

## A NEW NODOSAURID ANKYLOSAUR (DINOSAURIA: ORNITHISCHIA) FROM THE PAW PAW FORMATION (LATE ALBIAN) OF TEXAS

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**ABSTRACT**—*Pawpawsaurus campbelli* gen. et sp. nov. from the Paw Paw Formation (late Albian), Tarrant County, Texas, appears more primitive than other pre-Campanian nodosaurids, *Silvisaurus condrayi* and *Sauropelta edwardsi*. New cranial synapomorphies for the Nodosauridae are prominent W-shaped basioccipital tubera, anteriorly concave and anteroposteriorly flattened quadrate, and transversely continuous and straight posterior margin of the pterygoid aligned with the quadrate shaft. These synapomorphies are closely related to the downward orientation of the nodosaurid head in life. A pair of bony eyelids recovered with the skull are the first discovered for the Nodosauridae. Other Paw Paw Formation nodosaurid remains, including new postcranial elements and a baby nodosaurid, are taxonomically indeterminate.

### INTRODUCTION

In 1992 a nodosaurid skull (SMU 73203) was discovered in the upper Albian Paw Paw Formation, Tarrant County, Texas, by Cameron Campbell (Fig. 1). When first recovered, the left paroccipital process and premaxillary bones were missing, but were later found through the diligent searching of Robert Reid and John Maurice. The skull represents a new taxon that exhibits several unique characters, which elucidate the phylogeny of early nodosaurids. No lower jaws or postcranial elements were associated with the skull, but postcranial remains are known from the same formation. They include: a scapulocoracoid (SMU 73494), and a humerus and ilia (SMU 73057); a juvenile (SMU 72444) described by Jacobs et al. (1994); and most of a skeleton (USNM 337987). These cannot unambiguously be shown to belong to the same taxon as the skull. These specimens and their phylogenetic implications form the subject of this paper.

Both Early and Late Cretaceous Texas nodosaurids are poorly known. Specimens from the Campanian Aguja Formation and the Maastrichtian Javelina Formation of Big Bend National Park (Coombs, 1978a; Lehman, 1985) include a scapulocoracoid (OMNH uncatalogued) and a slightly crushed skull (AMNH 3076), which remain undescribed. Cenomanian nodosaurid remains occur in the Woodbine Formation of north central Texas. All Texas Early Cretaceous nodosaurid specimens are from the Albian Paw Paw Formation in the Fort Worth area.

The Paw Paw Formation lies near the top of the Washita Group, sharply delimited lithologically from the Weno Formation below and the Main Street Formation above (Fig. 2). In the Tarrant County area the Paw Paw is a brown to yellow fossiliferous clay (8 m thick), with scattered sandstone partings (Perkins and Albritton, 1955). The environment of deposition is interpreted to be predominantly nearshore marine (Scott et al., 1978). The Albian-Cenomanian boundary, as recognized from ammonite (Mancini, 1979; Birkelund et al., 1984) and foraminiferal assemblage zones (Michael, 1972), falls within the Grayson Formation overlying the Main Street Formation in the Dallas-Fort Worth area. The ages of the Albian-Cenomanian and Aptian-Albian boundaries are 97.5 Ma and 113 Ma, respectively (Kent and Gradstein, 1985). The age of the Kiamechi Formation, well below the Paw Paw, is approximately 100 Ma (Jacobs et al., 1991). The Paw Paw Formation is therefore late Albian.

### TAPHONOMY

Paw Paw nodosaurids have been recovered from marine sediments at four localities. There is no evidence of damage due to fluvial transport. Nodosaurids probably frequented coastal environments generally, as supported by several occurrences in marine sediments of western North America (Horner, 1979). The isolated skull lay palate-down on a shallow bottom where fine sand and clay were being deposited locally. Most of the teeth have fallen out. Bony eyelids that presumably attached to the orbits by ligaments were found near the skull. Scratch marks, most likely due to scavenging, are present on the condyle of the right quadrate and on the anterior proximal surface of a humerus (SMU 73507). Sharks and crabs would have been the most likely scavengers judging from their abundance at these sites. The defleshed skull roof and other bones were colonized by oysters. The diameters of these oysters are between 7 mm and 40 mm. Judging from the growth rates of modern oysters (Galtsoff, 1964), the skull remained exposed on the seafloor for a few years until it was completely covered with sand and clay. Small fish teeth, crab fragments, and oysters are found in the filling matrix of the skull.

**Abbreviations**—AMNH, American Museum of Natural History, New York; BMNH, Natural History Museum, London; CEU, College of Eastern Utah Prehistoric Museum, Price; GIPS, Geological Institute Section of Palaeontology and Stratigraphy, the Academy of Sciences of the Mongolian People's Republic, Ulan Bator; KUV, University of Kansas, Museum of Natural History, Lawrence; NMC, Canadian Museum of Nature, Ottawa; OMNH, Oklahoma Museum of Natural History, University of Oklahoma, Norman; ROM, Royal Ontario Museum, Toronto; SMU, Shuler Museum of Paleontology, Southern Methodist University, Dallas; USNM, National Museum of Natural History, Washington, D.C.; YPM, Peabody Museum of Natural History, Yale University, New Haven; ZPAL, Institute of Paleobiology (Zakład Paleobiologii) of the Polish Academy of Sciences, Warsaw.

