

## PYOZIA MESENENSIS, A NEW, SMALL VARANOPID (SYNAPSIDA, EUPELYCOSAURIA) FROM RUSSIA: “PELYCOSAUR” DIVERSITY IN THE MIDDLE PERMIAN

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**ABSTRACT**—*Pyozia mesenensis*, gen et sp. nov. is the second varanopid synapsid from the Middle Permian Krasnoschelsk Formation of Russia. *Pyozia* is a basal varanopid similar to *Archaeovenator* in having teeth that lack lateral compression or serration, lacking a caniniform tooth or region on the maxilla, and possessing four premaxillary teeth. *Pyozia* uniquely possesses a medial contact of the maxilla with the quadratojugal with no lateral exposure allowing the jugal to form part of the skull’s ventral margin, and rounded interpterygoid vacuities just anterior to the basiptyergoid articulations. Phylogenetic analysis places *Pyozia* as sister taxon to the terminal dichotomy of Mycterosaurinae and Varanodontinae. The newly described Upper Carboniferous *Archaeovenator* is again found to be the most basal varanopid.

The Permian saw a large-scale changeover of the synapsid fauna, with derived, but ecologically similar, taxa, replacing more primitive “pelycosaurs.” Leaf-shaped tooth-bearing caseids were replaced in the Middle and Late Permian by herbivorous pareiasaurs with similar dentition, and *Edaphosaurus* was replaced by therapsids capable of processing plant material. The large predators of Sphenacodontidae were similarly replaced by therapsid predators. The small to medium sized predator niche, however, was continuously occupied by varanopids. The discovery of the basal *Pyozia* suggests that varanopids maintained their diversity in the Middle Permian.

### INTRODUCTION

One of the more striking patterns to emerge from Paleozoic amniote paleontology is that basal synapsids (“pelycosaurs,” caseosaurians, varanopids, ophiacodontids, edaphosaurids, and sphenacodontians) diversified greatly during the Late Carboniferous and the Early Permian, whereas deposits of Middle to Late Permian age are dominated by a synapsid fauna predominantly comprised of therapsids (Reisz, 1986; Milner, 1993; Carroll, 1998). This pattern is notable because it corresponds with the general trend of increasing “mammalness” from a classic reptilian morphotype within synapsid phylogeny (Sidor and Hopson, 1998; Sidor, 2001), and was possibly driven by the emergence of a modern herbivore-based trophic structure in terrestrial ecosystems (Reisz and Sues, 2000). Past attempts to find deposits between those of the Early Permian of southwestern North America and the Middle and Late Permian of South Africa and Russia (e.g., Olson, 1962) have been called into question (Laurin and Reisz, 1996; Sidor and Hopson, 1995), thus reinforcing this faunal separation. Moreover, recent work suggesting that the Chickasha Formation of Oklahoma bridges this temporal hiatus (Reisz and Laurin, 2001) has been controversial (Lucas, 2002; Reisz and Laurin, 2002). Finally, the recent identification of a basal therapsid in the Lower Permian of North America (Laurin and Reisz, 1990, 1996) is equally controversial and not accepted by all workers (Sidor and Hopson, 1998; Condad and Sidor, 2001).

Caseids and varanopids do not follow this pattern; rather they extend from the Upper Carboniferous (varanopids) and Lower Permian (caseids) into the Middle Permian. The remains of the caseosaurian *Ennatosaurus* have been identified in Upper Kanizanian/Lower Tatarian sediments of Northern Russia (Olson, 1968; Ivakhnenko et al., 1997), in addition to the wide caseosaurian distribution in the Lower Permian of North America. Similarly, the varanopids *Mesenosaurus* (Efremov, 1938; Romer and Price, 1940; Reisz and Berman, 2001) and *Elliotsmithia* (Dilkes and Reisz, 1996; Reisz et al., 1998; Modesto et al.,

2001) are present in the Middle Permian of Russia and South Africa, respectively, which extends the varanopid lineage from the Upper Carboniferous (Reisz and Dilkes, 2003).

Varanopids are small to medium sized, carnivorous, basal synapsids that have recently attracted considerable attention. Currently recognized varanopids include *Varanops* (Williston, 1911, 1914; Watson, 1914; Romer and Price, 1940), *Varanodon* (Olson, 1965), *Aerosaurus* (Langston and Reisz, 1981), *Mycterosaurus* (Berman and Reisz, 1982; Reisz et al., 1997), *Mesenosaurus* (Reisz and Berman, 2001), *Elliotsmithia* (Dilkes and Reisz, 1996; Reisz et al., 1998; Modesto et al., 2001), and *Archaeovenator* (Reisz and Dilkes, 2003). The position of *Elliotsmithia* within varanopid phylogeny is controversial, being alternately placed within Varanodontinae (Reisz et al., 1998; Reisz and Dilkes, 2003) or Mycterosaurinae (Modesto et al., 2001). Additionally, Reisz and Dilkes (2003) have raised the possibility that the specimen referred to *Elliotsmithia* by Modesto et al. (2001) might not be the same species as the holotype.

