilian clade Anapsida (*sensu lato*). As a consequence of this rearrangement of amniote tree topology, the stem-based taxon Sauropsida is regarded to be in abeyance, because it now includes exactly the same taxa as Reptilia. Mesosaurs, at more than 275 million years of age, can be recognised as the oldest known anapsid reptiles.

KEYWORDS: *Stereosternum*, mesosaurs, Anapsida, phylogeny, Permian

INTRODUCTION

Stereosternum tumidum was described in 1886 by E. D. Cope on the basis of specimens collected from limestones of the Irati Formation, Sakmarian of Brazil. These initial materials preserved only the posterior half of the skeleton, but the following year he (Cope 1887) published a brief description of a skull that, unfortunately, lacked an illustration. Cope recognized that *Stereosternum* shared several characteristics with the aquatic reptile *Mesosaurus tenuidens* (Gervais 1865), known then only from a single specimen from the white-weathering black shales of the Whitehill Formation of southern Africa. Interestingly, *Mesosaurus* was later collected in great quantities from the black shales of the Irati Formation less than three decades later (MacGregor 1908), whereas a century passed before *Stereosternum* was described also from the limestones of the Whitehill Formation (Oelofsen & Araújo 1987).

Following Cope's (1886, 1887) early descriptions, only Osborn (1903) published a detailed description of *Stereosternum*. Osborn's material was only slightly more complete than that available to Cope, and thus many aspects of the anatomy of *Stereosternum* still remain poorly known, especially that of the skull. Current knowledge of mesosaurid anatomy is derived almost exclusively from specimens of *Mesosaurus* (Seeley 1892; MacGregor 1908; Wiman 1925; Huene 1941; Oelofsen 1981). This is surprising, considering that specimens of *Mesosaurus* must be studied from natural moulds that, prior to the adoption of latex casting technology (Heaton 1982), necessitated their study via relatively poor plaster and gutta percha casts. The friable nature of the black shale matrix also limits the number of specimens preserving the greater part of the skeleton. Thus, most of our knowledge of mesosaurid anatomy is based on relatively meagre materials. In strong contrast, complete skeletons of *Stereosternum* of exceptional preservation have been collected from the Irati Formation limestones. One of the best prepared specimens is reposited in the Black Hills Museum of Natural History in Hill City, South Dakota. This individual preserves an almost complete, well preserved skull, a rarity among most museum specimens of *Stereosternum*. A detailed description of the specimen is provided here, with supplementary information from less complete juvenile material.

MATERIALS

The specimens used in this study, BHM 999 (formerly 'BHI 999') and AMNH 11009, from the Black Hills Museum of Natural History and the American Museum of Natural History in New York, respectively, are from the Irati Formation of Brazil. No locality information is available. The Irati is thought by Oelofsen & Araújo (1987) to be Sakmarian in age (roughly 275 million years old). It was divided into two geographical zones by Barberena (1972): zone A consists mainly of black shales with exposures in the Brazilian states of Paraná, Santa Catarina, and Rio Grande do Sul, which have produced mainly *Mesosaurus brasiliensis*; fragmentary skeletons and isolated elements attributable to both *Stereosternum tumidum* and *Brazilosaurus sanpauloensis* have been collected from interbedded limestones at the Passo de São Borja locality in Rio Grande do Sul (Oelofsen & Araújo 1983). Zone B is comprised predominantly of limestone with exposures in the Brazilian states of Paraná and São Paulo, and have produced complete skeletons of *Stereosternum tumidum* and *Brazilosaurus sanpauloensis*. As the study specimens are reasonably complete, they probably come from localities in the latter two states. A complete specimen (NMS R4710) of *Stereosternum tumidum* in the Natur-Museum Senckenberg, Frankfurt was also examined, but because circumstances did not permit its illustration, mention of this specimen is limited to brief commentary on pedal morphology.

The genera *Mesosaurus*, *Stereosternum*, and *Brazilosaurus* are monotypic. Accordingly, these generic names are used henceforth in preference to their respective specific binomens.

DESCRIPTION

BHM 999 was exposed by previous workers who split the encasing limestone in order to produce a part and a counterpart. Most of the skeleton is present in the available block; it lacks part of the right side of the skull roof, the vertebral column distal to the twelfth cervical through to the first caudal, the tail distal to caudal 14, and portions of the hind limbs. The truncated tail ends at the edge of the block, and nothing can be said of the length of the tail. The other missing areas are presumably to be found on the counterpart, the whereabouts of which is unknown, but their former presence is marked by impressions. Missing elements of the right hind limb have been built up with bone-colored putty, presumably for display purposes. The veracity of these cosmetic restorations is uncertain, and so their outlines are not reproduced in Figure 1. The carpals and tarsals are well ossified, indicating that the skeleton is adult.

Skull (Figures 1 & 2)

The skull is roughly equal in length to the neck, a characteristic unique to *Stereosternum* among mesosaurs (Oelofsen & Araújo 1987). The antorbital region comprises just under three-quarters the total length of the skull. The external naris is positioned approximately at the halfway point of the skull roof. Accordingly, the snout is not as long in relative dimensions as that seen in *Mesosaurus*. Apart from some parasagittal grooves on the premaxilla, the skull roof is devoid of sculpturing. What appear to be lateral excavations at the bases of the premaxillary teeth are the result of crushing of the relatively thin bone forming the lateral walls of the tooth pits. What is visible of the right squamosal and left jugal suggests that a lower temporal opening was not present, unless it was very small. Well-preserved skulls of *Mesosaurus* reveal that a temporal opening was not present in that mesosaur either (Oelofsen 1981; pers. obsv.).

