

# *Archaeovenator hamiltonensis*, a new varanopid (Synapsida: Eupelycosauria) from the Upper Carboniferous of Kansas

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**Abstract:** Study of a nearly complete skeleton of a small amniote, preserved as part and counterpart in Upper Carboniferous limestone slabs of the Hamilton Quarry, Kansas, indicates that it is a new genus and species of varanopid synapsid.

*Archaeovenator hamiltonensis* gen. and sp. nov. is the oldest known varanopid. Phylogenetic analysis indicates that it is the sister taxon to all other known varanopids. Discovery of this new varanopid is important because it improves our knowledge of the terrestrial fauna of the Hamilton quarry, expands the known diversity of Late Carboniferous basal synapsids, and extends the fossil record of Varanopidae deeper within the Stephanian. Varanopidae has the longest fossil record (Late Carboniferous – upper Middle Permian) of all known clades of basal synapsids.

**Résumé :** L'étude d'un squelette presque complet d'un petit amniote, préservé sous forme d'empreinte et de contre-empreinte dans des dalles calcaires du Carbonifère supérieur de la carrière Hamilton, au Kansas, indique un nouveau genre et une nouvelle espèce de varanopide synapside. *Archaeovenator hamiltonensis* n. sp. et n. gen. est le varanopide le plus ancien connu et des analyses phylogénétiques montrent qu'il est le taxon frère de tous les autres varanopides connus. La découverte de ce nouveau varanopide est importante parce qu'elle accroît notre connaissance de la faune terrestre de la carrière Hamilton, étend la diversité connue des synapsides de base du Carbonifère tardif et prolonge la plage des fossiles Varanopidae plus profondément dans le Stephanien. Les fossiles Varanopidae sont les plus étendus (Carbonifère tardif – sommet du Permien médian) de tous les clades connus des synapsides de base.

[Traduit par la Rédaction]

## Introduction

The Upper Carboniferous (Upper Pennsylvanian) limestone beds that are exposed in a small quarry near Hamilton, Kansas have yielded a diverse assemblage of well-preserved plant, invertebrate, and vertebrate fossils. The abundance of well-preserved fossils has led geologists to designate this locality as a Fossil-Lagerstätte (Cunningham et al. 1993). Noteworthy among the fossils found in this locality are the superbly preserved plants, arthropods, and acanthodian fish (Zidek 1976; Schultze and Chorn 1988). Among this outstanding collection of fossils are the occasional remains of terrestrial vertebrates, some preserved in articulation, especially those sufficiently small to have been rafted as complete carcasses. One of these skeletons is a small diapsid reptile *Spinoequalis* (deBraga and Reisz 1995). Here we report on a second amniote that was identified originally as a small diapsid (Reisz 1988). However, additional study of the single known specimen of this new amniote has shown that the initial identification is erroneous, thus prompting the present study. Specifically, the medial process of the postorbital interpreted originally as evidence of a narrow upper temporal fenestra is actually overlain by the parietal and postfrontal, and there is

no upper temporal fenestra. Furthermore, knowledge of the morphology of varanopids has expanded significantly during the past 15 years, and features considered now to be diagnostic of varanopids were not recognized in the initial description of this amniote.

The new amniote from the Hamilton quarry consists of most of an articulated skeleton that was discovered by splitting pieces of the laminated limestone. As an unfortunate consequence of this method of collection, the skeleton was split through most of the bones and little external bone surface was exposed. Prior to the preparation undertaken by Ms Diane Scott in Toronto, resin was applied to the exposed surfaces of the split bone and acid was used to dissolve the limestone surrounding the skeleton with the goal of revealing the undamaged surfaces of fossilized bone. Regrettably, this acid preparation has resulted in extensive additional damage and the exposure of extremely delicate, unsupported skeletal elements. It was necessary to limit further preparation to mechanical methods to conserve those parts damaged by the acid.

The part and counterpart of the specimen preserve approximately the dorsal and ventral views of the skull and mandibles, lateral views of the curled up vertebral column,