### SYSTEMATIC PALEONTOLOGY

ORNITHISCHIA Seeley, 1888  
ANKYLOSAURIA Osborn, 1923  
NODOSAURIDAE Marsh, 1890

**Revised Diagnosis for the Cranium**—"Hourglass-shaped palate; hemispherical occipital condyle composed of basioccipital only, set off from braincase on a short neck and angled

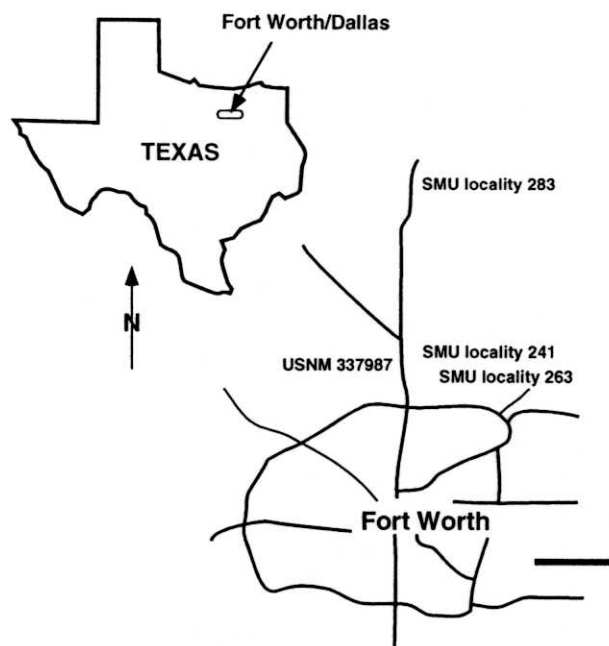


FIGURE 1. Nodosaurid localities in Tarrant County, Texas. Scale equals 6 km.

about 50° downward from the line of the maxillary tooth row; quadrate angled rostroventrally" (Coombs and Maryanska, 1990); prominent W-shaped basioccipital tubera; anteriorly concave and anteroposteriorly flattened quadrate; transversely continuous and straight posterior margin of the pterygoid aligned with the quadrate shaft. A postcranial diagnosis is given by Sereno (1986) and Coombs and Maryanska (1990).

#### PAWPAWSAURUS gen. nov.

**Type Species**—*Pawpawsaurus campbelli*, described below.

**Etymology**—Named for the Paw Paw Formation, which yielded the holotype; *sauros*, Greek lizard.

**Diagnosis**—Nodosaurid distinguished by prevomers with a rostral U-shaped ridge that opens posteriorly; oval prevomer foramen; and lack of a sagittal septum.

#### PAWPAWSAURUS CAMPBELLI sp. nov.

**Holotype**—SMU 73203, skull (Fig. 3)

**Type Locality and Horizon**—The Paw Paw Formation, late Albian, Tarrant County, Texas (SMU locality 263, all locality information on file at SMU).

**Etymology**—The species is named in honor of Mr. Cameron Campbell, who found the specimen.

**Diagnosis**—Type and only known species of genus as diagnosed above.

#### DESCRIPTION

The skull of *Pawpawsaurus campbelli* is well preserved, and judging from the circular orbits, there is no crushing or distortion. All skull elements are fused indicating a fully mature individual. The skull is approximately 250 mm long and 200 mm wide. The occiput projects posteriorly well beyond the skull roof so that most of the supraoccipital, paroccipital processes, and the lateral temporal fenestrae are visible in dorsal and lateral views. In posterior view, the cranium is much broader than high as is typical of ankylosaurian skulls.

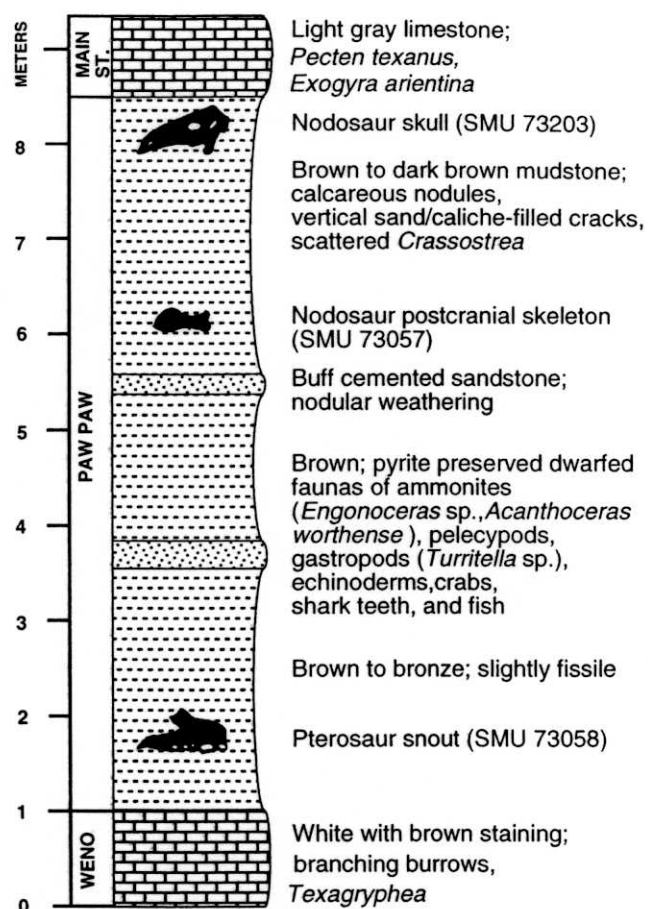


FIGURE 2. Stratigraphic section of the Paw Paw Formation at SMU locality 263, showing the level of the skull of *Pawpawsaurus campbelli* (SMU 73203) and nodosaurid indet. (SMU 73057). The other fossil shown is a pterosaur snout (*Coloborhynchus wadleighi*, SMU 73058).