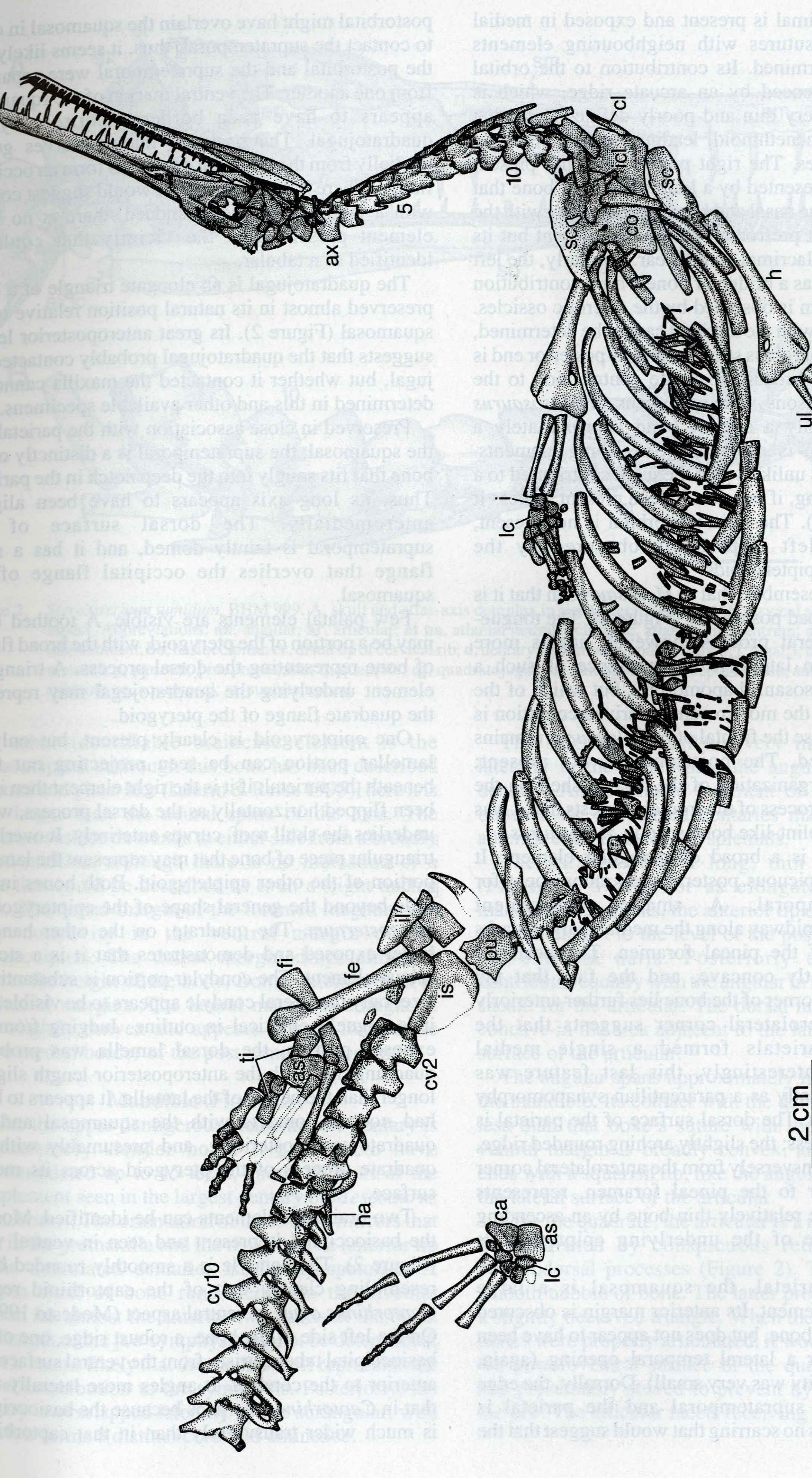
The premaxilla dominates the snout. It accommodates 12 teeth, with room for two or three additional teeth. This complement falls well short of the number (20+) found in the premaxilla of *Mesosaurus*. The teeth fall into two main types: long and short teeth, with the latter no longer than half the length of the former. The shorter teeth may be replacing teeth that were moving into position. Four of the long teeth are each preceded by shorter teeth and collectively they suggest a pattern of alternating long and short teeth. The anteriormost teeth extend almost directly ventrally, with no suggestion of the procumbency seen in *Mesosaurus*. Tooth morphology is described below.

The maxilla is a distinctly triangular bone in lateral view. As preserved it accommodates 14 teeth, with room for three more as evidenced by gaps. One or two additional teeth may have been present on the missing posterior portion. The specimen shows clearly that the anterodorsal margin was overlain slightly by the premaxilla. The primitive condition for amniotes is for the maxilla to overlap deeply the posterior process of the premaxilla. Thus, it appears that in association with the development of an extensive anterior process of the maxilla in mesosaurs, the nature of the suture with the premaxilla was modified as well. On average, the maxillary teeth are shorter than those in the premaxilla, with only a single anterior tooth rivalling the longest premaxillary teeth. However, it would be inappropriate to designate this tooth a caniniform in view of the similarly sized premaxillary teeth.

The septomaxilla comprises an elongate anterior footplate and a posterior facial process (Figure 2). A medial flange extends horizontally into the nares from the footplate. A prominent V-shaped excavation at the base of the facial process probably represents the external opening of the septomaxillary foramen.

Little can be said of the nasal apart from the observation that it shares a strongly serrate suture with the premaxilla that ranges the same anteroposterior extent as the external nares. At the posterior end, slight crushing has exaggerated the nature of the contact with the frontal, which is essentially a simple overlapping suture.

Figure 1. *Stereosternum tumidum*, BHM 999, skeleton with skull and vertebrae visible in right lateral view and appendicular elements seen largely in dorsal aspect. Note the gastralia dispersed among the dorsal ribs, along the ventral midline. Abbreviations: **as**, astragalus; **ax**, axis; **ca**, calcaneum; **cl**, clavicle; **co**, coracoid portion of scapulocoracoid; **cv2**, second caudal vertebra; **cv10**, tenth caudal vertebra; **fe**, femur; **fi**, fibula; **h**, humerus; **ha**, haemal arch and spine; **i**, intermedium; **icl**, interclavicle; **il**, ilium; **is**, ischium; **lc**, lateral centrale; **pi**, pisiform; **pu**, pubis; **ra**, radius; **sc**, scapular blade of scapulocoracoid; **sp**, splenial; **ti**, tibia; **ul**, ulna. Arabic numerals denote cervical vertebrae.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The left lacrimal is present and exposed in medial view, but its sutures with neighbouring elements cannot be determined. Its contribution to the orbital margin is evidenced by an arcuate ridge, which is covered by a very thin and poorly defined bone that may be the sphenethmoid, leading up to a series of sclerotic ossicles. The right prefrontal is not present unless it is represented by a long splinter of bone that lies alongside the nasal and has a small contact with the frontal. The left prefrontal is probably present but its suture with the lacrimal is not clear. Similarly, the left jugal is present as a bridge of bone whose contribution to the orbital rim is obscured by the sclerotic ossicles. Its relationship with the lacrimal cannot be determined, but its ventral margin is straight, and its posterior end is suggestive of a broadly spatulate contribution to the cheek. Comparisons with specimens of *Mesosaurus* suggest that only a narrow band approximately a millimeter deep is covered by overlying elements. Thus, it appears unlikely that the jugal contributed to a temporal opening, if one was indeed present (unless it was very small). The right postorbital is not present, whereas the left is probably obscured by the disarticulated epipterygoids.

The frontal resembles that of *Mesosaurus* in that it is transversely broad posteriorly (Figure 2). The tongue-like posterolateral process, however, angles more posteriorly than laterally. The presence of such a process is a mesosaurid apomorphy, but which of the two attitudes is the more recently derived condition is uncertain because the frontal of *Brazilosaurus* remains to be described. The postfrontal is not present; however, the organization of the narrow shelf on the posterolateral process of the frontal suggests that it was similar to the splint-like bone seen in *Mesosaurus*.

The parietal is a broad quadrangular element. It features a conspicuous posterolateral embayment for the supratemporal. A smaller embayment approximately midway along the medial margin marks the position of the pineal foramen. The posterior margin is faintly concave, and the fact that the posteromedial corner of the bone lies further anteriorly than the posterolateral corner suggests that the articulated parietals formed a single medial embayment. Interestingly, this last feature was recognized recently as a parareptilian synapomorphy (Modesto 1999). The dorsal surface of the parietal is flat and featureless; the slightly arching rounded ridge, seen running transversely from the anterolateral corner to just anterior to the pineal foramen, represents distortion of the relatively thin bone by an ascending process of one of the underlying epipterygoids (Figure 2).