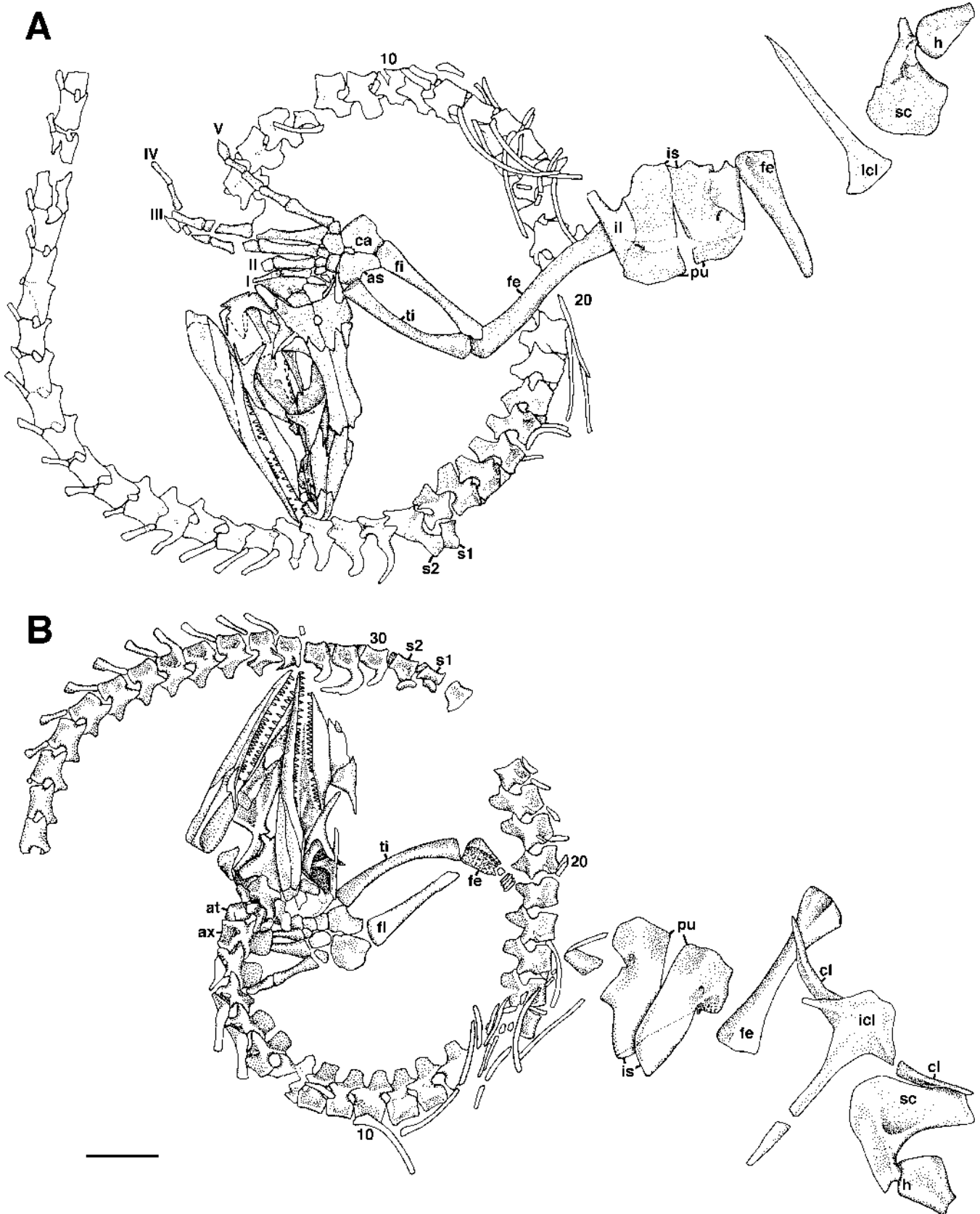
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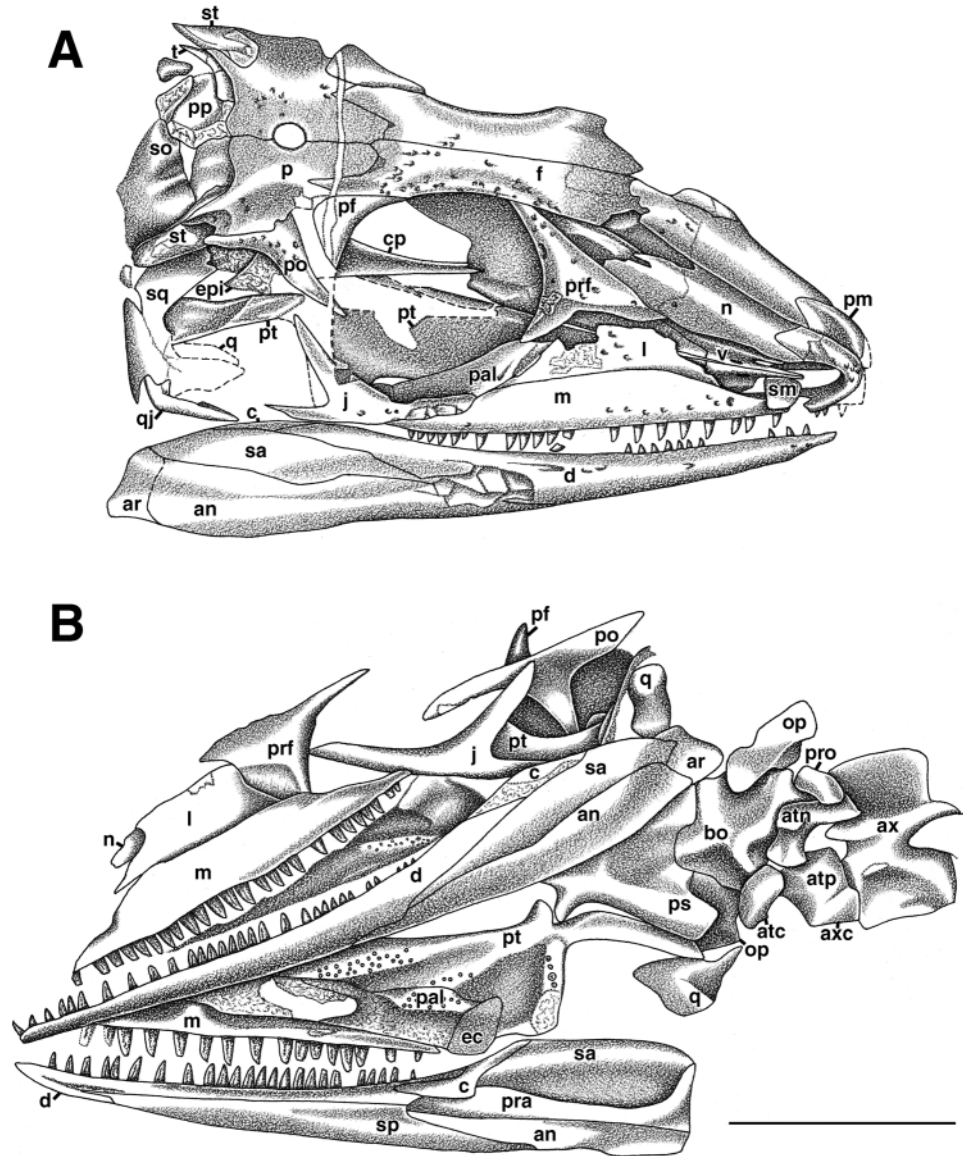
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**Fig. 1.** Holotype, KUVV 12483, *Archaeovenator hamiltonensis*. The skeleton has been preserved in part (A), and counterpart (B) slabs. as, astragalus; at, atlas; ax, axis; ca, calcaneum; cl, clavicle; fe, femur; fi, fibula; h, humerus; icl, interclavicle; il, ilium; is, ischium; pu, pubis; sc, scapulocoracoid; s1–s2, sacral ribs; ti, tibia; Roman numerals, digit numbers; arabic numerals, vertebral number. Scale bar = 1 cm.



**Fig. 2.** Holotype, KUVV 12483, *Archaeovenator hamiltonensis*. Skull in (A) dorsolateral, and (B) palatal views. an, angular; ar, articular; atc, atlantal intercentrum; atn, atlantal neural arch; atp, atlantal pleurocentrum; ax, axis; axc, intercentrum; bo, basioccipital, c, coronoid; cp, cultriform process; d, dentary; ec, ectopterygoid; epi, epipterygoid; f, frontal; j, jugal; l, lacrimal; m, maxilla; n, nasal; op, opisthotic; p, parietal; pal, palatine; pf, prefrontal; pm, premaxilla; po, postorbital; pp, postparietal; pra, prearticular; prf, prefrontal; pro, proatlas; ps, parasphenoid; pt, pterygoid; q, quadrate; qj, quadratojugal; sa, surangular; sm, septomaxilla; so, supraoccipital; sp, splenial; sq, squamosal; st, supratemporal; t, tabular; v, vomer. Scale bar = 1 cm.



and lateral and medial views of the preserved portions of the appendicular skeleton (Fig. 1). However, details of the part and counterpart skull do not match exactly due to loss of bone and teeth (Fig. 2). Most striking are the differences in the dentition and shape of the right lower jaw, with some loss of teeth and external surface near the anterior tip of the dentary, and loss of bone from the posterior section of the lower jaw in medial view.

### Systematic palaeontology

Synapsida Osborn, 1903  
Eupelycosauria Kemp, 1982  
Varanopidae Romer and Price, 1940

### *Archaeovenator*, gen.nov.

ETYMOLOGY: Archaeo, ancient (Latin); venator, hunter (Latin).

HOLOTYPE AND ONLY KNOWN SPECIES: *Archaeovenator hamiltonensis*, sp.nov.

DIAGNOSIS: As for the type and only known species  
*Archaeovenator hamiltonensis*, sp.nov.

ETYMOLOGY: Named after the type locality, the Hamilton Quarry, Kansas.

HOLOTYPE: KUVV 12483 (Kansas University Vertebrate Paleontology Collection, Lawrence, Kansas, U.S.A.), nearly

complete, articulated skeleton, with limbs and girdles slightly separated from axial skeleton.

**HORIZON AND TYPE LOCALITY:** Calhoun Shale, Shawnee Group, Virgilian Series (Stephanian of Europe), Upper Pennsylvanian; Hamilton Quarry near Hamilton, Greenwood County, Kansas, U.S.A.

**DIAGNOSIS:** Small varanopid eupelycosaur characterized by the presence of a large medial process of the postorbital that underlies the parietal and large nasal process of the premaxilla that forms a broad, expanded posterodorsal process. Differs from other varanopids in having simple conical, slightly recurved teeth, lacking maxillary dorsal process, lacking a lateral boss on the postorbital, and lacking excavation on the neural spines and arches.

**CORRECT SPELLING OF FAMILY VARANOPIDAE:** This family of Paleozoic synapsids was erected by Romer and Price in 1940, using the spelling Varanopsidae. More recently, Langston and Reisz (1981) argued for the spelling Varanopseidae. However, careful perusal of the literature, and the timely assistance provided by Dr. Hans-Dieter Sues led us to the discovery that the proper and correct family designation should be Varanopidae (Welles and Peachy 1953), the spelling used in this study.

**DESCRIPTION:** The skull and vertebral column remain in direct association, with the majority of the vertebrae properly articulated and in a tight spiral around the skull. Several of the ribs have been preserved in place, and numerous small intercentra are also preserved in their proper location between vertebrae. Much of the tail seems to have separated off and moved away from the rest of the skeleton. The pectoral girdle has moved away from the vertebral column and its components separated slightly. Only the proximal end of the right humerus remains of the pectoral limbs. The pelvic girdle and a nearly complete right hind limb have remained together as a unit and drifted only a short distance from the sacral region. We have been able to produce a reconstruction of the skeleton, although most of the forelimb is missing (Fig. 3).