The skull table becomes abruptly reduced in width anterior to the orbit, then it tapers rostrally to the truncated snout. The orbits are round (approximately 36 mm in diameter) and inclined forward and downward. The orbital rim bulges prominently posterior to a distinct preorbital constriction. It is bounded by postorbital and jugal dermal plates posteriorly. The external nares are large and anterolaterally placed. They are roughly trapezoidal in outline and open dorsolaterally.

**Dermal Skull Roof** (Fig. 4)—The dorsal surface of the skull is covered with dermal plates. They are thoroughly coossified to the skull so it is impossible to identify underlying cranial sutures. Grooves separating the plates on the top of the skull are complex and the pattern of cranial dermal plates of *Pawpawsaurus* does not closely resemble those of any other nodosaurids previously described. The antorbital and superior temporal fenestrae are closed.

The premaxillae flare slightly beneath the external nares and taper regularly toward the anterior margin of the snout. The dorsal portions of these bones bound the medial sides of the nostrils and meet the trapezoidal nasal dermal plate posterodorsally. The thin anterior edge curves ventrally to the premaxillary tooth row forming a shallow scooped premaxillary palate. The rugose and pitted anterior margin of each premaxilla was probably covered with a horny beak.

In anterior view, between the anterior extremities of the external nares, the premaxillae form a ventrally opened U-shaped excavation in front of the nasal dermal plate. Along the lateral