Like the parietal, the squamosal is a large quadrangular element. Its anterior margin is obscured by an overlying bone, but does not appear to have been emarginated for a lateral temporal opening (again, unless this vacuity was very small). Dorsally, the edge contacting the supratemporal and the parietal is straight. There is no scarring that would suggest that the postorbital might have overlain the squamosal in order to contact the supratemporal; thus, it seems likely that the postorbital and the supratemporal were separated from one another. The ventral margin of the squamosal appears to have been bordered entirely by the quadratojugal. The posterior margin curves gently medially from the temporal portion to form an occipital flange. There is no scarring that would suggest contact with a large tabular bone. Indeed, there is no large element preserved in the vicinity that could be identified as a tabular.

The quadratojugal is an elongate triangle of a bone preserved almost in its natural position relative to the squamosal (Figure 2). Its great anteroposterior length suggests that the quadratojugal probably contacted the jugal, but whether it contacted the maxilla cannot be determined in this and other available specimens.

Preserved in close association with the parietal and the squamosal, the supratemporal is a distinctly ovoid bone that fits snugly into the deep notch in the parietal. Thus, its long axis appears to have been aligned anteromedially. The dorsal surface of the supratemporal is faintly domed, and it has a short flange that overlies the occipital flange of the squamosal.

Few palatal elements are visible. A toothed bone may be a portion of the pterygoid, with the broad flange of bone representing the dorsal process. A triangular element underlying the quadratojugal may represent the quadrate flange of the pterygoid.

One epipterygoid is clearly present, but only its lamellar portion can be seen projecting out from beneath the parietal; if it is the right element then it has been flipped horizontally as the dorsal process, which underlies the skull roof, curves anteriorly. It overlies a triangular piece of bone that may represent the lamellar portion of the other epipterygoid. Both bones impart little beyond the general shape of the epipterygoid in *Stereosternum*. The quadrate, on the other hand, is better exposed and demonstrates that it is a stocky, robust element. The condylar portion is substantial in size; only the lateral condyle appears to be visible, and it is vaguely elliptical in outline. Judging from the exposed portion, the dorsal lamella was probably quadrangular, with the anteroposterior length slightly longer than the height of the lamella. It appears to have had normal contacts with the squamosal and the quadratojugal posteriorly, and presumably with the quadrate process of the pterygoid across its medial surface.

Two braincase elements can be identified. Most of the basioccipital is present and seen in ventral view (Figure 2). The condyle is a smoothly rounded boss, resembling closely that of the captorhinid reptile *Captorhinus aguti* in ventral aspect (Modesto 1998b). On the left side of the bone, a robust ridge, one of the basioccipital tubera, arises from the ventral surface just anterior to the condyle. It angles more laterally than that in *Captorhinus*, perhaps because the basioccipital is much wider transversely than in that captorhinid.

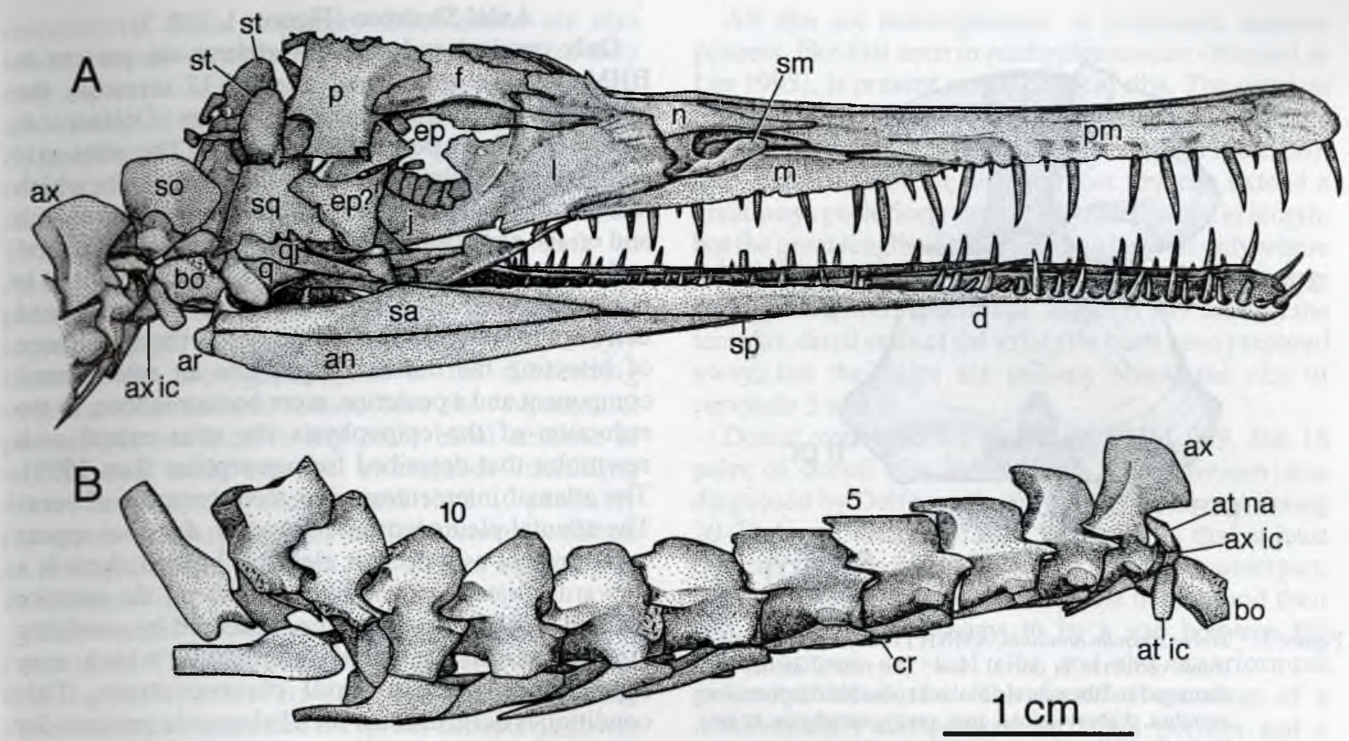

Figure 2. *Stereosternum tumidum*, BHM 999. A, skull and atlas-axis complex in right lateral view, and B, cervical series in right lateral aspect. Abbreviations: **an**, angular; **ar**, articular; **at na**, atlantal neural arch; **at ic**, atlantal intercentrum; **ax**, axis; **ax ic**, axial intercentrum; **bo**, basioccipital; **cr**, distal tip of cervical rib; **d**, dentary; **ep**, epipterygoid; **f**, frontal; **j**, jugal; **l**, lacrimal; **m**, maxilla; **n**, nasal; **p**, parietal; **pm**, premaxilla; **q**, quadrate; **qj**, quadratojugal; **sa**, surangular; **sm**, septomaxilla; **so**, supraoccipital; **sp**, splenial; **sq**, squamosal; **st**, supratemporal.

The other identifiable braincase element is the supraoccipital. Although this bone has been described as broad and plate-like (Laurin & Reisz 1995), here it is little larger than the neural spine of the axis. The posterior surface descends to either side from a broadly raised midline, although there is no indication of a ridge that could be described as even a slight nuchal crest. The dorsal margin of the foramen magnum is a deep concavity in the ventral margin of the supraoccipital. The dorsal margin drops almost a quarter the height of the bone, from a midline peak to the lateral margins. The lateral margin is straight or only slightly convex and appears to have formed the entire medial border of the post-temporal opening.