**SKULL AND LOWER JAWS (FIGS. 2A, 2B):** The right side and the skull table of the dermal skull roof are only slightly disarticulated. However, most of the left side is displaced and distorted because the skull has been bent along the line formed by the edge of the left nasal, frontal, and parietal bones, pushing the skull onto the left side. This partial disarticulation and distortion is undoubtedly due to flattening of the remains of this animal, a process that characterizes most of the articulated specimens from this locality.

The paired dorsal series of skull roof bones have been exposed only in dorsal view. The premaxillae are unusual in that their dorsal nasal processes are very broad in comparison to their slender maxillary and palatal processes. The overall result of these unique proportions is that the anterior region of the snout is entirely occupied by the premaxillae, without any visible anteroventral or anterolateral contribution of the nasal. Thus, the overall shape and slender appearance of the snout is defined by the premaxillae rather than a combination of the premaxilla and nasal. Although the maxillary process is delicate in comparison with the dorsal process, it has

room for 4 teeth, and has the characteristic varanopid feature of a rounded ventrolateral surface. The palatal process is also quite slender, and matches in slenderness the delicate anterior process of the vomer, exposed through the right external naris. Two teeth are preserved on the right premaxilla with only the anterior one preserved intact. It is conical with no discernable recurvature. Height of this tooth only slightly exceeds the diameter of its base.

The nasals are elongate elements when compared with those of basal synapsids, such as caseosaurs, but the slender appearance is caused by the narrow contribution that these elements provide to the top of the snout. A significant part of the transversely curved nasal surface contributes to the height of the antorbital region, giving the snout the tall, narrow appearance that characterizes eupelycosaur. The lateral edge of the nasal is unusual in having a long free edge that extends from the anterolateral contact with the premaxillae more than half way along the length of the bone. Normally, in other Permian–Carboniferous synapsids this area would form a sutural contact with the elongate lacrimal, or in the case of sphenacodontids, with the maxilla. Instead, the nasal of *Archaeovenator* forms the upper border of an enlarged external naris, and its contact with the lacrimal bone is very short. This greatly enlarged external naris is partly interrupted by a small, sheet-like septomaxilla that straddles the premaxillary–maxillary contact, and probably extended to the edge of the nasal bone.

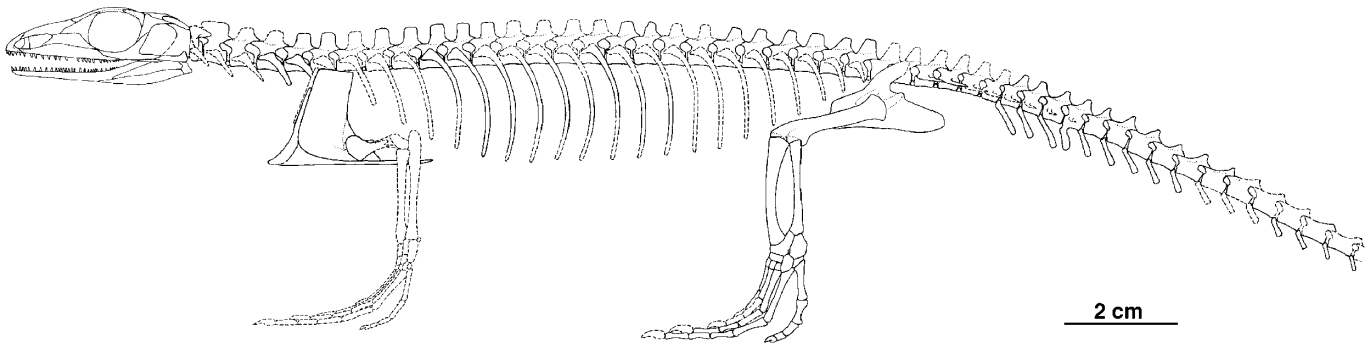
Nasals with similar morphology to those of *Archaeovenator* are also present in *Varanodon*, as well as *Aerosaurus* and *Varanops* (Olson 1965; personal observation). Consequently, all these taxa have an elongated external naris that is expanded posterodorsally and a similar, sheet-like septomaxilla. The morphology of the external naris in *Mesenosaurus* and *Mycterosaurus* also bear some resemblance to the condition seen in the other varanopids in the presence of a posterodorsal elongation, but neither of these taxa has a preserved septomaxilla.

The frontal is the longest of the paired dermal skull roof bones, extending over the top of the skull from the antorbital region to the level of the postorbital bar. Anteriorly, its sutural contact with the nasal is poorly preserved, but appears acuminate. It forms most of the gently concave upper orbital margin. A well-developed elongated posterolateral process extends along the medial edge of the postfrontal and continues onto the surface of the parietal to nearly reach the level of the anterior border of the pineal foramen.

The paired parietals have the typical morphology of all basal amniotes. Three features are noteworthy: the relatively large posterolateral depression on the parietal wings for the supratemporal, the slightly concave lateral shelf that extends posteriorly from the postfrontal–postorbital contact and includes the depressed surface for the supratemporal, and the gentle ventral inflection of the skull table posterior to the pineal foramen. The lateral shelf of the parietal covers a significant portion of the postorbital, whereas the postfrontal forms a wedge-like indentation into the body of the parietal. Therefore, while the postfrontal is clearly exposed in dorsal view, little of the postorbital would be visible from above, certainly much less than in caseosaurs.

It is difficult to determine if the postparietal is paired or a single median element. There is a large, plate-like element

**Fig. 3.** Skeletal reconstruction of *Archaeovenator hamiltonensis* in left lateral view.



preserved between the right parietal and the large supraoccipital that is likely a portion of the postparietals. This plate-like element appears to have a slightly raised medial edge. If the postparietals are paired, then this element is the right postparietal and the raised edge is the medial contact with the left postparietal. This ridge matches a median ridge on the supraoccipital.

The left tabular is nearly complete, although fractured, and is a relatively long, slender structure, as in *Elliotsmithia*. It appears to have an acuminate posterior tip. Similarly, the right tabular is a sliver of bone that is situated along the posterior face of the parietal wing. The supraoccipital is a plate-like structure that occupies much of the occipital surface. It has a medial ridge that is flanked by depressions.

The maxilla is a slender, elongate element with room for at least 29 teeth (25 preserved teeth and spaces for an additional four teeth on the left maxilla). Maxillary teeth are larger than those on the premaxilla. Most show a noticeable recurvature of the tip, but this recurvature is reduced somewhat in the more posterior maxillary teeth. Those teeth under the orbit are simple cones lacking any recurvature whose height is slightly greater than the basal diameter. There is little variation in the height of the teeth with the exception of those ventral to the contact between the maxilla and the jugal, which are distinctly smaller. The dorsal expansion of the maxilla is modest and is restricted to the area where the maxilla contacts the lacrimal. Anteriorly, there is an elongate narial shelf where the maxilla is not covered by the lacrimal and forms instead most of the ventral rim of the external naris. A lateral row of small foramina is present along the anterior half of the maxilla. The anteriormost foramen in this row is larger than the others and opens anteriorly into a pronounced groove that nearly reaches the tip of the maxilla. Posteriorly, the dorsal edge of the maxilla is recessed to accept the anterior process of the jugal. This region of the maxilla is expanded laterally and projects beyond the surface of the remainder of the maxilla. Although damaged on the right maxilla, this lateral expansion is clearly visible on the undamaged left side.