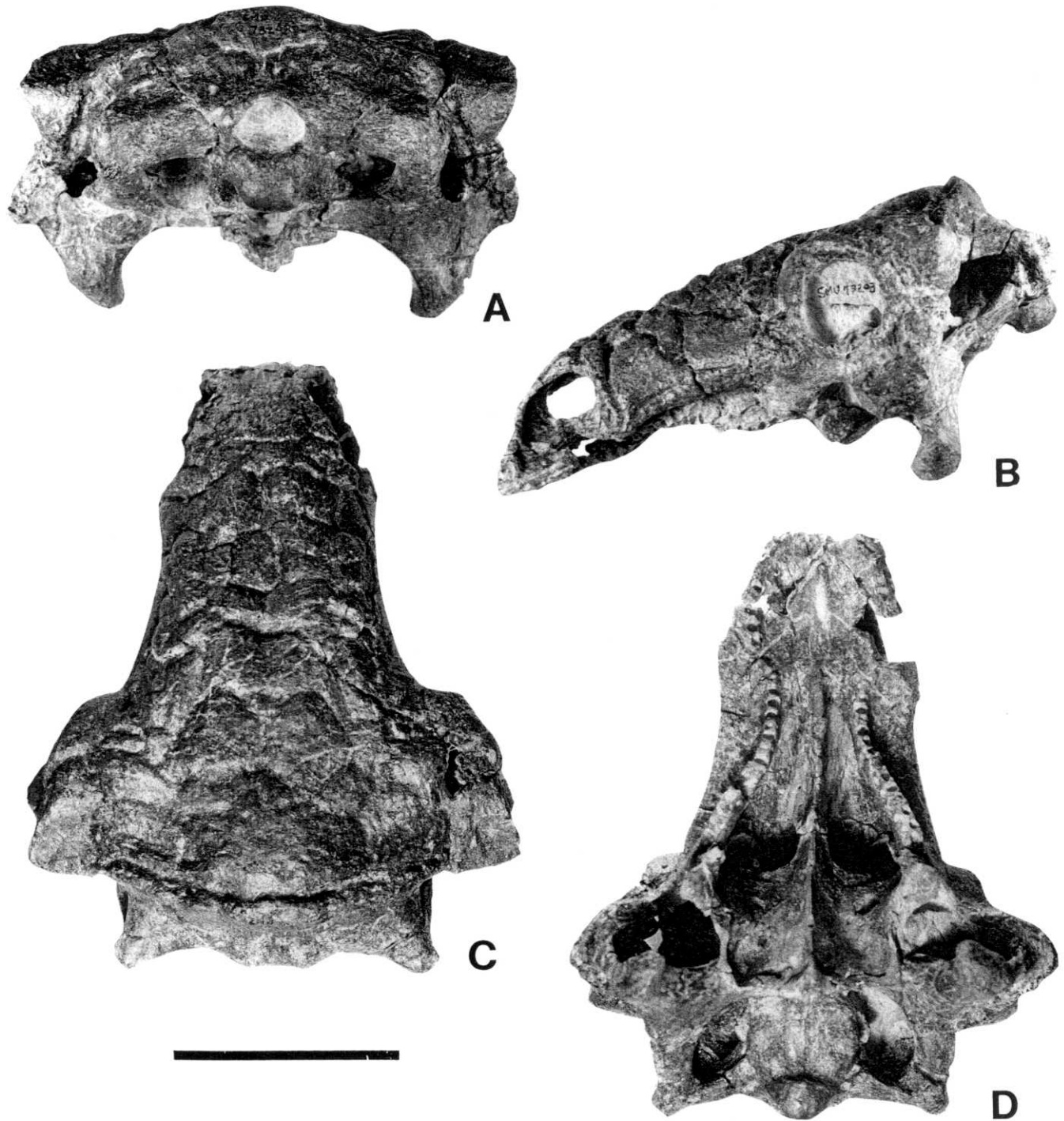


FIGURE 3. Holotype of *Pawpawsaurus campbelli* gen. et sp. nov., SMU 73203. Skull in posterior (A), lateral (B), dorsal (C), and ventral (D) views. Scale equals 10 cm.

edges of the excavation, two pairs of openings pierce the premaxillae. A dorsally situated opening, the premaxillary foramen, opens medially at the anteroventral corner of the external naris as occurs in most ornithischians. An incised canal from the premaxillary foramen passes ventrally to the lower opening, the anterior premaxillary foramen. It opens into a canal through the premaxilla and expands into the anterior palatal cavity between the first premaxillary tooth and the anterior portion of the prevomers. These premaxillary foramina probably served

the vascular system to the upper beak. The subnarial portion of the premaxilla inclines ventrally to meet the narial emargination.

The maxilla (Fig. 5) has the dorsal surface hidden by dermal plates. Its lateral edge is curved inward ventrally and forms the deep buccal emargination and a rounded linear eminence. A shallow groove is developed just above the buccal emargination between the external naris and the orbit, which is here considered to represent the ventral suture of the central dermal plates.

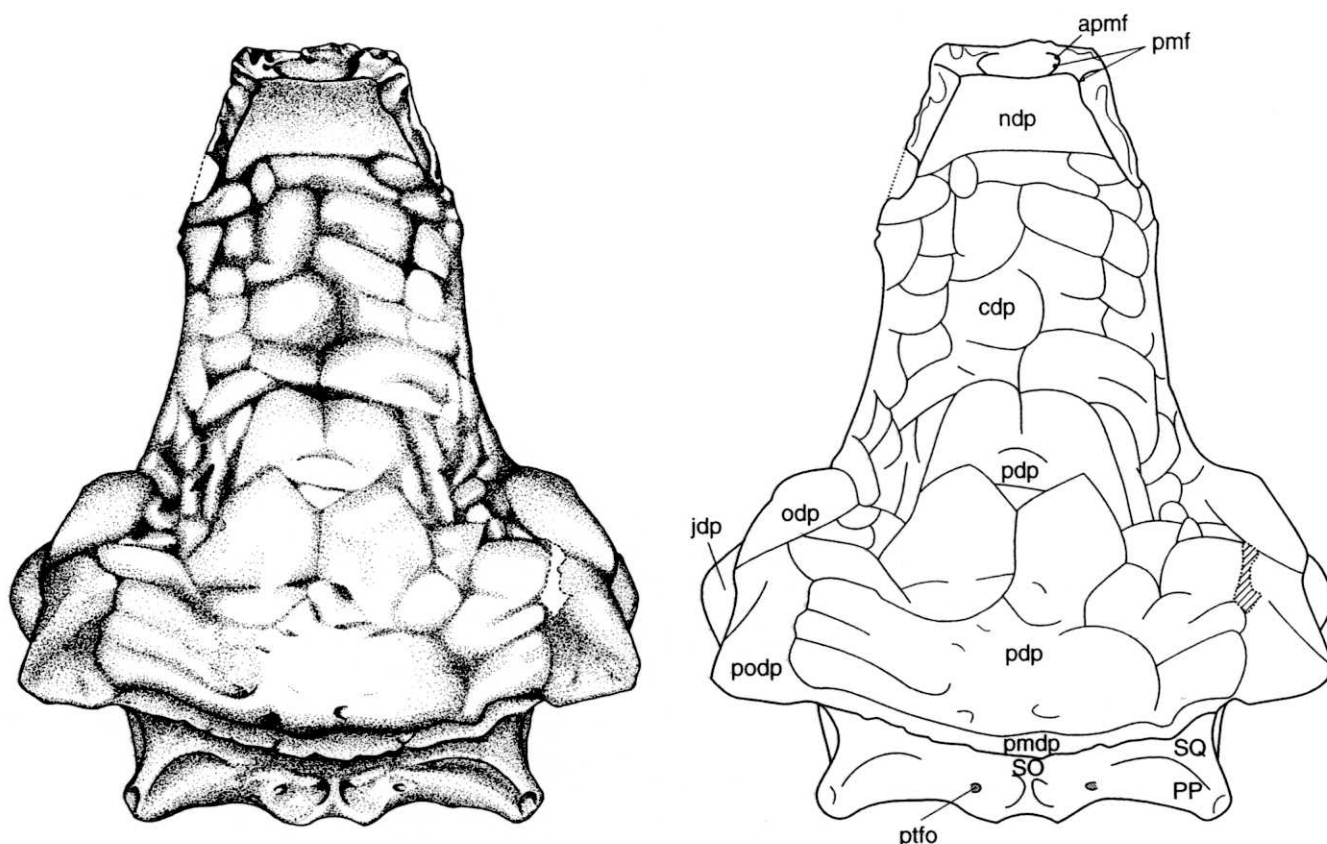


FIGURE 4. Skull of *Pawpawsaurus campbelli* (SMU 73203) in dorsal view. Abbreviations: **apmf**, anterior premaxillary foramen; **cdp**, central dermal plates; **jdp**, jugal dermal plate; **ndp**, nasal dermal plate; **odp**, orbital dermal plate; **pdp**, posterior dermal plates; **pmf**, premaxillary foramen; **pmdp**, posteriormost dermal plate; **podp**, postorbital dermal plate; **PP**, paroccipital process; **ptfo**, posttemporal foramen; **SO**, supraoccipital; **SQ**, squamosal.