Mandible (Figure 2)

Like the upper dentigerous elements, the dentary is an extremely slender bone. It appears to have accommodated up to 45 teeth, about 10 short of the complement seen in the largest dentary of *Mesosaurus* (pers. obsv.). The orientation of these teeth mirrors that seen in the premaxilla and the maxilla. The anterior tip of the articulated dentaries is slightly spatulate. A smooth shelf of bone runs medial to the alveolar portion for almost the anterior two-thirds of the bone. The length of the jaw symphysis cannot be determined, but it is seems likely that the medial shelf represents the dorsal contribution to the symphysis. Posteriorly, the dentary is overlapped laterally by the surangular, with which it forms a distinct coronoid eminence.

The splenial has only a very narrow exposure laterally in the area where the angular contacts the dentary. An acuminate fragment of bone extending between the articulated dentaries may represent the anterior end of one of the splenials.

The surangular is a long, thin sheet of bone (Figure 2). While not as elongate as the other mandibular elements, the anterior tip of the surangular extends almost to the level of the posterior margin of the external naris. Posteriorly the surangular contributes equally with the angular in forming a lateral sheath for the articular. The dorsal margin is slightly concave in the area adjacent to the lateral articulating surface of the articular.

The angular spans approximately half the length of the mandible. Its contact with the dentary is markedly less than that bone's suture with the surangular. Its ventral margin is broadly convex, and posteriorly it ends with a squarish tip, like the angular, that sheathes the lateral surface of the articular.

Like the quadrate, the articular is a robust bone. It is distinguished by conspicuous retroarticular and posterodorsal processes (Figure 2). The former is a smooth nubbin of bone. The latter projects dorsally as a slightly decurved triangle. When the jaw suspension bones were properly articulated, it would have hugged the posteroventral surface of the quadratic condyles and presumably served to prevent hyperadduction of the jaw. The articular facets receiving the condyles are

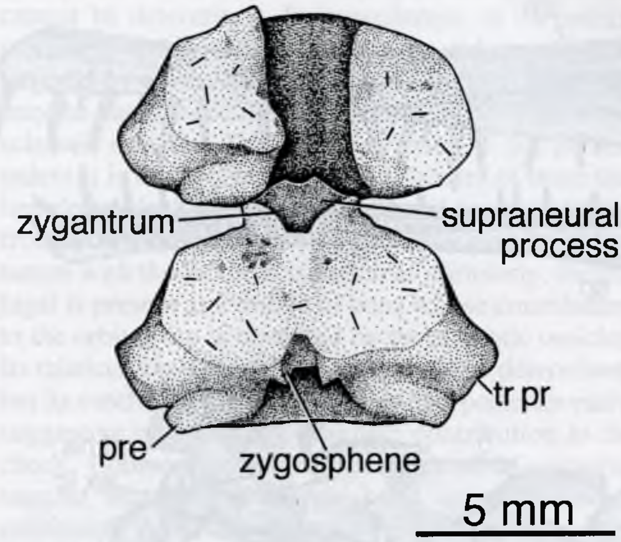

Figure 3. *Stereosternum tumidum*, AMNH 11009, two articulated trunk vertebrae in dorsal view. The neural arches are damaged and the neural canal is exposed in the posterior vertebra. Abbreviations: **pre**, prezygapophysis; **tr pr**, transverse process.

not well exposed, but what is visible suggests that it facilitated only orthal movements of the lower jaw.

Dentition (Figure 2)

The homodont marginal teeth are slender with sharply pointed, slightly recurved tips. The longest teeth are roughly three tooth positions in length (measured from base to tip), and so are absolutely shorter than those in *Mesosaurus* where they exceed five tooth positions in length (pers. obsv.). Basal tooth diameter is about 14 percent total tooth length. Oelofsen & Araújo (1987) described the teeth as oval in cross section. However, the tooth bases of all teeth are subcircular in cross sections. Some of the larger teeth do appear laterally compressed (distal to their subcircular bases), but close examination under light microscopy reveals that this is an artifact of crushing: the teeth are expanded slightly anteriorly and posteriorly and there is a conspicuous furrow that runs down the lateral surface, features strongly suggestive of transverse compression of the teeth. Uncrushed teeth display a gradual decrease in diameter from base to tip. There is the expected reduction in length and diameter towards the posterior end of the dentition in each jaw, in addition to the alternation between long and shorter teeth observed for upper and lower jaws. The shorter teeth may represent replacement teeth, but their is no evidence of remodeling of the alveolar bone, as characteristic of newly ankylosed or ankylosing replacement teeth in other early reptiles (e.g., Modesto 1996a). The marginal teeth appear to be implanted in subthecodont fashion in shallow, regularly spaced sockets. The palatal teeth that can be examined are much smaller than the majority of marginal teeth. They are sharp, straight, homodont structures with subcircular cross sections.

Axial Skeleton (Figures 1, 2 & 3)

Only cervical and caudal vertebrae are present in BHM 999. An articulated series of 12 cervicals, the normal complement for *Stereosternum* (Oelfosen & Araújo 1987), is present (Figure 2B). The atlas-axis complex is complete except for the proatlas, for which there is an articulating facet on the atlantal neural arch and on the exoccipital (Figure 2B). The atlantal neural arch has a small transverse process, although no rib is preserved. There is no distinct epipophysis, and instead there is a low angular mound that gives the appearance of bisecting the dorsal margin into an anterodorsal component and a posterior, more horizontal one. In the reduction of the epipophysis the atlas neural arch resembles that described for parareptiles (Lee 1997). The atlantal intercentrum is a stout crescent of bone. The atlantal pleurocentrum, however, does not appear to be present as a distinct element. Instead, there is a forward-projecting cone-like process on the anterior tip of the axial pleurocentrum, obscured by overlying atlantal neural arch and intercentra, which may represent a fused atlantal pleurocentrum. This condition is quite unusual for a Palaeozoic amniote, for primitively the atlantal pleurocentum is either fused to the anterodorsal surface of the axial intercentrum or it is a discrete element positioned immediately dorsal to the intercentrum, and thus the organization of the atlas described here appears to be unique to *Stereosternum*. In specimens of *Mesosaurus* in which this area is adequately exposed, a single structure comprising a fused atlantal pleurocentrum and axial intercentrum is present (pers. obsv.), the primitive condition for amniotes (Sumida *et al.* 1992).

The axis comprises a small pleurocentrum with co-ossified neural arch and a discrete intercentrum (Figure 2B). The neural spine is hatchet-shaped. A conspicuous ridge arises on its lateral surface and curves posteroventrally onto the postzygapophyses. The ridge may be serially homologous with the mammillary processes that surmount the postzygapophyses in succeeding vertebrae. Postaxial vertebrae lack intercentra. The third cervical appears to have an organization transitional between the axis and the fourth cervical vertebrae. Neural spine height decreases dramatically over the succeeding three vertebrae, and then increases again posteriorly from the seventh cervical. The axial pleurocentrum is the shortest cervical, and the centra gradually increase in sagittal length posteriorly along the series (Figure 2B).