The lacrimal of *Archaeovenator* is similar to those seen in other varanopids (personal observation), but unusual in comparison to non-varanopid synapsids. Although appearing as a slender, elongate element, it forms a very short contact with the nasal anterior to the prefrontal. Anterior to this contact, the lacrimal has a concave dorsal edge that slopes gently anteroventrally to form a portion of the border of the enlarged external naris. Posterior to the naris, the dorsal edge of the lacrimal overlaps the robust prefrontal. The lacrimal is virtually

excluded from the orbital margin by the long ventral process of the prefrontal, although it likely contacted the anterior process of the jugal. In contrast, the lacrimals of other varanopids have a more substantial entrance into the orbital margin.

The jugal is one of the distinctive varanopid features of *Archaeovenator*. It is an exceedingly slender element, with narrow orbital, postorbital, and subtemporal rami. Of particular significance is the slender appearance of the subtemporal ramus that probably contacts both the reduced quadratojugal and the anteroventral process of the squamosal. A narrow subtemporal bar is a diagnostic feature of varanopids.

The prefrontal is a robust element that forms the anterior and anterodorsal borders of the orbit and contacts the lacrimal, frontal, and nasal. Both prefrontals are preserved, showing clearly the extent to which they underlay the lacrimal, and the way they contributed to both the dorsal and lateral surfaces of the skull roof. There is no evidence to suggest that the prefrontal made contact with the palate.

Both postfrontals are preserved in their proper articulation. Each is a small, but robust, element that is wedged in the anterolateral corner of the parietal and along the posterolateral edge of the frontal. Although an element of the skull table, the postfrontal slopes gently ventrally in line with the slightly concave lateral flange of the parietal.

In contrast to the postfrontals, both postorbitals have moved out of position. The right postorbital has moved slightly posteriorly, and somewhat medially, so that a large portion now lies beneath the right parietal. The left postorbital is disassociated from the other temporal bones and has completely flipped out of position so that the concave internal surface is visible. The postorbital of *Archaeovenator* is a triradiate structure with robust ventral and posterior rami, and a short anteromedial process. The anteromedial process of the right postorbital is hidden underneath the parietal, but is visible on the left postorbital extending medially under the left parietal. When articulated properly with the other skull elements, the short anteromedial process would partly underlie the parietal and the posterior edge of the postfrontal. The posterior ramus is sufficiently long to have made contact with the supratemporal along the dorsal border of the temporal fenestra, whereas the robust ventral ramus would have contacted the anterior edge of the jugal dorsal process.

The squamosal is preserved only on the right side, and its anteroventral portion is preserved only as an impression. The anteroventral process is sufficiently large to have excluded the quadratojugal from the temporal fenestra, allowing the

squamosal to make contact with the slender suborbital ramus of the jugal. The contributions of the squamosal to the dorsal and posterodorsal borders of the temporal fenestra are clearly visible. Overall, the squamosal is a relatively small element, especially when compared with that in *Eothyris* and the early ophiacodontid *Archaeothyris*. Its proportions are comparable to those of the squamosal in the other small varanopid *Mycterosaurus*. Although the posteromedial part of the bone is incomplete, it is sufficiently preserved to indicate that its occipital component is modest, as in other varanopids. The quadratojugal is also preserved only on the right side as a narrow, sliver-like element that underlies the squamosal. A short dorsal process of the quadratojugal is covered by the sheet-like squamosal. The supratemporal is a surprisingly large element, anteroposteriorly elongated, as in all other Permian–Carboniferous eupelycosaur. Anteriorly, it lies in a deeply recessed groove along the posterolateral surface of the parietal.

The palate is exposed in dorsal view on one half of the split skull and in ventral view in its counterpart, but it is partly obscured dorsally by the skull roof and ventrally by the left cheek and left lower jaw.

The pterygoid is greatly elongated in *Archaeovenator*, extending far anteriorly between the vomers. As in other basal amniotes, there are three ridged areas with teeth on the ventral surface of the pterygoid, extending laterally, diagonally, and anteriorly from the region of the basicranial articulation. Although poorly preserved, the teeth on the transverse flange seem to form a single row, whereas the diagonal and anterior ridges seem to carry fields of teeth rather than distinct rows. Although nearly all teeth are damaged, those on the transverse flange may be slightly larger than those on the palatal ramus. The diagonal ridge extends onto the palatine, which also carries teeth, but it is not possible to determine if the anterior ridge extends onto the vomer because the left mandible hides the ventral side of the vomers. The medial edge of the palatal ramus defines a long and relatively narrow interpterygoid vacuity that extends nearly to the posterior border of the external naris. In contrast, the significantly shorter interpterygoid vacuity of *Mesenosaurus* does not reach as far as the anterior limit of the ectopterygoid (Reisz and Berman 2001). The right palatine and ectopterygoid are exposed in ventral view. The ectopterygoid is a small, edentulous element wedged between the palatine and pterygoid. The palatine is elongate and generally resembles that in *Mesenosaurus*. Anteriorly, the palatine is deeply emarginated for the posterior margin of the internal naris. The posterior limit of the internal naris is well within the limits of the orbit, at approximately the level of the 6th tooth from the posterior tip of the maxilla.

Parts of the parasphenoid and basisphenoid complex and the basioccipital and exoccipital complex are exposed, but little significant information can be derived from the specimen. The basipterygoid processes project laterally and have an anteriorly facing articular facet. The width of the parabasisphenoid increases dramatically posterior to the basicranial articulation, but unlike other varanopids, such as *Aerosaurus* (Langston and Reisz 1981) and *Mesenosaurus* (Reisz and Berman 2001), this increase in width is gradual. A gradual increase in width of the parabasisphenoid is also present in *Mycterosaurus* (Berman and Reisz 1982).

*Archaeovenator* shares with *Mycterosaurus* and *Mesenosaurus*, but not *Aerosaurus*, the presence of thickened lateral edges of the parabasisphenoid that form basisphenoidal tubera. In sharp contrast to *Aerosaurus*, *Mycterosaurus*, and *Mesenosaurus*, there are no teeth on the parabasisphenoid of *Archaeovenator*.

Only the articular surfaces of the condyles of the quadrates are exposed. Both condyles are have slightly damaged surfaces. The lateral condyle is hemispherical with a prominent pit. The medial condyle is less rounded and slightly elongated anteroposteriorly.

Both the left and right lower jaws are exposed in lateral view, but only part of the right half is exposed in medial view. As in all varanopids, the dentary is a slender, long element that occupies slightly more than 3/4 of the mandibular length, and has space for 37 teeth. There is a slight elevation of the posterior part of the dentary as a coronoid eminence. Most dentary teeth are damaged. Height of the dentary teeth appears to be uniform throughout most of the length of the dentary with the exception of those situated more posteriorly and beneath the smaller maxillary teeth. Anteriorly, the dentary has a short, very narrow symphysis. The posterior coronoid is a small element in *Archaeovenator* and is visible in both lateral and medial views above the dentary and surangular. No anterior coronoid is present, but its absence may be an artifact of preservation because the region of the dentary immediately anterior to the posterior coronoid is damaged. The splenial appears to be an unusually long element and is restricted entirely to the medial side of the lower jaw. It extends posteriorly from the symphysis and has a long, tapering contact with the angular and a very small contact with the prearticular. The articular bone is exposed only in lateral view and extends well beyond the posterior limits of the angular and surangular bones. There appears to be a modest, posteriorly directed retroarticular process that is absent in caseid and ophiacodontid synapsids. This process is elongate and well developed among varanopids. It is unfortunate that the medial aspect of this element is not preserved in the medial view of the mandible because this structure is generally poorly known among varanopids. The ventral edge of the angular in *Archaeovenator* is like those of caseid and ophiacodontid synapsids in forming a ridge posteriorly next to the articular. This form of the angular may represent the primitive condition because, in more derived Permian varanopids, the ventral region of the angular is rounded.