The antorbital fenestra is closed externally by central dermal plates but visible on the internal lateral wall of the maxilla. The maxilla meets the premaxilla anteriorly and the jugal and lacrimal posteriorly. With the exception of the premaxilla, maxillary sutures with surrounding bones are not visible. The anteromedial process of the maxilla projects into the premaxillary palate, but does not reach the vomer medially. Thus, the anterior border of each choana is formed by the premaxilla and maxilla.

In *Pawpawsaurus*, the maxilla is not expanded lingually beyond the strong tooth ridge. As in *Sauropelta*, therefore, there is no evidence of a secondary palate between the vomers and the internal alveolar margin of the maxillae. Two large choanae separated by the vomers lie between the maxillary tooth rows. The tooth row extends ventrally and slightly outward posteriorly and it is inclined approximately 25° from the vertical plane. The cheek pouch of the maxilla is well developed anteriorly but it is gradually reduced posteriorly as the maxillary tooth row flares. Thus, the horizontal portion of the cheek forms a narrow crescentic surface lying lateral to the maxillary tooth row and the posterior portion of the premaxillary tooth row.

The nasal bones are concealed externally by a trapezoidal nasal dermal plate and central dermal plates. No ethmoid ossifications are observable. The nasal dermal plate between the nares is fused to the premaxillae at the rostral tip of the snout. It forms the dorsal margins of the external nares but does not extend to the lateral margin of each maxilla. Central dermal plates between a nasal dermal plate and posterior dermal plates are generally more rounded and smaller than other dermal

plates. Laterally, they extend down to the border of the cheek emarginations.

The space between the orbits is covered with several small posterior dermal plates, not a subcircular plate as in *Panoplosaurus* and *Edmontonia longiceps*. Although their shapes and sizes are not equal, bilateral symmetry is retained. There are three plates anteriorly, two laterally, and one posteromedially. The latter is distinctly domed above the braincase. Behind these is a long narrow plate (posteriormost dermal plate), which forms the posterior border of the skull roof and the dorsal margin of the occipital region. Laterally, it extends to the postorbital dermal plate.

The postorbital dermal plate covers the posterior rim of the orbit. In nodosaurids, the degree of its development is variable, but this plate is larger in *Pawpawsaurus* and *Sauropelta* than in other taxa. In *Pawpawsaurus*, it forms the posterolateral apex of the skull roof as a pyramidal-shaped caudolateral "horn," but does not project beyond the posterior margin of the skull roof as in ankylosaurids. A rhombic orbital dermal plate is on the anterolateral margin of the orbital roof. It overlaps the anterior aspect of the postorbital dermal plate. Thus, the orbital roof is covered with the orbital and postorbital dermal plates. Small tubercles and wrinkles extend between the orbital dermal plates and the anterior portion of the posterior dermal plates.

None of the palpebral components in the dorsal orbital region can be determined, but a pair of bony eyelids was found detached from the skull (Fig. 6). They are the first discovered for nodosaurid ankylosaurs. They are rhombic in shape (35 mm in length, 15 mm in height, and 9 mm in width). The medial sur-



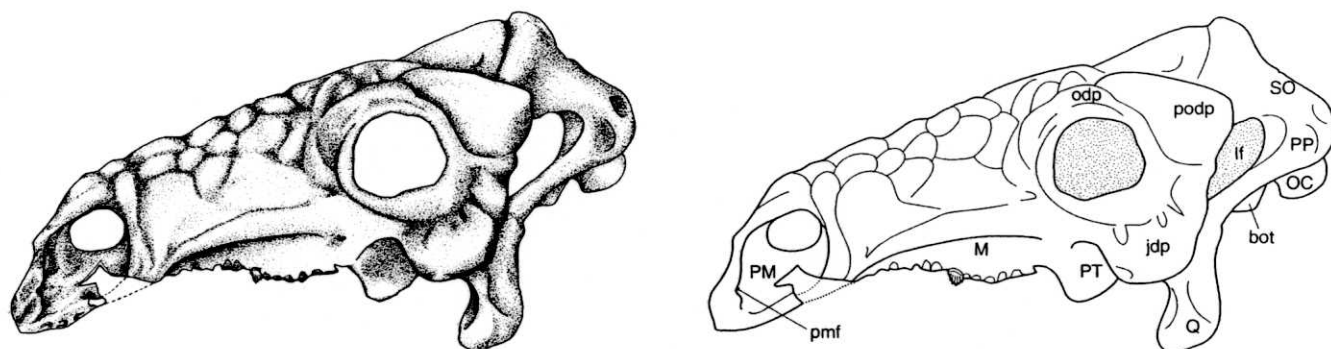


FIGURE 5. Skull of *Pawpawsaurus campbelli* (SMU 73203) in lateral view. Abbreviations as in Figure 4 plus: **bot**, basioccipital tubera; **lf**, lateral temporal fenestra; **M**, maxilla; **OC**, occipital condyle; **PM**, premaxilla; **PT**, pterygoid; **Q**, quadrate.

face is rather smooth and slightly concave to conform to the outer surface of the eyeball but the dorsal surface is coarsely textured. The dorsal surface is longitudinally grooved for articulation with the dorsal orbital margin.