BHM 999 is missing the entire series of dorsal vertebrae. Examination of other referred specimens of *Stereosternum* indicates that, outwardly, the dorsals of this mesosaur do not differ from those of *Mesosaurus* (von Huene 1941). However, a fortuitous horizontal section through two dorsals in the articulated vertebral column of a juvenile, AMNH 11009, reveals two important anatomical features of the neural arch (Figure 3). The first is the presence of zygosphenes and zygantra, small accessory articulations that flank the supraneural pits anteriorly and posteriorly, respectively. These accessory articulations are also seen in dorsal vertebrae of *Mesosaurus*, and so they may represent a mesosaurid synapomorphy (neural arch morphology of *Brazilosaurus* is unknown). Zygosphenes and zygantra are present also in mosasaurs, where they are thought to have helped to dampen twisting movements of the column (Russell 1967). The second vertebral feature seen in AMNH 11009 is a narrow but broad tongue-like process that floors the zygantra and posterior supraneural pit, and projects posteriorly to fit snugly between the prezygapophyses of the succeeding vertebra. This feature, termed here the 'supraneural process', is not seen in any other basal amniote in which this area can be examined, including *Mesosaurus* (pers. obsv.), and thus it probably represents an autapomorphy of *Stereosternum* (albeit an ambiguous one, because this area is unknown in *Brazilosaurus*).

The caudal vertebrae (Figure 1) are robustly constructed. The anterior six of the preserved series are missing their neural spines, but the succeeding vertebrae demonstrate that the spines become narrower and increase slightly in height posteriorly. The tips of several spines are slightly curved anteriorly. Only the anteriormost preserved member of the series (the second caudal) is visible in dorsal aspect and reveals that the arch is approximately as wide as long; mammillary processes are present on this and the succeeding caudal, but are absent on the remainder of the series. Ribs were borne by the proximal 11 caudals, but all ribs are damaged and little can be said of their morphology apart from the observation that they are dorsoventrally compressed anteriorly but become subcircular in cross section in the posterior four of the series. Intercentra are absent and haemal arches are fused indistinguishably to the preceeding vertebra. There is no evidence that caudal intercentra have fused with the pleurocentra (if such intercentra were ever present). The posterior part of each caudal centrum is accentuated by a slight trough that runs down the lateral surface of the centrum, an excavation that was interpreted as a fracture line for facilitating caudal autotomy (Osborn 1903; Broom 1904). However, the fine cracks representing lines of weakness in extant lizards that can autotomize the tail (Etheridge 1967; Bellairs & Bryant 1985) are absent here, suggesting strongly that caudal autotomy was not present in *Stereosternum*.

Haemal arches are present from the fourth caudal to the last preserved vertebra. They have the appearance of slightly swollen wishbones. The haemal spines are short and the tips of some are conspicuously expanded anteroposteriorly. The haemals of caudals 12 and 13 are twisted and co-ossified for most of their length. This may be a result of ankylosing spondylitis (Stuart Sumida, pers. comm.) or may have resulted from some trauma to the underside of the tail. Either conjecture lends support to the idea that *Stereosternum* was incapable of caudal autotomy.

All ribs are holocephalous. A prominent anterior process, like that seen in pachypleurosaurs (Rieppel & Lin 1995), is present on all cervical ribs. The cervical ribs are slender, rod-like structures, except those on the last two cervicals, which are broad and flat (Figure 2B). The distal ends of the anteriormost ribs can extend a great ways posteriorly, up to 4 cervical centra in length, but the great length of these ribs can be seen only where the cervical vertebrae have been carefully prepared as in several AMNH specimens. In BHM 999 most of the tenuous, distal ends of the axial ribs have been prepared away, but their tips are present below the ribs of cervicals 5 and 6.

Dorsal vertebrae are absent in BHM 999, but 18 pairs of dorsal ribs are present. *Stereosternum* was diagnosed by Oelfosen & Araújo (1987) as possessing 20-22 dorsal vertebrae, so it seems likely that at least two pairs of ribs ended up on the missing counterpart. Possible candidates are anteriormost dorsals and their ribs, because there seems to be a gap between the posteriormost cervical ribs and the anteriormost preserved dorsal ribs. The dorsal ribs consist of a dorsoventrally compressed proximal portion and a distal, thickened portion. The latter is essentially circular in cross section, but crushing has left prominent grooves in many of the ribs from overlying, missing portions of other ribs. An elongate dimple is present on the posterior surfaces of well-preserved ribs. It may mark the former attachment site for intercostal cartilage. The posteriormost left dorsal rib is oriented laterally, in parallel with the sacral ribs. This suggests that the last pair of dorsal ribs are fused to their vertebra in adult *Stereosternum*, as in *Mesosaurus* (pers. obsv.).

The two left sacral ribs are partially preserved and maintain their contact with the ilium. Both are dorsoventrally compressed and subequal in anteroposterior breadth. The fragment of the second sacral rib is smaller than that of the first, to which it is firmly attached for almost all of its preserved length.

Gastralia litter the former ventral midline of the trunk between the left and right series of dorsal ribs. Most are preserved loosely in their former area, but several remain in articulation and collectively are suggestive of the imbricate pattern seen in other early reptiles. Each dermal riblet is a dorsoventrally flattened splint of bone, and there is no evidence of chevron-shaped midline elements (as seen in neodiapsids). Most riblets are no longer than a typical metacarpal, but a few exceed the length of the longest manual digit.

Appendicular Skeleton (Figure 1)

The shoulder girdle is well-preserved apart for the clavicle, of which only a fragment remains of the right element. No cleithrum is in evidence, but, considering the state of the remaining clavicle, the absence of the cleithrum may be either taphonomic or an artefact resulting from the manner in which the specimen was exposed by the original collectors. The well preserved interclavicle comprises a diamond-shaped head and a posterior parasternal stem. The former is flat and featureless, and the latter is slightly constricted proximally and ends posteriorly with a truncated tip.

The scapulocoracoid is present as a single unit. The scapular portion is dorsoventrally short and curves posteriorly almost as far as the posterior end of the coracoid. There is no supraglenoid foramen. The anterodorsal margin of the scapula merges almost indistinguishably with the anterior margin of the coracoid; a faint notch (partly obscured by two gastralia) may mark the border between the two component elements. The coracoid is large and plate-like. Anteriorly it is suboval in outline, but the posterior end appears quadrangular, albeit with broadly rounded corners. Just anteromedial to glenoid angle, the coracoid is pierced by the coracoid foramen. Subcoracoscapular and coracoid fossae and their associated ridges, prominent in other early tetrapods, are absent.

Among non-mesosaurid amniotes the humerus resembles most closely that of romeriid reptiles (*sensu* Gauthier *et al.* 1988) in relative slenderness. The diameter of the shaft is about 10 per cent the total length of the bone. The distal width of the bone is comparable to that seen in romeriids, being slightly less than 35 per cent the total length of the humerus. The distal end is angled slightly more postaxially, resulting in a relatively straight anterior margin and a slightly more concave posterior margin. The proximal head of the humerus is only slightly expanded compared to the shaft, and it is set at a right angle to the distal end; a small tubercle visible on its dorsal surface may have served for the insertion of the scapulohumeralis muscle. The entepicondyle is relatively small and, as in other reptiles, the supinator process is directed distally.

Both the radius and the ulna are rod-like, narrowly waisted elements that are just under half the length of the humerus (Figure 1). The shafts of both are smooth and featureless, with truncated proximal and distal ends.