Here we report on a second varanopid species from the Middle Permian fossil-bearing deposits of the Mesen River Basin in Russia (Ivakhnenko et al., 1997). This new varanopid is a basal form, falling outside the terminal dichotomy of Mycterosaurinae and Varanodontinae, and in many ways resembles the recently described *Archaeovenator* from the Upper Carboniferous Hamilton Quarry of Kansas (Reisz and Dilkes, 2003). This new species is important because it suggests that Middle Permian varanopids were not simply relicts of an older fauna, but they maintained significant diversity throughout the Permian. Throughout this study we follow the amended spelling of Varanopidae (from Varanopseidae) of Reisz and Dilkes (2003).

### SYSTEMATIC PALEONTOLOGY

AMNIOTA Haeckel, 1866  
SYNAPSIDA Osborn, 1903  
EUPELYCOSAURIA Kemp, 1982  
VARANOPIIDAE Romer and Price, 1940  
*PYOZIA MESENENSIS* gen. et sp. nov.

**Holotype**—PIN 3717/33.

**Locality**—Ust-Nyafra, Arkhangelsk Region, Mezen District, Pyoza River.

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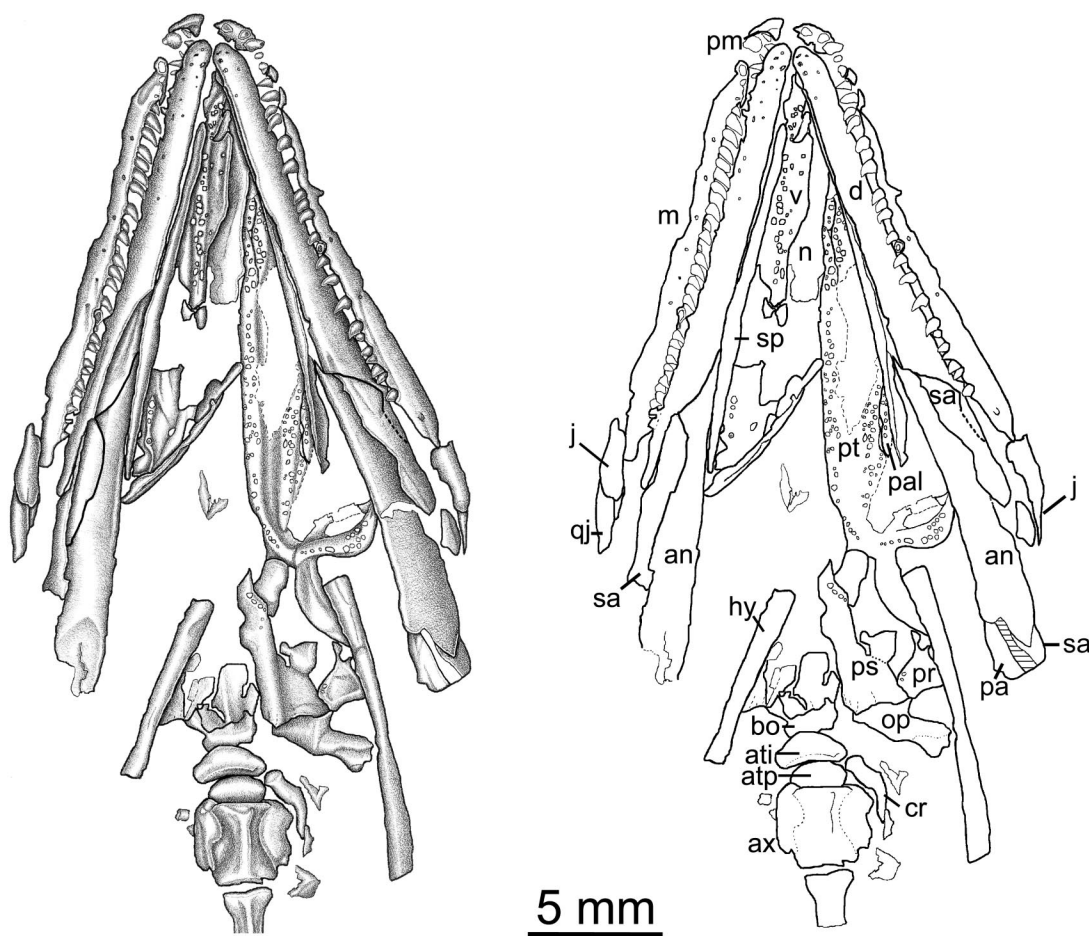


FIGURE 1. *Pyozia mesenensis*, new genus and species, holotype PIN 3717/33. Skull in ventral view. **Abbreviations:** an, angular; ati, atlantal intercentrum; atp, atlantal pleurocentrum; ax, axial pleurocentrum and neural arch; axi, axial intercentrum; bo, basioccipital; cr, cervical (atlantal) rib; d, dentary; hy, hyoid; j, jugal; m, maxilla; n, nasal; op, opisthotic; pal, palatine; pm, premaxilla; pr, prootic; ps, parasphenoid; pt, pterygoid; qj, quadratojugal; sa, surangular; sp, splenial; v, vomer.

**Formation and Age**—Krasnoschelsk Formation, Leshukonsk Member, Lower Tatarian, Middle Permian.

**Etymology**—Genus named for the Pyoza River, site of the discovery locality, feminine. Species named to acknowledge the importance of the fossils from the Mesen River Basin.