The bony eyelid of *Pawpawsaurus* differs from that of the ankylosaurid *Euoplocephalus tutus* in size and shape. The latter is shaped like a quarter section of a sphere and is large enough to cover the outer surface of the eyeball completely. Because the diameter slightly exceeds the diameter of the orbital opening of *Euoplocephalus*, it has been interpreted to lie internal to the orbital cavity like a shutter (Fig. 7C, D; Coombs, 1972). The bony eyelid of *Pawpawsaurus* occupies approximately one third of the eye socket, projecting outward like a protective awning (Fig. 7A, B). Although it has a different shape from that of *Euoplocephalus*, it must have served to protect the eyeball, overhanging the dorsal rim of the eye socket in life. It does not appear to have been capable of closing the orbital opening completely. Nevertheless, considering the passive defensive strategy of nodosaurids—clutching and keeping the head down near the ground, and difficult-to-overturn body conformation (Coombs and Maryanska, 1990)—bony coverings for the eyes would be of great value from attack by predatory theropods.

The origin of the bony eyelid has been interpreted as a hypertrophied palpebral bone (Coombs, 1972). Palpebral bones in Ankylosauria are identified only in a juvenile ankylosaurid *Pinacosaurus*, which has three palpebrals (Maryanska, 1977:fig. 2A1). If three palpebrals have been incorporated in the orbital

roof of other ankylosaurs, the bony eyelid would represent a fourth palpebral, at least in *Euoplocephalus* and *Pawpawsaurus*. The presence of four palpebral bones might then be an apomorphy distinguishing Ankylosauria from Stegosauria (three palpebral bones).

The squamosal, seen along the dorsal border of the lateral temporal fenestra, projects beyond the posterior margin of the skull roof. The squamosal, the paroccipital process, and the head of the quadrate are firmly fused as in other nodosaurids.

The jugal projects anteriorly to contact the maxilla but its dorsal extension to the postorbital cannot be determined due to fusion of the postorbital dermal plate. Most of the jugal is covered with the jugal dermal plate at the ventral portion of the orbit. The crescentic jugal dermal plate projects ventrolaterally to the level of the maxillary tooth row under the posteroventral corner of the orbit. Although not big enough to hide the quadrate shaft as in ankylosaurids, the jugal dermal plate of *Pawpawsaurus* is expanded laterally so that the broadest portion of the skull is across these plates.

The transversely wide quadratojugal forms a bridge between the quadrate and the jugal and forms the lower margin of the lateral temporal fenestra. These bones are completely fused so precise boundaries cannot be determined. The quadratojugal contacts about three-fourths of the length of the lateral edge of the quadrate shaft posteriorly and extends laterally to the jugal dermal plate. The mandibular condyle of the quadrate is continuous with the ventral edge of the quadratojugal.

**Palatal Complex** (Fig. 8)—The scoop-shaped premaxillary palate is surrounded by the anterior cutting margin and premaxillary tooth rows. Posteriorly it is bounded by ridges connecting the maxillary tooth rows. Anteriorly, the prevomers rise on the anterior fifth of the premaxillary palate as a posteriorly opening U-shaped ridge, and extend backward to the junction with the vomers behind the premaxillae. There is a large, deep oval opening (prevomer foramen) in the center of the prevomers.

The vomers extend back from the prevomers and continue smoothly to the median ridge of the pterygoids, but they do not extend posteriorly beyond the last maxillary tooth. The anterior portion of the vomers is ventrally inclined but the posterior portion arches upward to the median ridge of the pterygoids. The vomers are laterally compressed, form a short vertical wall, and lie above the level of the maxillary tooth row but ventral to the respiratory passage. In lateral view, they form a narrow bridge between the premaxilla and the pterygoid. The respiratory passage is therefore not fully separated longitudinally in the snout as in *Scelidosaurus* (BMNH R1111, Owen, 1861:pl. 5, fig. 2).