The manus is well ossified. In dorsal aspect the curved digits and their metacarpals describe an almost perfect ovoid; it probably formed a stout paddle. The carpus is comprised of nine elements. The three largest are the ulnare, the intermedium, and the lateral centrale. The perforating foramen resembles more the spindle-shaped passage that has been restored for the synapsid *Ophiacodon*, rather than the distinctly circular opening bounded by the intermedium and ulnare that is seen in the reptiles *Labidosaurus* and *Petrolacosaurus* (Sumida 1997). The radiale is unossified, judging from the conspicuous gap between the end of the radius and the first distal carpal, whereas the medial centrale was either unossified as well, or it was entirely absent. Five distal carpals are present, of which the first is the largest. A pisiform is present, well ossified, and larger than the fifth distal carpal. The metacarpals and phalanges are relatively much shorter than those of other amniotes. Those of the first digit are fairly robust, whereas the metacarpals and phalanges become more slender postaxially. The phalangeal formula differs from the plesiomorphic amniote pattern of 2·3·4·5·3 with the loss of a single phalanx from the fourth digit. The unguals are spade-shaped. The first four digits curve postaxially, whereas the fifth is strongly divaricate, as in some mosasaurs (Russell 1967).

The pelvic girdle did not survive as well as the pectoral elements the splitting process used to expose the specimen originally (Figure 1). The entire right side of the girdle is missing, as are portions of the left pubis and ischium, although the associated ilium is very well preserved. None of the remaining pelvic elements are co-ossified. The medial portion of the pubis is absent and the remaining dorsal part has rotated almost 90 degrees from its normal position; the larger of the two notches neighbouring the ischium represents part of the formerly enclosed obturator foramen. Most of the ischium is present and the extent of the missing portion can be restored from its impression. This bone does not differ notably from those of other basal amniotes, apart from having a more gracile dorsal margin. Although it is well preserved, the ilium is not well exposed. The dorsal margin is only marginally longer than the region receiving the sacral ribs and is slightly roughened for muscle attachment. The posterior process tapers abruptly. The ventral portion contributing to the acetabulum appears to be the thickest part of the bone.

Only the left femur is present and it is visible in anteroventral aspect. It is notably more slender than those of contemporaneous terrestrial amniotes; the widths of the proximal and distal ends are both roughly one-fifth, and the shaft about one-tenth, the total length of the bone. The internal trochanter is a weak, rounded ridge and the shaft is smooth and devoid of the adductor ridge system that characterizes terrestrial forms. The distal end is broadly rounded; the medial and lateral condyles are subequal and conjoined with no sign of the notch that separates the condyles of terrestrial basal cotylosaurs. The distal condylar surfaces together form a single, hourglass-shaped articulating surface.

The tibia is about two-thirds the length of the femur. The proximal end appears to be no broader than one-fifth the total length of the bone. Its articulating surface is broadly elliptical and moderately convex in side view. The fibula is as long as the tibia but is broader than that bone throughout most of its length, with the proximal end conspicuously expanded. The fibula is dorsoventrally compressed for most of its length apart from the slightly thicker proximal end. These two elements are essentially indistinguishable from those of *Mesosaurus* (pers. obsv.).

Although the right propodial and epipodials are missing, the right tarsus is well preserved with the exception of the first distal carpal, of which only its impression remains. Of the disarticulated left tarsus only the astragalus, two of the larger distal tarsals, and the calcaneum can be seen, the last of which is mostly obscured by the left tibia. The right astragalus is a distinctly quadrangular bone, with the proximal end slightly narrower than the distal margin. There is no dorsal component to the articulating surface for the tibia. The lateral margin bears a small notch, the astragalar contribution to the perforating foramen, approximately midway along its length, whereas the distal margin is slightly convex for the reception of the lenticular lateral centrale. The left astragalus is less quadrangular in outline, marginally broader, and conspicuously longer proximodistally than its counterpart in the right tarsus. The distal margin is mostly obscured by overlying metapodials and so the left astragalus was marginally longer than what is visible. It is at least equal in length to the articulated astragalus and lateral centrale in the right tarsus, suggesting strongly that the astragalus and laterale centrale in the left pes were indistinguishably fused. Augmentation of the astragalus by incorporation of the lateral centrale is invariably seen in *Mesosaurus* (Rieppel 1993; Modesto 1996b), and so this individual of *Stereosternum* appears to be polymorphic with respect to the two conditions. The same polymorphism appears to be present in NMS R4710, where the left lateral centrale is distinct but the right is co-ossified with its respective astragalus (pers. obsv.).

The calcaneum is markedly smaller than the astragalus. It is triangular in outline, with broadly rounded corners (Figure 1), and thus differs dramatically in both shape and size from the distinctly plate-like calcanea of terrestrial basal amniotes (Rieppel 1993). The notch for the perforating foramen is positioned just distal to the midway point of the margin contacting the astragalus.

Of the four distal tarsals present in the right tarsus, the fourth is only slightly larger than the second and third elements, which are subequal in size; the fifth distal tarsal is by far the smallest of the series. The impression of the first distal tarsal suggests that it is intermediate in size between the fifth element on one hand and the second and third elements on the other. However, the first distal tarsal is always the largest in specimens of *Mesosaurus*, doubtless because it is associated with the most robust metatarsal (Modesto 1996b), and so the unexpectedly small size of the impression is most likely an artifact resulting from when the specimen was exposed by the splitting of its encasing matrix.

Four of the five metatarsals are preserved between the two pedes. The first metatarsal is present on the left side. It is the broadest and shortest of the series, and is distinctly flattened dorsoventrally. The remaining metatarsals are elongate rods that increase in length postaxially. Between the two pedes the phalangeal formula can be determined to be 2·3·4·5·5, the standard pedal formula for mesosaurs (Modesto 1996b). The digits increase in length postaxially. The phalanges comprising each digit become narrower as one progresses postaxially, such that the longest, the fifth toe, is also the most gracile. The unguals of the first three toes are, as in the manus, spade-like, with the fourth somewhat less so, and the fifth present as tiny claw that resembles the unguals of terrestrial reptiles. The toes were embedded in a web of skin that was strengthened by rays, or fibres, which run parallel to the toes in rare specimens that preserve skin fragments (Rösler & Tatizana 1989). Presumably this condition also applied to the manus.

DISCUSSION

Study of BHM 999 supports most of the identifying characteristics that have been observed for *Stereosternum* by previous workers. The most salient of these is the head to neck ratio of approximately 1:1 (MacGregor 1908; Oelofsen & Araújo 1987). The trunk ribs and haemal arches are also conspicuously thickened, or pachyostotic, as recognized by Oelofsen & Araújo (1983, 1987). However, the pachyostotic nature of the former is shared also with *Mesosaurus*, whereas the condition of thickened haemal arches is shared with *Brazilosaurus*. In contrast to statements by Oelofsen & Araújo (1987) that the marginal teeth of *Stereosternum* are compressed transversely (i.e., the teeth have oval cross sections), the slightly compressed appearance of the teeth appears to be an artifact of crushing in BHM 999; the teeth of this individual were circular in cross section throughout their entire length, as described for *Mesosaurus* (Oelofsen and Araújo 1987).