AXIAL SKELETON (FIGS. 1A, 1B): As in most Permian–Carboniferous eupelycosaur, there are 27 presacral vertebrae. The two sacral vertebrae are partly preserved, and there are 22 caudals in articulation with the rest of the skeleton. Approximately two-thirds of the tail is missing in the specimen. Anteriorly, the atlas–axis complex has the same morphology as in Permian varanopids: The axis has a hatchet-shaped neural spine and a massive neural arch fused to the axial centrum; the axial intercentrum is suturally attached and beneath the atlantal centrum; there is a well-developed pair of atlantal neural arches that are sitting above the short, fused atlantal centrum – axial intercentrum. A large atlantal intercentrum is found anteroventrally to the atlantal centrum – axial intercentrum, and the small, paired proatlas is attached anterodorsally to the atlantal neural arch.

The dorsal vertebrae have modestly developed, blade-like

neural spines, only slightly shorter than those in *Mycterosaurus* in the mid-dorsal region and similar to those in *Mesenosaurus*. The mid-dorsal neural spines of *Aerosaurus*, *Varanodon*, and *Varanops* are taller and narrower than in *Archaeovenator*, *Mycterosaurus*, and *Mesenosaurus*. Shape of the neural spines of the posterior dorsal vertebrae of *Archaeovenator* and *Mesenosaurus* differ little from those of the mid-dorsal region in contrast to the posterior dorsals of *Mycterosaurus* (Berman and Reisz 1982; Reisz et al. 1997) that are taller and narrower than the mid-dorsals. A prominent mid-ventral ridge is present on the centra of the cervicals, dorsals, sacrals, and anterior caudals. There is little variation in vertebral length along the column, with a slight shortening of individual vertebrae near the sacrum, and slight elongation in the caudal series. Occasionally, intercentra are lodged between cervical and dorsal centra, along the ventral edge of the vertebral column. Presumably, they were present throughout the presacral region. Intercentra are preserved between the sacral vertebrae, and numerous haemal arches are found in place in the caudal region. The haemal arch of the eighth caudal vertebra has apparently fused to its centrum.

Typical cervical and dorsal ribs are preserved along the vertebral column. The cervical ribs have expanded, blade-like shafts that end abruptly. There is no separation between the capitular and tubercular heads. The dorsal ribs are thin, in accordance with the general slenderness and light build of the skeleton. Two subequal sacral ribs are fused to their respective centra. As in other varanopids, they are expanded distally, deflected ventrally, and gently scooped in lateral view. Only four anterior caudal ribs are present. They are fused to the transverse processes and are recurved.

**APPENDICULAR SKELETON:** The girdles and limbs have drifted in the same direction from the axial skeleton, and the preserved portions of the limbs have stayed in rough articulation with their respective girdles (Figs 1A, 1B). The preserved portions of the pectoral girdle and forelimb consist of the right scapulocoracoid, the shafts of the clavicles, the interclavicle, and the proximal head of the right humerus.

There is no suture between the co-ossified scapula and coracoid. In terms of overall proportions, the scapulocoracoid of *Archaeovenator* most closely resembles that of *Mycterosaurus* (Berman and Reisz 1982; Reisz et al. 1997). The scapulocoracoids of the more derived varanopids *Varanodon* and *Varanops* are significantly taller dorsoventrally. An additional similarity between the scapulocoracoids of *Archaeovenator* and *Mycterosaurus* is found in the anterior edge of the scapular blade, which is slightly concave in both genera. There is no supraglenoid foramen in the scapulocoracoid of *Archaeovenator*, and the triceps process is slightly larger than in *Mycterosaurus*. The interclavicle has a broad, diamond-shaped proximal end and a long, slender stem. Clavicles are tall and narrow distally, and although the portions that articulate with the interclavicle are absent or not exposed, the shape of the anterior end of the interclavicle suggests only a modest expansion of the clavicles.

Little information can be garnered from the preserved proximal end of the right humerus. The humerus of *Archaeovenator* has a narrow head in relation to the small portion of preserved shaft. The deltopectoral crest is prominent, but

the scapulocoracoid obscures the area where a secondary ridge along the deltopectoral crest that is characteristic of varanopids and caseids is expected (Reisz et al. 1997).

Significantly more morphological data are found in the preserved hind appendages that include complete pelves, left femur, and nearly complete right limb. All three elements of each half of the pelvic girdle are tightly sutured together with co-ossification between the ischium and pubis. The suture between the ilium and the pubis and ischium remains discernable and aids in an approximation of the location of the puboischial suture. The iliac blade is only partially preserved on the right side. It appears to be an elongate, posteriorly directed blade with prominent scars along the dorsal edge that are likely for epaxial musculature. There is no anterior expansion of the iliac blade. Along the dorsal margin of the iliac blade and above the acetabulum is a small, rounded and dorsally developed projection. Iliac with similar morphologies are present in varanopids and ophiacodontids and differ strongly from the ilia of caseids and sphenacodontids (Reisz 1986). The pubis of *Archaeovenator* is unusual among basal synapsids in that it is very short in relation to the ischium with a ratio between the pubis and ischium of ~0.57. In other basal synapsids, the ratio between the pubis and ischium may vary from ~0.75 to 1.0. The free edge of the pubis is greatly thickened, and a lateral process (pubic tubercle) is present at the anterolateral edge. In *Mycterosaurus*, the lateral process of the pubis is situated approximately at the midpoint of the pubis (Berman and Reisz 1982). An oval obturator foramen is located beneath the acetabulum and near the approximate posterior edge of the pubis. The elongate ischium has a thickened dorsolateral margin comparable to that of the pubis. Its symphyseal edge is straight for at least three-quarters of the total length of the ischium. The puboischial symphysis is straight and uninterrupted for its entire length; there is no gap at the junction between the pubis and ischium.

The elongate femur of *Archaeovenator* has a slender shaft with a slight sigmoidal curvature and the proximal end turned upwards and the distal end turned downwards. Proximal and distal heads are narrow (~22% and 29% of the total femoral length, respectively, based upon the left femur). An adductor crest and fourth trochanter are absent, and an internal trochanter is situated proximally and virtually confluent with the head of the femur. In all of these features, the femur of *Archaeovenator* is extremely similar to the femur of *Mycterosaurus* (Berman and Reisz 1982). The intertrochanteric fossa is deep and broad, but its distal extent is uncertain due to crushing. A small foramen penetrates the left femur within the intertrochanteric fossa distal to the internal trochanter. The femur of *Varanops* has wider proximal and distal ends that are ~32% of total femoral length based upon illustrations in Williston (1911) and an internal trochanter that is distal to the femoral head and clearly demarcated from the head.

Tibia and fibula are relatively short in comparison to the femur (~75% and 73%, respectively), similar to the hind limb proportions of *Mycterosaurus* (Berman and Reisz 1982). More derived varanopids appear to have a slightly more elongate crural segment of their hind limbs; the tibia and fibula of *Varanops* are ~82% and 89% of the length of the femur, respectively, based upon measurements in Romer and Price (1940) and the tibia and fibula of *Aerosaurus welllesi* are ~84%

and 102% of the length of the femur, respectively, based upon the holotype (Langston and Reisz 1981). The tibia and fibula of *Archaeovenator* are slender bones with only modest expansion of the proximal and distal ends. The tibia has a pronounced medial curvature.