**Diagnosis**—Small varanopid with contact of maxilla and quadratojugal unexposed laterally, homodont dentition lacking serration, four premaxillary teeth, anteriorly directed basipterygoid processes, and interpterygoid vacuity laterally rounded directly anterior to basipterygoid articulations.

**Description**—The specimen is preserved in a red siltstone that was split through the skeleton on a transverse plane. Unfortunately, the counterpart was not recovered. Dr. Michael Ivakhnenko embedded the exposed surface in epoxy, and the specimen was prepared from the opposite side, revealing the ventral surface. The specimen is in two pieces, one containing the skull and anterior few vertebrae, and the other containing parts of the pectoral girdle and a few dorsal vertebrae.

The skull (Fig. 1) is preserved in palatal view but some of the lateral surface may also be seen. The lower jaws are preserved in place, obscuring details of the palatal morphology. Unfortunately, not all of the palate was in the plane of the fracture, resulting in some additional bone loss. The skull appears to have undergone minimal dorsoventral compression.

The specimen does not show the pinched and truncated rostrum diagnostic of *Mesenosaurus* (Reisz and Berman, 2001;

Fig. 2). In *Mesenosaurus*, the premaxillae are tightly apposed to each other, forming a slender, anteriorly attenuated snout, and each bears 6 teeth. In contrast, the rostrum of *Pyozia* is broadly rounded, and the narrowly triangular skull gradually tapers to its termination from the posterior (Fig. 1). The premaxilla of *Pyozia* is anteriorly broad and holds four teeth of equal size, a low count for a varanopid. The premaxilla floors the external naris ventrally. This subhorizontal shelf passes ventrolaterally to meet the tooth row, so that there is no lateral wall of the premaxilla beneath the external nares, which is a unique feature of varanopids (Reisz et al., 1998; Reisz and Berman, 2001). In all other amniotes, including the parareptile *Macroleter* (pers. obs.), there is a lateral surface of the premaxilla ventral to the external nares continuous with that of the more anterior premaxilla and the maxilla, which is distinct from the subnarial shelf.

The maxilla is long, being approximately three-quarters the total length of the lower jaw. The maxilla contacts the medial surface of the quadratojugal, and this contact is not visible in lateral view. It cannot be determined if the dorsal lamina of the maxilla contacted the nasal, but it is clear that *Pyozia* lacks both the lateral maxillary buttress that characterizes varanodontines, and the type of thickening of the maxillary lamina that characterizes mycterosaurines. The anterolateral surface of the right maxilla has worn away, revealing the passage, and slightly exaggerating the size, of an anteriorly directed foramina, similar

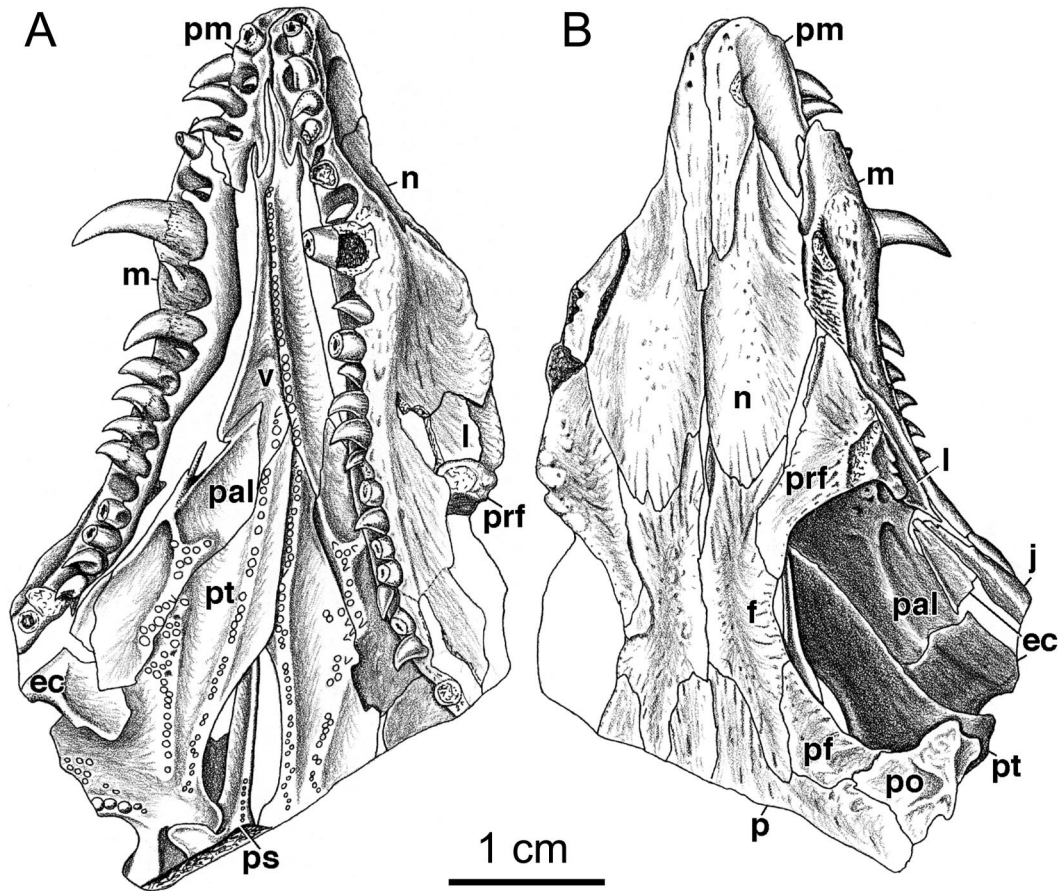


FIGURE 2. *Mesenosaurus romeri*, PIN 3586/8a, in (A) ventral view, showing the characteristic narrow rostrum that is absent from *Pyozia*, and (B) dorsal view, displaying the unique varanopid premaxillary morphology.