The most unusual and intriguing feature of BHM 999 is the structure of the atlas-axis complex. Whereas *Mesosaurus* displays a normal organization of a distinct and well ossified atlantal pleurocentrum and crescentic atlantal and axial intercentra, and the anterior end of the axial pleurocentrum is normally developed in *Brazilosaurus* (pers. obsv. of the holotype), there is no distinct atlantal pleurocentrum in BHM 999. In its place is a conspicuous anterior process protruding from the axial pleurocentrum. Although this process resembles the odontoid of mammals, it is clearly not the relatively small, peg-like process of the mammalian axis. Because only the base of the 'odontoid' of *Stereosternum* is known, its functional significance is far from clear. It may correlate with the presence of a long skull on a long neck in *Stereosternum*. The head of *Mesosaurus*, being larger both in absolute and relative terms, is mounted on a relatively shorter, slightly more robust neck, and the neck of *Brazilosaurus* is relatively longer and it supports a skull that is absolutely smaller (Oelofsen & Araújo 1987). The 'odontoid' process of *Stereosternum*, therefore, may have served to minimize movement at the junction between skull and neck. Although the skull must have been fairly hydrodynamic, it was relatively large in relation to the neck and still had to plough through water as the animal moved forwards, quite possibly with the jaws making lateral sweeps during foraging maneuvers.

Fortuitous breakage of dorsal vertebrae in a juvenile specimen reveals a second autapomorphy for *Stereosternum*: the presence of a supraneural process on the neural arch of trunk vertebrae. This feature must be regarded for the time being as an ambiguous autapomorphy of *Stereosternum*, as the vertebral column of *Brazilosaurus* remains to be described in detail. Similarly, the presence of accessory vertebral articulations, zygosphenes and zygantra, are considered an ambiguous apomorphy uniting *Stereosternum* and *Mesosaurus*, given that the presence of these accessory articulations cannot be determined in *Brazilosaurus* using the available materials.

In addition to the absence of a maxillary caniniform tooth and a supraglenoid foramen, there are two features in BHM 999 that are suggestive of parareptilian affinities for mesosaurs. The first is the modification of the posterior margin of the parietals to form a single median posterior emargination of the skull roof. This character, present also in *Mesosaurus* (pers. obsv.), was identified only recently as a parareptilian synapomorphy (Modesto 1999). The second is the absence of an atlantal epipophysis, identified by Lee (1997) as a synapomorphy of parareptiles (regarded by Lee 1995, only as a potential parareptilian apomorphy). It should be noted here that, *contra* Lee (1997), an epipophysis is indeed present in millerettids: personal examination of BP/1/3821, the most complete skeleton of *Milleretta rubidgei* (and the only millerettid specimen that preserves the atlas-axis complex), reveals that a small epipophysis is present on the left atlantal neural arch, as reconstructed by Gow (1972); the right arch is damaged and its epipophysis appears to have been spalled off.

In the first phylogenetic analysis to include mesosaurs with other amniote taxa (Gauthier *et al.* 1988), they were grouped together with millerettids, pareiasaurs, and procolophonids. A subsequent study by Laurin & Reisz (1995) grouped the last three taxa together in a clade to which the authors applied Olson's (1947) nomen 'Parareptilia'; mesosaurs were regarded as the sister group of Reptilia and thereby thought to be only distantly related to Parareptilia. However, in an alternate tree that was only a single step longer than their most parsimonious resolution, Laurin & Reisz (1995) acknowledged that mesosaurs subtended a clade formed by millerettids, pareiasaurs, and procolophonids, thereby resurrecting the basic complement of taxa grouped together as 'parareptiles' by Gauthier *et al.* (1988). The two additional parareptilian synapomorphies, present in BHM 999 and not utilized by Laurin & Reisz (1995), therefore have the potential to alter the topology of the most parsimonious tree of those authors by grouping mesosaurs with parareptiles. Furthermore, a redescription of the skull of the basal eureptile *Captorhinus aguti* (Modesto 1998b) revealed that two of the reptilian synapomorphies identified by Laurin & Reisz (1995) are problematic and, therefore, might not serve to exclude mesosaurs from Reptilia. The first of these concerns the breadth of the parasphenoid wings (their character 51): new material demonstrates that the captorhinid parasphenoid differs little in general dimensions from those of mesosaurs and basal synapsids (Modesto 1998b; *contra* Laurin & Reisz 1995). The second, the presence of supraoccipital anterior cristae (their character 54), is in all likelihood a saurian apomorphy that does not apply to Paleozoic reptiles (Modesto 1998b). Considering the doubtful nature of these two characters in barring mesosaurs from Reptilia, the admittedly weak position of mesosaurs as the most basal sauropsids (Laurin & Reisz 1995), and the identification of two additional potential parareptilian apomorphies that are shared also with *Stereosternum*, it would appear that there is a good case for parareptilian affinities for mesosaurs.

With this in mind, the two new characters were added to the data matrix of Laurin & Reisz (1995), one of their characters (character 51) was modified by recoding captorhinids as '0', and the other problematic character (no. 54) was deleted entirely; distributions of states for the two new characters are listed in the appendix. The modified data matrix was analyzed by PAUP 3.1 following all the options outlined by those authors, except that all characters were run unordered. A single most parsimonious tree of 330 steps was discovered (Figure 4*a*), in which mesosaurs form a sister-group relationship with parareptiles (*sensu* deBraga & Reisz 1996). The topology of the preferred tree of Laurin & Reisz (1995), where mesosaurs are excluded from Reptilia, is replicated in an alternative tree of 332 steps. Thus, with only minor additions and modifications to the data matrix of Laurin & Reisz (1995), a slightly different picture of mesosaurid relationships arises. This re-analysis is not intended to serve as a critical re-evaluation of the interrelationships of early reptiles; that is the subject of a forthcoming paper. It does, however, suggest that there is strong evidence that mesosaurs are reptiles and that their closest relatives are most likely to be found among the reptilian taxa now known formally as the Parareptilia (deBraga & Reisz 1996).

Following the tenets of phylogenetic taxonomy (De Queiroz & Gauthier 1990, 1992) and the principle of priority, Williston's (1925) term 'Anapsida' can be applied to the clade of mesosaurs and parareptiles. That nomen was defined by Gauthier *et al.* (1988, p. 142) to include 'extant turtles, and all other extinct reptiles that are more closely related to them than they are to other reptiles'. Thus, Anapsida is the nomen that should have been applied to the clade that Laurin & Reisz (1995) named Parareptilia, which was defined by the latter authors as a stem-based group that includes all reptiles related more closely to Testudines than to other reptiles. Accordingly, Parareptilia *sensu* Laurin & Reisz (1995) can be considered to be preoccupied by Anapsida *sensu* Gauthier *et al.* (1988). The node-based redefinition of deBraga & Reisz (1996) is regarded here as the valid definition of Parareptilia.