The pes of *Archaeovenator* has an overall slender morphology with elongate digits compared with other varanopids, such as *Aerosaurus welllesi* (Langston and Reisz 1981) and *Varanops* (Reisz 1986). This slender morphology is due primarily to its combination of relatively more slender metatarsals and phalanges and distal phalanges that are more elongate compared with the proximal phalanges. The tarsus and metatarsals are exposed in both dorsal and ventral views and the digits are exposed best in dorsal view. The astragalus is distinctly L-shaped with a taller proximal neck than in other varanopids. Near the distal end of the lateral edge is a notch that along with a corresponding notch on the calcaneum forms the perforating foramen. Most of the distal edge of the astragalus contacts the large lateral centrale. The fourth distal tarsal has a small area of contact with the distolateral corner of the astragalus. There is no evidence for the large, concave surface on the astragalus for the fourth distal tarsal that is present in *Mycterosaurus*. The calcaneum has a fibular facet that is slightly larger than the fibular facet of the astragalus. Distally, there is a large articular surface for the fourth distal tarsal next to the perforating foramen and no discernable contact surface for the fifth distal tarsal. The lateral edge of the calcaneum is not broadly rounded, as in the majority of basal amniotes, but has distinct proximolateral and distolateral surfaces. The lateral centrale is a large, rectangular bone that contacts the astragalus proximally, the fourth distal tarsal laterally, and distal tarsals 1–3 distally. No other centrale is preserved; the medial edge of the single centrale is smoothly rounded finished bone with no evidence of a contact surface for a medial centrale. Distal tarsals 1–3 are rectangular with their long axes oriented proximodistally. The greatly enlarged fourth distal tarsal is an oblong pentagonal bone with clearly defined articular facets for the astragalus, calcaneum, lateral centrale, fourth metatarsal, and fifth distal tarsal. Contact between the fourth and third distal tarsals is less well defined. The small, triangular fifth distal tarsal contacts the fifth metatarsal and fourth distal tarsal and possibly the fourth metatarsal. This last possible contact between the fifth distal tarsal and fourth metatarsal is uncertain due to damage to the fifth distal tarsal.

Metatarsals I–V increase in relative length from the first to fourth. The length of the fifth metatarsal is intermediate between the lengths of the second and third metatarsals. The proximal and distal ends of the metatarsals are expanded modestly with some overlap of the proximal ends. The width of the proximal end is at most only 33% of the total length of the metatarsal, whereas in other varanopids, it is typically greater than 40%. The phalangeal formula is uncertain as only the third and fifth digits have a complete set of phalanges. However, it is most likely the primitive amniote pattern of 2:3:4:5:4 because digit 3 has four phalanges, digit 4 has at least five phalanges (assuming that only the ungual is missing), and digit 5 has four phalanges. Each preserved phalanx is unusually slender and significantly elongated. Differences in the proportions of the phalanges among *Archaeovenator* and other varanopids are more pronounced than with the metatarsals.

Comparison of the proximal width to total length of the first phalanx shows that in *Archaeovenator* this value does not appear to exceed 40%, whereas in other varanopids the proximal width is at least 65% of the total length. These differences in proportions hold true for the remaining phalanges and are emphasized further in the distal phalanges of the fourth digit that are remarkably elongate compared with corresponding phalanges in other varanopids. Partial pedal unguis are associated with digits 3 and 5. Each ungual is lateromedially compressed with a large flexor tubercle at the base. Neither preserved ungual is complete towards the distal tip, but the ungual for digit 3 indicates that the tip has a slightly expanded dorsal surface and a narrower ventral portion.

## Phylogenetic analysis

A skull of a second varanopid (BP/1/5678) from South Africa was assigned recently to *Elliotsmithia* (Modesto et al. 2001). However, this new skull is different in several aspects from the holotype of *Elliotsmithia* (TM 1438), as described by Reisz et al. (1998), and reinterpretation of the holotype was required to reconcile these differences. Specifically, it was argued by Modesto et al. (2001) that failure to take into account damage and distortion of the holotype led to erroneous conclusions. The primary area of disagreement is the differing interpretations of the squamosal and the shape of the temporal fenestra. It is certainly true that the holotype of *Elliotsmithia* is distorted. However, it is unlikely that the form of distortion is sufficient to account for the different shapes of the squamosals of BP/1/5678 and TM 1438. As shown by fig. 5 of Modesto et al. (2001), the outlines of the temporal fenestrae formed by the squamosals of BP/1/5678 and TM 1438 are different. The squamosal of BP/1/5678 has an anterior extension of its base that is clearly absent in TM 1438, the anterodorsal process of TM 1438 reaches significantly anterior to the base of the squamosal, whereas in BP/1/5678 the upper and lower portions of the squamosal (unfortunately incomplete) appear to extend anteriorly an equal amount, and the angle between the long axis of the anterodorsal process and the occipital margin of the squamosal is more acute in BP/1/5678 than in TM 1438. The holotype of *Elliotsmithia* has been dorsoventrally compressed, as shown by the displacement of the postorbital-jugal contact, the convexity of the subtemporal bar, slight separation of the jugal and quadratojugal, and the rotation of the squamosal clockwise (in right lateral view) away from its contact with the postorbital. There is no evidence that the right squamosal of TM 1438, which served as the basis for the description of this bone in Reisz et al. (1998), has been plastically deformed, nor does this form of distortion account for the absence of an anterior extension of the base of the squamosal on TM 1438. Accordingly, we consider the differences between the squamosals of TM 1438 and BP/1/5678 to be real, and we have included BP/1/5678 as a separate taxon in our phylogenetic analysis.

The overwhelming skeletal evidence supporting the identity of *Archaeovenator* as a varanopid synapsid permits us to evaluate the phylogenetic relationships of this form through the use of the data matrix employed in the restudy of the anatomy and relationships of *Elliotsmithia* (Reisz et al. 1998). Two caseosaurs, two ophiacodontids and BP/1/5678 were added

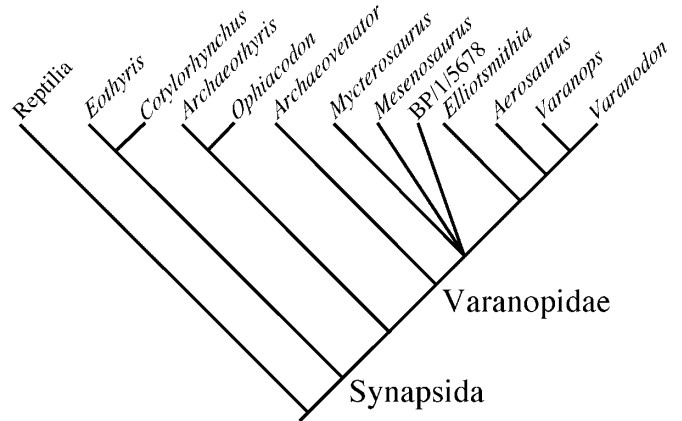
as new taxa. In addition, we modified characters 2, 7, 15, 20, and 21 to include the coding for *Elliotsmithia*, as suggested by Modesto et al. (2001). Character 3 was modified to indicate the presence or absence of a lateral temporal fenestra. We disagree with the suggestion of these authors that characters 8 and 24 should be eliminated since they describe different, although clearly related, aspects of the fenestra. Furthermore, we disagree with their measurement of 55° for the inclination of the squamosal of *Elliotsmithia*. Our estimation of the angle of inclination is approximately 50°. Thus the inclination of the squamosal of *Elliotsmithia* is closer to those of *Aerosaurus*, *Varanops*, and *Varanodon*, and we have modified the wording of character 27 to indicate the derived state of the character as an angle of inclination of 50° or less. Characters 2, 7, 15, 20, and 21 were coded for *Elliotsmithia* according to Modesto et al. (2001). We have also added two new characters (Nos. 32, 33) included by Modesto et al. (2001) in their analysis. The coding for character 33 differs from that suggested by Modesto et al. (2001) to incorporate information based upon observations of the taxa by the first author. Thirteen new characters (34–46), as well as seven characters from previous analyses (47–53), were incorporated, as indicated in Appendix 1. The resulting matrix (Appendix 2, Table A1) consisting of 13 taxa and 53 characters was analyzed using the test version of PAUP 4.0 (Swofford 2001) with the branch-and-bound algorithm. All multistate characters were treated as polymorphic and run unordered. DELTRAN was selected for character-state optimization.