The palatine forms a transverse wall between the orbital area

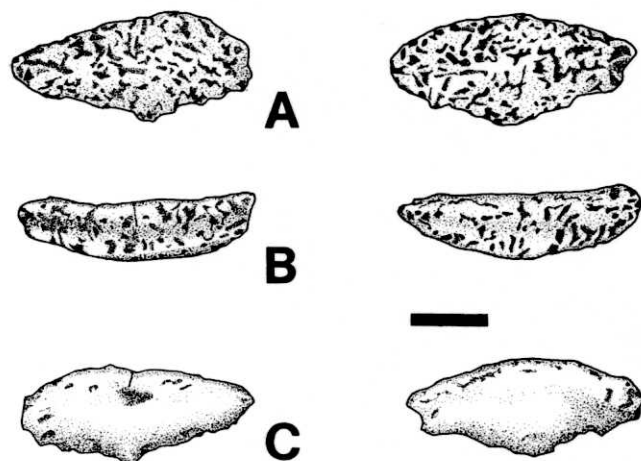
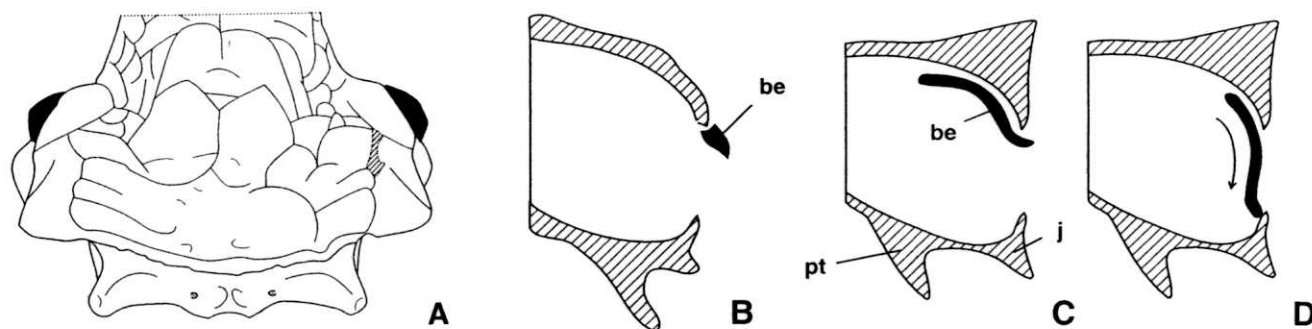


FIGURE 6. Right and left bony eyelids of *Pawpawsaurus campbelli* in external (A), dorsal (B), and internal (C) views. Scale equals 10 mm.



and the respiratory passage. It contacts the underside of the skull roof dorsally, the pterygoid ventrally, and the anterior end of the braincase dorsomedially. An anterior process contacts the jugal and maxilla laterally. A round opening pierces the palatine dorsomedially so that the orbital cavity opens into the air passage.

In nodosaurids the pterygoids are fused along the midline and generally appear as a single large oblique plate. *Pawpawsaurus* is distinguished from other nodosaurids in that the pterygoid has a well expanded anterior flange containing a ptery-

goid foramen. The mandibular process of the pterygoid projects ventrolaterally toward the adductor fossa of the lower jaw. It is concave medially forming a "spout," the apex of which is rugose marking the attachment of musculature. The ectopterygoid has an anterior edge that is vertically flattened and terminates behind the maxillary tooth row, and lacks a prominent anteriorly projecting process.