to that seen in many other basal amniotes, including the varanopids *Aerosaurus* and *Varanodon* (pers. obs.). The maxilla holds 30 teeth, which are slightly recurved and lack visible serration. Recurvature is not as strongly expressed as in other varanopids, such as *Aerosaurus* (Langston and Reisz, 1981) and *Varanodon* (pers. obs.), but it is more pronounced than seen in other amniotes, including *Hylonomus* and the paretile *Millerosaurus*. As in *Archaeovenator* (Reisz and Dilkes, 2003) the teeth are not laterally compressed; there is no caniniform region in the maxillary dentition, and no lateral swelling of the maxilla where the canines would usually occur. This is in contrast to the condition in *Mesenosaurus* where there is a single dominant canine tooth, and to all other varanopids where a caniniform region is present (Reisz and Berman, 2001). Tooth size is uniform except for the posterior-most seven, which are reduced in size.

The subtemporal margin is narrow, as in all varanopids (Reisz and Dilkes, 2003), and is formed by the jugal, squamosal, and quadratojugal. The contact between the squamosal and the jugal prevents the quadratojugal from participating in the lower margin of the fenestra. Like *Mesenosaurus* but unlike other varanopids, the jugal forms part of the ventral margin of the skull. In *Mesenosaurus*, this is due to the maxilla failing to contact the quadratojugal, whereas in *Pyozia* the maxillary contact with the quadratojugal is not exposed laterally.

The palate of *Pyozia* is similar to that seen in *Mesenosaurus* (Reisz and Berman, 2001; Fig. 2b). The vomer is anteroposteriorly elongate. It sutures medially with its counterpart for the anterior half of its length, and with the lateral surface of the pterygoid for the remaining posterior distance. The vomer bears

a single irregular row of teeth on a ridge along its medial margin. Between the vomers another elongate bone protrudes ventrally. It is smooth and toothless and either represents the sphenethmoid or the ventral surface of a nasal. The lower jaws obscure the morphology of the choana.

The pterygoid is the longest bone of the palate, spanning three-quarters the total length of the skull. It borders an interpterygoid vacuity that is very narrow except posteriorly, where it widens laterally just anterior to the basiptyergoid articulation. Anteriorly the pterygoid is narrow and laterally bordered by the vomer. More posteriorly it widens and is laterally bordered by the palatine. As in *Mesenosaurus*, *Archaeovenator*, and many basal amniotes such as *Petrolacosaurus* (Reisz, 1977), the pterygoid bears three raised rows of teeth that radiate from the region of the basicranial articulation: the first row runs parasagittally towards the vomer, the second row runs anterolaterally towards the palatine, and the third row runs along the bone's transverse flange. These teeth are uniformly small, except for those on the transverse flange, where they are much larger. Small accessory teeth lie along the anterolateral surface of the transverse flange. The transverse flange extends below the plane of the palatal surface, unlike the derived condition in *Mesenosaurus* where it is at the same level (Reisz and Berman, 2001). The quadrate ramus of the pterygoid extends posterolaterally at a 35° angle to the longitudinal axis. The quadrate itself is placed even with the occiput, similar to the condition in *Mycterosaurus* (Berman and Reisz, 1982).

Only a fragment of the palatine is exposed. It is sutured to the lateral surface of the pterygoid along the anterolateral tooth

ridge, but it is mainly obscured by the splenial. A single row of teeth can be seen running parallel to the anterolateral pterygoid tooth row, which is a more medial location than is inferred for *Mesenosaurus* (Reisz and Berman, 2001; Fig. 2).

The parasphenoid is incompletely preserved. The basal plate is triangular, with the apex oriented towards the unpreserved cultriform process. The basiptyergoid processes are directed anteriorly and slightly laterally, at an angle more similar to that in *Haptodus* (Currie, 1979) or *Archaeovenator* (Reisz and Dilkes, 2003) than in derived varanopids, which have more laterally directed processes. A row of teeth is present on the lateral margin of the parasphenoid at the basiptyergoid process, but the region that would bear a transverse row of teeth as in *Aerosaurus* (Langston and Reisz, 1981) is not preserved. The suture between the parasphenoid and basioccipital is visible, as are longitudinal striations running anteriorly from that suture.

A portion of the opisthotic is seen on the left side of the skull. The base of the paroccipital process is columnar and projects dorsolaterally out of the plane of preservation. Anterior to it is the prootic. As preserved, it is a trapezoidal element that reaches from the parasphenoid and anterior opisthotic laterally towards the quadrate. A large fenestra ovalis is formed between the prootic and opisthotic. No additional braincase features can be seen.