The realignment of turtles with the taxa that Gauthier *et al.* (1988) regarded as 'parareptiles' has the potentially confusing effect of removing from the group taxa that have long served as exemplary anapsids (*e.g.*, captorhinids). Moreover, the phylogenetic

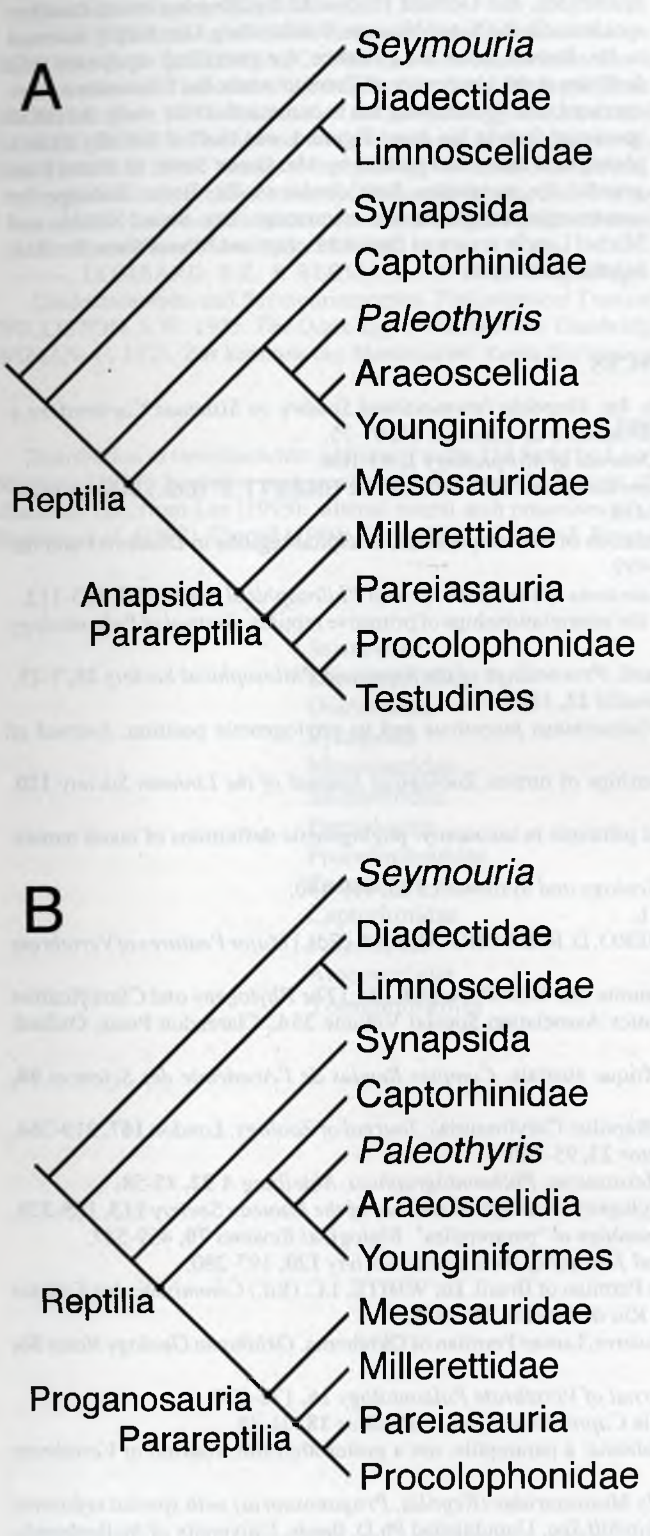

Figure 4. A. Cladogram illustrating the most parsimonious tree obtained from a PAUP 3.1 analysis of a data matrix modified slightly from Laurin & Reisz (1995). Anapsida is diagnosed by characters 24, 25, 91, 97, 113, and 125 of Laurin & Reisz (1995) and the appendix. B. Corresponding phylogeny in which turtles are recognised as diapsid reptiles, illustrating the alternative nomenclature for major amniote groups necessitated by the repositioning of Testudines and the tenets of phylogenetic taxonomy.

definition of a taxon that has long been regarded as unnatural may not be well received by many workers, and it is not inconceivable that a move may be made to suppress the name 'Anapsida' under the aegis of the International Committee for Zoological Nomenclature. However, such an action may be moot given the current controversy over the phylogenetic position of turtles within Reptilia. If the hypothesis that turtles are aberrant diapsid reptiles (Rieppel & deBraga 1996; deBraga & Rieppel 1997) comes to represent the consensus view, Gauthier *et al.*'s (1988) definition of Anapsida may have to be abandoned, for turtles would be nested well within the reptilian crown group. Should this unorthodox view come to pass, then the clade of mesosaurs and parareptiles will be without a name. In contingency, Baur's (1887) nomen 'Proganosauria' would serve as a appropriate name for this 'turtleless' sauropsid clade. Created by Baur (1887) to receive mesosaurs and their close relatives, the taxon included only mesosaurs for most of its history. Proganosauria is defined here as a stem-based group that includes all amniotes related more closely to *Mesosaurus tenuidens* than to saurian reptiles. The alternate nomenclature is labelled on a phylogeny in which turtles are not members of Parareptilia (Figure 4*b*). Thus, Anapsida is the correct name for the clade of mesosaurs and parareptiles, but only as long as turtles are included in the latter group. For the time being, *Stereosternum* and other mesosaurs can be recognised as the most basal anapsid reptiles.

Finally, as a consequence of this minor rearrangement of amniote phylogeny, the nomen 'Sauropsida' now encompasses exactly the same complement of taxa as Reptilia as the latter is regarded in the present work. The former nomen was defined as a stem-based taxon (Gauthier 1994), whereas the latter was defined as a crown-group (node-based) taxon (Gauthier *et al.* 1988). Reptilia clearly has priority here, both as a phylogenetically-defined taxon and as the older, more established taxonomic name. Accordingly, the nomen 'Sauropsida' is regarded to be in abeyance, bearing in mind that that there is no longer a non-synapsid amniote taxon that falls outside of the reptilian crown group. However, the discovery of such a taxon would allow 'Sauropsida' to be resurrected again as one of the two major clades of Amniota.

The identification of mesosaurs as the closest relatives of the parareptiles has two important consequences. The first is that it eliminates the substantial ghost lineage for Mesosauridae that is necessitated by the 'sauropsid' tree of Laurin & Reisz (1995): according to that tree, mesosaurs must have originated sometime during the Westphalian, implying that over 40 million years of their evolutionary history is unknown (Laurin & Reisz 1995: Figure 9). The preferred tree of the present analysis (Figure 4) suggests that such a severe estimate of unrecorded history is unwarranted. If one distinguishes between 'ghost taxa' and 'ghost lineages' (*sensu* Norell 1992), then a ghost lineage for Mesosauridae is absent, and the ghost taxon for anapsids extends from the late Westphalian until the first appearance of mesosaurs in the late Sakmarian. The oldest known parareptiles are the acleistorhinids from the South Grandfield and Richards Spur localities in Oklahoma (Modesto 1999), which appear some 7 or 8 million years after the mesosaurs. Consequently, the anapsid identification of mesosaurs also reduces the ghost lineage for Parareptilia, which now extends from the late Sakmarian to the early Artinskian.

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APPENDIX

Distribution of two characters additional to the 124 listed by Laurin & Reisz (1995). Their description is as follows: character 125, from Modesto (1999): posterior margin of skull roof roughly straight (0), with a single, median embayment (1), or embayed bilaterally (2); character 126, from Lee (1995): atlantal neural arch possesses (0) or lacks (1) an epipophysis. Sources, in addition to the present work: Berman *et al.* (1992), Carroll (1969), Gow (1972), Laurin & Reisz (1995), Lee (1995), and Sumida (1990).

	125	**126**
Seymouria	0	0
Limnoscelidae	1	0
Diadectidae	2	0
Synapsida	2	0
Mesosauridae	1	1
Millerettidae	1	0
Pareiasauria	1	1
Procolophonidae	0	1
Testudines	0	1
Captorhinidae	2	0
Paleothyris	2	1
Araeoscelidia	2	0
Younginiformes	1	0