Five most parsimonious trees were discovered (Fig. 4), each consisting of 89 steps, with a consistency index of 0.71 excluding uninformative characters, a rescaled consistency index of 0.59, and a retention index of 0.83. A polytomy exists consisting of *Mycterosaurus*, *Mesenosaurus*, BP/1/5678 and *Varanodontinae*. *Elliotsmithia* is a basal varanodontine. The results indicate that *Archaeovenator* is a sister taxon to all other varanopids and falls outside the clades *Varanodontinae* and *Mycterosaurinae* (Reisz and Berman 2001). This position of *Archaeovenator* is well supported by the data, and it takes 4 extra steps (in MacClade Version 4.0) to move this taxon into the *Mycterosaurinae*, and 6 extra steps to move it into the *Varanodontinae*. In addition, it takes 7 extra steps to make it into a stem eupelycosaur. A bootstrap analysis using 1000 replicates, with 10 random addition sequences, was performed for each replicate resulting in values of 95% for the clade *Varanopidae* and 87% for *Archaeovenator* as the sister taxon of all other varanopids. Removal of BP/1/5678 results in a single most parsimonious tree (Fig. 5).

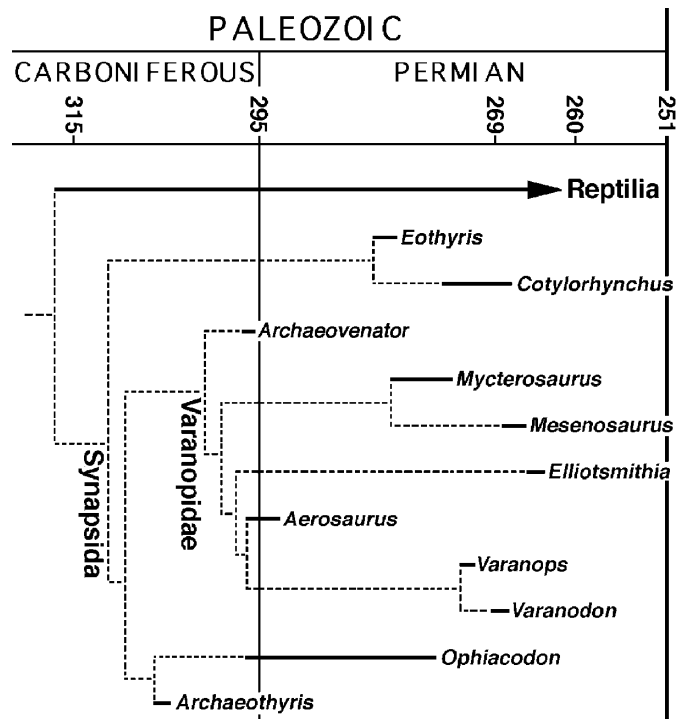
**Discussion**

The skeletal anatomy of *Archaeovenator hamiltonensis* provides convincing evidence that this small Pennsylvanian amniote is a varanopid synapsid. Varanopid autapomorphies of the skeleton include (1) the maxillary process of the premaxilla has a rounded ventrolateral surface; (2) the septomaxilla is greatly modified to form a sheet-like structure that extends across the external naris, from the premaxillary–maxillary ventral edge to the nasal bone above; (3) the external naris is greatly expanded posterodorsally; (4) the subtemporal bar is very slender, with a narrow, sliver-like quadratojugal; (5) the occipital shelf of the squamosal is reduced; (6) the

**Fig. 4.** Strict consensus cladogram of the five most parsimonious trees of an analysis of varanopid relationships.



**Fig. 5.** Varanopid phylogeny and the fossil record. Ghost lineages are indicated by dashed lines. *Cotylorhynchus* and *Eothyris* have been selected as representatives of the caseasaurian families Caseidae and Eothyrididae, respectively; *Archaeoethyris* and *Ophiacodon* have been selected as representatives of the eupelycosaurian family Ophiacodontidae. Other synapsid taxa were not included because the basic pattern of eupelycosaurian relationships, including the position of ophiacodontids, is well resolved (Berman et al. 1995). The primitive character states for the clade Reptilia were reconstructed by examining *Mesosaurus*, *Milleretta*, and *Captorhinus*. In this phylogeny, Reptilia and Synapsida are sister taxa, representing a basal dichotomy of Amniota.



parietal extends anteriorly over the orbital region; (7) the slender lower jaw is unusually slender, and the splenial does not contribute to slender symphysis; (8) the retroarticular process is modestly developed and is oriented in line with the length of the mandible; (9) the tabular bone is reduced to

sliver-like proportions; (10) the femur is long and slender with a length-to-distal width ratio greater than 3:1; and (11) two subequal sacral ribs are present.

Of particular interest here are the cranial features in the snout region. The morphology of the septomaxilla in *Archaeovenator* is identical to that seen in *Varanodon*. In both taxa, the septomaxilla has been modified from the primitive amniote condition, not only in developing a sheet-like morphology, but also by taking up a superficial position in the external narial opening and straddling the opening between its ventral and dorsal borders. Reexamination of the skulls of *Varanops* and *Aerosaurus* reveals the presence of essentially the same septomaxillary morphology, although not as well preserved as in the former two taxa. This type of septomaxilla has not been seen in any other Paleozoic tetrapod and seems to be associated in all of the above taxa with a dramatic posterodorsal expansion of the external naris. More modest posterodorsal expansion of the external naris is present in both *Mycterosaurus* and *Mesenosaurus*, but neither has a preserved septomaxilla. In these two taxa, the posterior border of the narial opening is formed by the massive dorsal expansion of the maxilla. This is in strong contrast to the condition in the varanodontines and in *Archaeovenator*, where the posterior border of the narial opening is formed by the lacrimal bone. The results of the phylogenetic analysis indicate that the condition seen in *Archaeovenator* is primitive for varanopids, with a large posterodorsal expansion of the narial opening and no dorsal expansion of the maxilla. This expanded narial opening is retained in varanodontines, but modified slightly through the development of a narrow dorsal process of the maxilla that overlies a portion of the lacrimal, but does not exclude it from the narial opening. The condition seen in mycterosaurines appears to be derived in the presence of a massive, anteroposteriorly expanded dorsal process of the maxilla that also excludes the lacrimal from the narial opening. Nevertheless, these mycterosaurines appear to retain a modest posterodorsal expansion of the narial opening.

*Archaeovenator* exhibits the synapsid autapomorphies of a well developed lateral temporal fenestra, in which the quadratojugal is excluded from the temporal fenestra by the anteroventral process of the squamosal and a broad supraoccipital. Eupelycosaurian features include the presence of a narrow snout, a long posterolateral process of the frontal, a broad contribution of the frontal to the orbital margin, location of the pineal foramen near the posterior edge of the parietal bone, the presence of an elongate, slender supratemporal bone, and sharply divided lateral and dorsal surfaces of the postorbital bone. This large body of evidence makes us confident of the broadly defined position of *Archaeovenator hamiltonensis* as both a basal eupelycosaur and a basal member of the clade Varanopidae.

## Conclusions

The description of this new varanopid extends the fossil record of this clade of basal synapsids well into the Pennsylvanian (Upper Carboniferous). Its position as a sister taxon to all other varanopids is consistent with its age (Fig. 5), but the next oldest varanopid is *Aerosaurus*, a highly derived, large form whose fossil remains have been found in El Cobre Canyon and Arroyo de Agua, New Mexico. Recent discoveries (Reisz

et al. 1998; Reisz and Berman 2001; Modesto et al. 2001) indicate that varanopids form a clade of basal synapsids that had a wide geographic and temporal distribution, ranging from the Late Carboniferous to the upper Middle Permian and from Central U.S.A. to South Africa and northern Russia. Our recognition of the Middle Permian follows the current biostratigraphic scheme for the Permian endorsed currently (e.g., Erwin et al. 2002). In comparison to the other Permian–Carboniferous clades with a distinctive morphotype, Caseasauria (Caseidae and Eothyrididae), Ophiacodontidae, Edaphosauridae and Sphenacodontidae, Varanopidae has the longest known fossil record.