The mandible is preserved only in ventrolateral aspect. Each ramus is shallowest at the symphysis and gradually increases in depth posteriorly, until it passes above the plane of separation. Both rami are overlapped by the maxillae, so few dentary teeth are visible. The pattern of sutures is similar to that seen in *Mesenosaurus* (Reisz and Berman, 2001). The dentary is the largest bone of the mandible, extending posteriorly at least as far as the maxilla does. Only the dentary forms the symphysis. On the lateral surface of the dentary just below the tooth row run a series of small foramina; at the symphysis there are three additional mental foramina ventral to the main row.

The angular extends from the articular to the last quarter of the upper tooth row. It has a blade-like ridge running the length of the preserved portion of its ventral surface. The surangular just reaches the most posterior part of the maxillary tooth row. The splenial is a long element, spanning from just posterior to the symphysis to a level even with the last maxillary tooth, about two-thirds the length of the lower jaw. The presence of a retroarticular process cannot be determined because of a lack of preservation of the relevant areas.

On either side of the parasphenoid lies a hyoid element, probably the ceratohyal. It is a long, slender cylindrical bone that is not expanded at either end. It lies parallel to the jaws and extends from the basicranial articulations well beyond the posterior margin of the skull to the caudal end of the axis. A basihyal element is not preserved.

Portions of six vertebrae represent the axial skeleton: the three anterior-most vertebrae and three dorsal vertebrae. The crescentic atlantal intercentrum lies posterior to the basioccipital (Fig. 1). To the left of the atlantal intercentrum is an atlantal rib. Posterior to the atlantal intercentrum lies the atlantal pleurocentrum. It is comprised of unfinished bone, and bears articulations for the atlantal and axial intercentra. The axial intercentrum is not preserved.

The entire length of the axis is preserved. The centrum is laterally excavated, and a well-formed median ridge is present. The neural arch is partially visible lateral to the centrum but little else can be seen beyond its presence. The other vertebrae seem more strongly keeled and are larger than the axis, but no other features are preserved.

Elements of the pectoral girdle are preserved in ventral view (Fig. 3). The interclavicle is a cross-shaped structure with a laterally elongate diamond-shaped head and a long posterior stem (which is covered posteriorly by a limb element). The

head is about as wide as the visible portion of the stem. It bears two prominent ridges, one running along the midline, on the ventral surface of the stem and positioned between the clavicles, whereas the other runs transversely. Most of the preserved head is found anterior to the transverse ridge. In most features it resembles the interclavicles of *Aerosaurus* (Langston and Reisz, 1981) and *Ophiacodon uniformis* (Romer and Price, 1940).

The left clavicular head is preserved (Fig. 3). It lies in the hollow found between the interclavicular ridges, anterior of the transverse ridge, and covers most of that area. The clavicle is thickened along its anterior edge and thins posteriorly. The anterior margin is relatively straight, except for a small process near the midline of the interclavicle; the posterior margin is broadly convex. To the right of these bones are fragments of a scapula and coracoid. Supraglenoid and coracoid foramina are not evident.

Other elements of the pectoral girdle and forelimb are present, but are poorly preserved. Just lateral to the left clavicle is a fragment that is either part of the right clavicle or left scapulocoracoid. Along the right lateral margin of the interclavicle lie three long bones that might represent the forelimb. The element that lies caudally is the largest and might represent the humerus. None of the ends of the three bones is ossified, suggesting this specimen is not fully mature.

## DISCUSSION

*Pyozia* shares a number of features with varanopids, justifying its placement within this taxon. *Pyozia* shares with all other varanopids a narrow, triangular skull shape in dorsoventral view, in contrast with the extremely broad triangular shape of the parareptiles common at Mesen. This new species has the unique varanopid subnarial shelf formed by a dorsomedial process of the premaxilla that smoothly grades to the tooth row, rather than having a distinct vertical surface on the lateral skull margin that aligns with that of the maxilla and more anterior portions of the premaxilla. The elongate, gracile hyoids running posteriorly beyond the skull margin are characteristic of varanopids. In more basal synapsids such as *Casea* (Sigogneau-Russell and Russell, 1974:plate 2A), captorhinids, and basal parareptiles, the hyoids are relatively short, are proximally or distally expanded, and are directed laterally towards the quadrates. The teeth in *Pyozia* are recurved. In all varanopids, the inflection point where teeth begin to curve posteriorly is found on the proximal third of the tooth. In outgroup taxa such as the protorothyridid *Hylonomus* and the parareptile *Millerosaurus*, inflection, if it is found at all, is placed distal to the half way point of the tooth, producing much less recurvature (pers. obs.). However, the teeth of the new taxon are not laterally compressed, similar to those of the basal varanopid *Archaeovenator* (Reisz and Dilkes, 2003) but unlike those of all other varanopids. Like that of all eupelycosaur, the axial pleurocentrum is spool-shaped. This new species has restricted the atlantal pleurocentrum from reaching the ventral margin of the vertebral column, like other synapsids.

A number of features are unique to *Pyozia*, justifying its establishment as a new species. The rounded interptyergoid vacuities just anterior to the basiptyergoid processes are autapomorphic. Additionally, all varanopids possess a caniniform region or tooth; the absence of a canine in this new taxon, shared with *Archaeovenator*, is striking and may represent the primitive condition for the family. *Pyozia* possesses a low number of premaxillary teeth. This is a plesiomorphy as more basal synapsids such as caseosaurians also have a low count of premaxillary teeth.

Data from *Pyozia* were incorporated into the matrix of Reisz and Dilkes (2003; Table 1). One new character was added, de-



TABLE 2. Coding for *Pyozia* and other taxa for the new character added to the matrix of Reisz and Dilkes (2003). Character (54), retroarticular process: present and formed by articular, angular and surangular: absent (0); present (1).

Character	54
Reptilia	0
<i>Cotylorhynchus</i>	0
<i>Eothyris</i>	0
<i>Archaeothyris</i>	0
<i>Ophiacodon</i>	0
<i>Mycterosaurus</i>	?
<i>Mesenosaurus</i>	1
<i>Elliotsmithia</i>	1
<i>Aerosaurus</i>	1
<i>Varanops</i>	1
<i>Varanodon</i>	1
<i>Archaeovenator</i>	0
<i>Pyozia</i>	?

Varanodontinae. Because the purpose of the present study is to examine the position of *Pyozia* within Varanopidae, we will leave the question of the specific identity of BPI/1/5678 to future work.

The result of the present phylogenetic analysis is significant because it introduces a long ghost lineage to the base of the varanopid tree that extends from the Late Carboniferous to the Middle Permian. The presence of *Archaeovenator* in North America suggests a Laurasian origin of varanopids, and the presence of a basal varanopid in Russia is evidence for long-term maintenance of the basic varanopid morphotype. If our interpretation of the second specimen recently attributed to *Elliotsmithia* is correct, it suggests that the diversity of varanopids persisted throughout the Permian, including within Gondwana. Rather than relicts of an earlier fauna, the varanopids from Russia and South Africa represent a portion of the trophic structure that remained unchanged worldwide, while pareiasaurs and therapsids replaced basal synspsids such as caseids, ophiacodontids, edaphosaurids, and sphenacodontids. The strongly recurved dentition of varanopids is unique among both Permian-Carboniferous and Middle Permian amniotes, suggesting a distinct predatory behavior in these small synspsids. Thus, while caseosaurians were eventually replaced by pareiasaurs with similar dentition, edaphosaurs were replaced by various therapsids that process plant material, and sphenacodontids were replaced by the large predatory therapsids, small predatory varanopids maintained their niche within the Middle Permian fauna.

CONCLUSIONS

*Pyozia mesenensis* is the second varanopid known from the Middle Permian deposits of the Mesen Basin, bringing the number of basal synspsid genera found in faunas dominated by the more advanced therapsids to at least four: *Pyozia*, *Mesenosaurus*, *Elliotsmithia*, and *Ennatosaurus*. This evidence strengthens the argument against some sort of ecological factor that restricted Permian-Carboniferous synspsids to equatorial regions free from therapsids. *Pyozia* represents evidence for a Laurasian origin for varanopids, and suggests that at least in Russia, varanopid diversity persisted unabated. If Reisz and Dilkes (2003) are correct in their suggestion that BPI/1/5678 is distinct from *Elliotsmithia* and affiliated with mycterosaurines, then members of both varanopid subfamilies would be present in the Middle Permian of South Africa, making varanopids ubiquitous, if relatively rare, members of the Middle Permian terrestrial fauna. The fossil record of varanopids is therefore extraordinarily long among basal synspsids. In contrast to other "pelycosaurs," which are restricted either to the Permian-Carboniferous or the Middle Permian, varanopids extend from the Carboniferous into