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## Appendix 1: List of characters used in the phylogenetic analysis

The numbers in brackets refer to the state for a character. Most characters are taken from Reisz et al. 1998, unless otherwise indicated. Character descriptions that have been modified are also indicated.

- Marginal dentition: conical and slightly recurved (0); strongly recurved and mediolaterally compressed (1).
- Premaxillary narial shelf: ventral shelf of external naris separated from sculptured lateral surface (0); rounded ventral narial shelf that extends smoothly to ventral edge of skull (1).
- Lateral temporal fenestra: absent (0); present (1). Modified from Reisz et al. 1998.
- Frontal: posterolateral process short or absent (0); posterolateral process long and narrow, matching length of postfrontal, and between parietal and postfrontal (1).
- Maxilla dorsal process: absent (0); present, extends to level of dorsal narial margin (1). Modified from Reisz et al. 1998.
- Maxilla–prefrontal contact: contact absent (0); contact present (1).
- Prefrontal contribution to orbit: restricted to anterodorsal corner of orbit (0); long ventral process of prefrontal extends ventrally to reduce lacrimal contribution to orbit (1). Modified from Reisz et al. 1998.
- Anterodorsal process of squamosal: absent or short and does not extend along the entire length of the posterior process of the postorbital (0); present and extends to the corner between the posterior and anteroventral processes of the postorbital (1).
- Temporal fenestra shape: subcircular (0); posteroventral expansion resulting in triangular outline of fenestra (1); oval, height greater than length (2). Modified from Reisz et al. 1998.
- Lateral buttress of maxilla: external dorsally oriented maxillary buttress absent (0); present (1).
- Quadratojugal: contribution to fenestra absent (0); present (1).
- Antorbital region: broad antorbital region, nasal largely dorsal element (0); antorbital region narrow and tall, nasal has nearly vertical contribution to snout (1).
- Frontal–orbital border: frontal contribution to orbit absent or narrow (0); frontal contribution to orbit broad and forms most of dorsal edge (1).
- Circumorbital ornamentation: tuberos ornamentation on prefrontal and jugal absent (0); present (1). Modified from Reisz et al. 1998.
- Squamosal occipital shelf: occipital process of squamosal present and contributes to occipital surface of skull (0); narrow (1); absent (2).
- Parietal: extension over orbital region absent (0); present (1). Modified from Reisz et al. 1998.
- Pineal foramen: located on anterior or mid-region of midline parietal suture (0); pineal located in posterior region of midline parietal suture (1).
- Lower temporal bar: zygomatic arch or subtemporal bar tall, occupying at least 30% of skull height (0); bar narrow, occupying less than 20% of postorbital skull height (1).
- Lacrimal duct: lacrimal duct opens on posterior edge of lacrimal (0); duct opens laterally near posterior edge of lacrimal (1); opens laterally on concave surface of lacrimal (2).
- Basal tubera: short, broad, with short articulating facets facing anterolaterally (0); long, wing-like, with long articulating facets facing anteriorly (1).
- Dimensions of femur: broad and short, maximum length/distal width ratio less than 3:1 (0); femur long and slender, length/distal width ratio more than 3:1 (1).
- Supratemporal: broad element of skull table (0); slender, in parietal and squamosal trough (1).
- Postorbital: long posterior process present, extending over temporal fenestra (0); long posterior process absent (1).
- Squamosal: contact with jugal absent anterodorsally (0); squamosal–jugal contact present on postorbital bar (1).
- Dorsal and lateral surfaces of postorbital: form smooth curve (0); dorsal and lateral surfaces sharply divided (1).
- Dimensions of paroccipital process: tall, blade-like, and attached dorsolaterally to tabular (0); narrow, blade-like, and unattached (1).
- Quadrate: occipital margin with an anterior slope that is greater than 60° (0); occipital edge with anterior slope that is 50° or less (1).
- Maxillary tooth row: 23 maxillary teeth or fewer (0); 26 maxillary teeth or more (1).
- Supraglenoid foramen: absent (0); present (1).

30. Teeth on transverse flange: single row on edge (0); additional teeth anterior to single row (1).
31. Neural spine height of mid-dorsal vertebrae from base of zygapophysis / maximum centrum height: equal or less than 1 (0); 1.5 or greater (1). Modified from Reisz et al. 1998.
32. Serrations on teeth: absent (0); present (1). Modesto et al. 2001.
33. Squamosal posterodorsal process: absent (0); present (1). Modesto et al. 2001.
34. Marginal dentition lateral compression: present distally (0), present over 2/3 of tooth (1). New
35. Quadratojugal: superficial anterodorsal process absent (0); present (1). New.
36. Anterior extent of quadratojugal: equal to anterior extent of ventral portion of squamosal (0), quadratojugal longer extending anterior to ventral portion of squamosal (1). New.
37. Postorbital: lateral boss at orbital margin absent (0); present (1). New.
38. Angular posteroventral edge: ridged, or keeled (0); rounded (1). New.
39. Caniniform region: absent (0), present (1). New.
40. Hyoid: short, directed to quadrate region (0), long directed posteriorly beyond skull (1). New.
41. Premaxillary teeth: five or more (0), four or fewer (1). New.
42. Septomaxilla: lateral, sheet-like exposure absent (0); present (1). New.
43. Narial posterodorsal expansion: absent (0); present, but modest, pinched between nasal and maxilla (1); greatly enlarged, between nasal and lacrimal (2). New.
44. Dorsal centra midventral margin: rounded (0), ridged but without keel (1) New.
45. Parasphenoid dentition posterior to level of transverse flange: absent (0), present along edges (1), present on edges and posterior body (2). New.
46. Tabular: large sheet-like (0); narrow, slender (1). New.
47. Vertebral neural spine excavation: absent (0); present (1). Reisz 1986.
48. Sacral ribs: two unequal (0); two equal (1); three (2); four (3). Reisz 1986.
49. External narial shelf on nasal: absent (0); present (1). Reisz 1986.
50. Nasal length: shorter or equal to frontal (0); longer than frontal. Berman et al. 1995.
51. Premaxillary rostral process: absent (0); present (1). Reisz 1986.
52. Ventral margin of postorbital region: straight (0); concave (1). Berman et al. 1995.
53. Snout proportions: snout width > height (0); snout width < height (1). Reisz 1986.

## Appendix 2.

**Table A1.** Data Matrix

Node	123456789	1111111111	2222222222	3333333333	4444444444	5555
Reptilia	00000000?	0?01000000	0000?01000	0000000000	0100100000	0000
<i>Cotylorhynchus</i>	001010000	0100010010	0000000000	1001001000	0100000031	0110
<i>Eothyris</i>	001000000	0000000000	0?0000000?	1001001001	?100?0?0?1	0100
<i>Archaeothyris</i>	0?1100000	00110?0100	0010011010	010?00?001	??01?0000	1011
<i>Ophiacodon</i>	001100002	0011000100	0010011?10	0100101001	?000100000	1011
<i>Mycterosaurus</i>	111111102	0011111111	1110011001	?11?1001?1	10?1111110	0001
<i>Mesenosaurus</i>	111111102	0011111111	1110011001	1011100101	10?1111110	0001
<i>Elliotsmithia</i>	1?11??111	?0?111111?	??100111??	0?111011??	1?????1??0	?01
<i>Aerosaurus</i>	111110011	1111021112	1111110100	010?111111	1012121120	0001
<i>Varanops</i>	111110011	1111021112	1111110110	110?111111	1012121120	0001
<i>Varanodon</i>	111110011	1111021112	1111110110	110?111111	10121?1120	0001
<i>Archaeovenator</i>	011100102	0011011110	011001?011	000?000000	?112101010	0001
BP/1/5678	1?10?1?2	?????11??	??00?00?	?1110??1	?????????	???