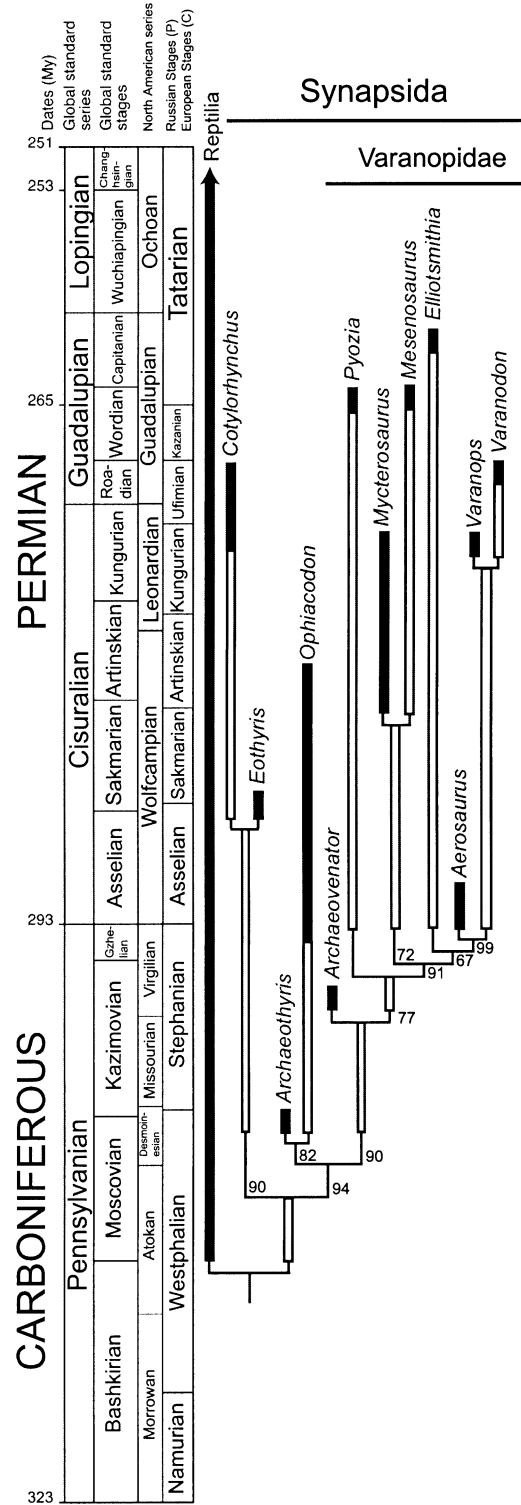


FIGURE 4. Stratigraphically most parsimonious tree (86 steps, C.I. = 0.709, R.I. = 0.831) of the three MPTs found in the phylogenetic analysis. *Pyozia mesenensis* is identified as the sister taxon to Varanodontinae + Mycterosaurinae, with the Upper Carboniferous *Archaeovenator* placed farther stemward. White bars show ghost lineages necessitated by this topology, and the geologic time scale shows their relative duration. Numbers at each node are bootstrap values after 1,000 random replicates. Correlation of Permian stages from Reisz and Laurin (2002), and Upper Carboniferous stages from Peppers (1996).

the Middle Permian, suggesting that they were able to adapt to the ecological and climatic changes that characterize the late Paleozoic (end of ice-age, dispersal of tetrapods to high latitude, temperate zones, dramatic changes in terrestrial fauna and flora).

Although the diversity of Permo-Carboniferous synapsids is spectacular within the Carboniferous and Early Permian of Laurasia, only the two most basal clades were apparently able to extend into the Middle Permian. One is a highly specialized herbivore, the caseosaurian *Ennatosaurus*; it is present in Mezen and Pinega (Reisz and Laurin, 2002), where there are no pareiasaurs (eco-equivalent to caseosaurians as a leaf-toothed herbivore). Small varanopids survive well into the Middle Permian as small predators, and there are no eco-equivalents until the appearance of small diapsid predators in the uppermost Permian. This is a particularly fascinating aspect of synapsid evolution during the initial stages of amniote evolutionary history, when synapsids were clearly the dominant terrestrial vertebrates.

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#### LITERATURE CITED

- Berman, D. S., and R. R. Reisz. 1982. Restudy of *Mycterosaurus longiceps* (Reptilia, Pelycosauria) from the Lower Permian of Texas. *Annals of Carnegie Museum* 51:423–453.
- Carroll, R. L. 1998. Summary; pp. 187–205 in P. Wellnhofer and R. L. Carroll (eds.), *Encyclopedia of Paleoherpptology*, Vol. 1: Lepospondyli. Verlag Dr. Friedrich Pfeil, München.
- Conrad, J., and C. A. Sidor. 2001. Re-evaluation of *Tetraceratops insignis* (Synapsida: Sphenacodontia). *Journal of Vertebrate Paleontology* 21(3, Supplement):42A.
- Currie, P. J. 1979. The osteology of haptodontine sphenacodonts (Reptilia: Pelycosauria). *Palaeontographica Abteilung A* 163:130–168.
- Dilkes, D. W., and R. R. Reisz. 1996. First record of a basal synapsid ('mammal-like reptile') in Gondwana. *Proceedings of the Royal Society London B* 263:1165–1170.
- Efremov, J. A. 1938. Some new Permian reptiles of the U.S.S.R. *Comptes Rendus (Doklady)* 19:771–776.
- Haackel, E. H. P. A. 1866. *Generelle Morphologie der Organismen: allgemeine Grundzüge der organischen Formen-Wissenschaft, mechanisch begründet durch die von Charles Darwin reformirte Descendenz-Theorie*. Druck und Verlag von Georg Reimer, Berlin.
- Ivakhnenko, M. F., V. K. Golubev, Y. M. Gubin, I. V. Novikov, A. G. Sennikov, and A. S. Rautian. 1997. Permian and Triassic Tetrapods of Eastern Europe. GEOS, Moscow, 216 pp.
- Kemp, T. S. 1982. *Mammal-like Reptiles and the Origin of Mammals*. Academic Press, London, 363 pp.
- Langston, W., Jr., and R. R. Reisz. 1981. *Aerosaurus wellesi*, new species, a varanopsid mammal-like reptile (Synapsida: Pelycosauria) from the Lower Permian of New Mexico. *Journal of Vertebrate Paleontology* 1:73–96.
- Laurin, M., and R. R. Reisz. 1990. *Tetraceratops* is the oldest known therapsid. *Nature* 345:249–250.
- Laurin, M., and R. R. Reisz. 1996. The osteology and relationships of *Tetraceratops insignis*, the oldest known therapsid. *Journal of Vertebrate Paleontology* 16:95–102.
- Lucas, S. G. 2002. Discussion and reply: the reptile *Macroleter*: first evidence for correlation of Upper Permian continental strata of North America and Russia. *Geological Society of America Bulletin* 114:1174–1176.
- Milner, A. R. 1993. Biogeography of Paleozoic tetrapods; pp. 324–353 in J. A. Long (ed.), *Vertebrate Biostratigraphy and Biogeography*. The Johns Hopkins University Press, Baltimore.
- Modesto, S., C. A. Sidor, B. S. Rubidge, and J. Welman. 2001. A second varanopsid skull from the Upper Permian of South Africa: implications for Late Permian 'pelycosaur' evolution. *Lethaia* 34:249–259.
- Olson, E. C. 1962. Late Permian terrestrial vertebrates, U. S. A. and U. S. S. R. *Transactions of the American Philosophical Society (New Series)* 52(2):3–224.
- Olson, E. C. 1965. New Permian vertebrates from the Chickasha Formation in Oklahoma. *Oklahoma Geological Society* 70:3–70.
- Olson, E. C. 1968. The family Caseidae. *Fieldiana: Geology* 17:225–349.
- Osborn, H. F. 1903. The reptilian subclasses Diapsida and Synapsida and the early history of the Diaptosauria. *Memoirs of the American Museum of Natural History* 1:449–507.
- Peppers, R. A. 1996. Palynological correlation of major Pennsylvanian (Middle and Upper Carboniferous) chronostratigraphic boundaries in the Illinois and other coal basins. *Memoir of the Geological Society of America* 188:1–111.
- Reisz, R. R. 1977. *Petrolacosaurus kansensis* Lane, the oldest known diapsid reptile. *Science* 196:1091–1093.
- Reisz, R. R. 1986. Pelycosauria, Vol. 17A. *Handbook of Paleoherpptology*. P. Wellnhofer (ed.). Gustav Fischer Verlag, Stuttgart and New York, 102 pp.
- Reisz, R. R., and D. S. Berman. 2001. The skull of *Mesenosaurus romeri*, a small varanopsid (Synapsida: Eupelycosauria) from the Upper Permian of the Mesen River Basin, northern Russia. *Annals of Carnegie Museum* 70:113–132.
- Reisz, R. R., and D. W. Dilkes. 2003. *Archaeovenator hamiltonensis*, a new varanopsid Synapsida: Eupelycosauria from the Upper Carboniferous of Kansas. *Canadian Journal of Earth Science*, in press.
- Reisz, R. R., D. W. Dilkes, and D. S. Berman. 1998. Anatomy and relationships of *Elliotsmithia longiceps* Broom, a small synapsid (Eupelycosauria: Varanopsidae) from the Late Permian of South Africa. *Journal of Vertebrate Paleontology* 18:602–611.
- Reisz, R. R., and M. Laurin. 2001. The reptile *Macroleter*: first vertebrate evidence for correlation of Upper Permian continental strata of North America and Russia. *GSA Bulletin* 113:1229–1233.
- Reisz, R. R., and M. Laurin. 2002. Discussion and reply: the reptile *Macroleter*: first evidence for correlation of Upper Permian continental strata of North America and Russia. *Geological Society of America Bulletin* 114:1176–1177.
- Reisz, R. R., and H.-D. Sues. 2000. Herbivory in late Paleozoic and Triassic terrestrial vertebrates; pp. 9–41 in H.-D. Sues (ed.), *Evolution of Herbivory in Terrestrial Vertebrates: Perspectives from the Fossil Record*. Cambridge University Press, Cambridge.
- Reisz, R. R., H. Wilson, and D. Scott. 1997. Varanopsid skeletal elements from Richards Spur, a Lower Permian fissure fill near Fort Sill, Oklahoma. *Oklahoma Geology Notes* 57:160–170.
- Romer, A. S., and L. I. Price. 1940. Review of the Pelycosauria. *Geological Society of America Special Paper* 28, 538 pp.
- Sidor, C. A. 2001. Simplification as a trend in synapsid cranial evolution. *Evolution* 55:1419–1442.
- Sidor, C. A., and J. A. Hopson. 1995. The taxonomic status of the Upper Permian eotheriodont therapsids of the San Angelo Formation (Guadalupian), Texas. *Journal of Vertebrate Paleontology* 15(3, Supplement):53A.
- Sidor, C. A., and J. A. Hopson. 1998. Ghost lineages and "mammalness": assessing the temporal pattern of character acquisition in the Synapsida. *Paleobiology* 24:254–273.
- Sigogneau-Russell, D., and D. E. Russell. 1974. Étude du premier Caséidé (Reptilia, Pelycosauria) d'Europe occidentale. *Bulletin du Muséum National d'Histoire Naturelle* 230:145–214.
- Swofford, D. L. 1998. PAUP\*. *Phylogenetic Analysis Using Parsimony (\*and Other Methods)*. Version 4. Sinauer Associates, Sunderland, Massachusetts.
- Watson, D. M. S. 1914. Notes on *Varanosaurus acutirostris* Broili. *Annals and Magazine of Natural History* 8:297–310.
- Williston, S. W. 1911. *American Permian Vertebrates*. Chicago University Press, Chicago, 145 pp.
- Williston, S. W. 1914. Osteology of some American Permian vertebrates. *Contributions from the Walker Museum* 1:107–162.