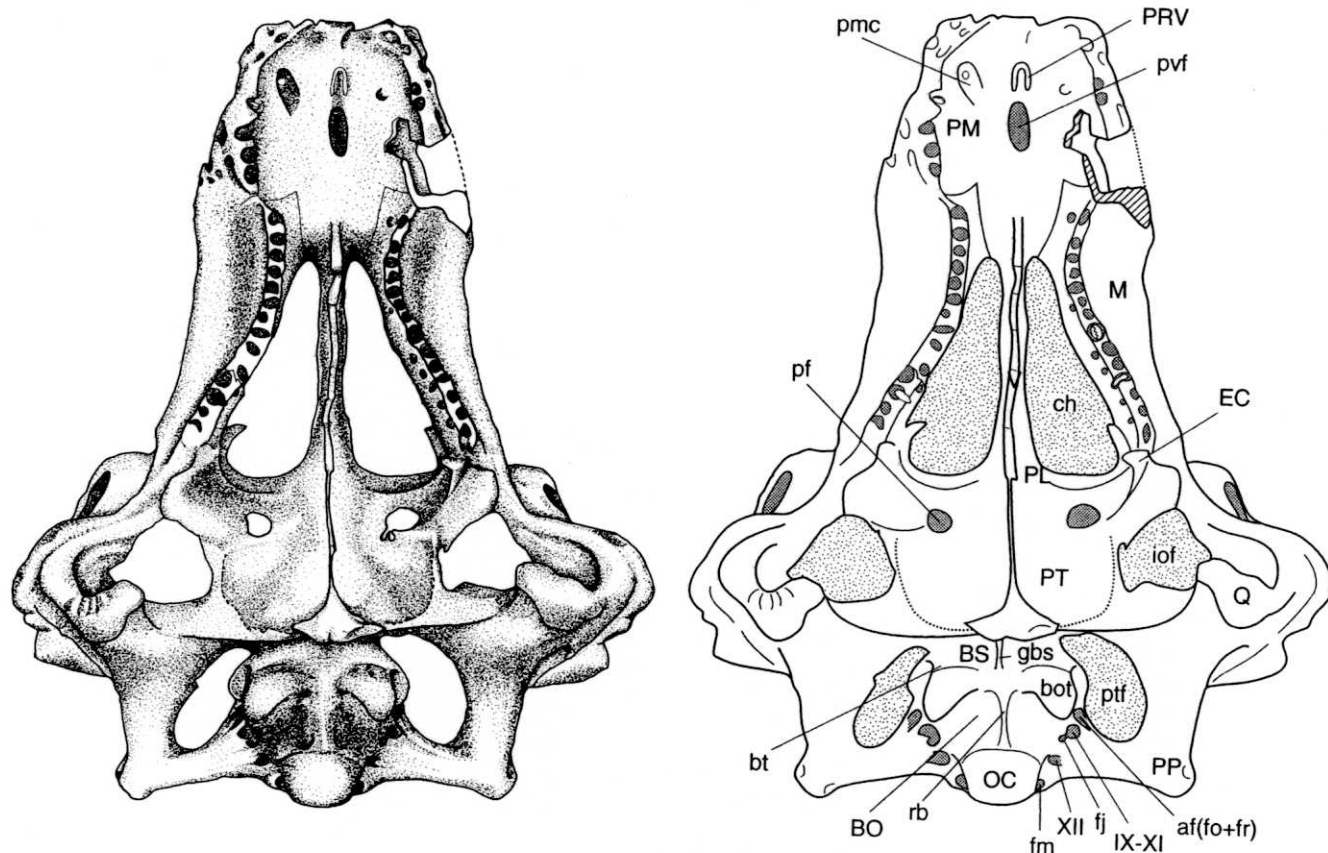


FIGURE 8. Skull of *Pawpawsaurus campbelli* (SMU 73203) in ventral view. Abbreviations as in Figures 4 and 5 plus: **af**(**fo**+**fr**), auditory foramen (fenestra ovalis+fenestra rotunda); **BO**, basioccipital; **BS**, basisphenoid; **bt**, basal tubera; **ch**, choana; **EC**, ectopterygoid; **fm**, foramen magnum; **fj**, foramen jugular for vena jugularis internus; **gbs**, groove on basisphenoid; **iof**, intraorbital fossa; **pf**, pterygoid foramen; **PL**, palatine; **pmc**, premaxillary palatal cavity; **PRV**, prevomer; **ptf**, posttemporal fenestra; **pvf**, prevomer foramen; **rb**, ridge of basioccipital; **IX–XI**, XII, cranial nerves.

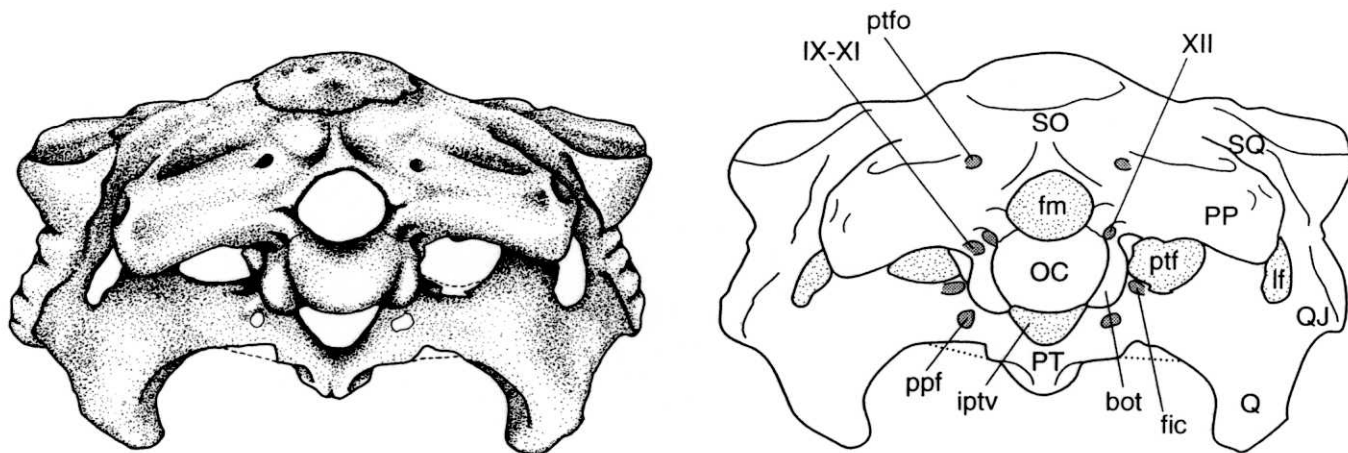


FIGURE 9. Skull of *Pawpawsaurus campbelli* (SMU 73203) in occipital view. Abbreviations as in Figures 4, 5 and 8 plus: **fic**, foramen for internal carotid; **iptv**, interpterygoid vacuity; **ppf**, postpterygoid foramen; **QJ**, quadratojugal.

triangular junction is formed. The transverse ridge forms a shallow recess on the posterolateral corner of the pterygoid. The posterior margin of the pterygoid is continuous laterally with the pterygoid ramus of the quadrate. A triangular-shaped interpterygoid vacuity is completely closed by the pterygoids and the basisphenoid. The postpterygoid foramen, lateral to the interpterygoid vacuity, pierces the posterior wall of the pterygoid ventral to the braincase.

The quadrate shaft is angled slightly anteroventrally, but almost perpendicular to the long axis of the skull. It is transversely broad with the anterior face concave and the posterior face convex. The mandibular condyle of the quadrate is massive and thicker than the quadrate shaft. The articular surface is roughly ovoid in shape and its long axis extends anteromedially and posterolaterally rather than transversely. It angles strongly ventromedially as in ankylosaurids and stegosaurids. The quadrate articulates with the pterygoid medially, forming the dorsoventrally narrow pterygoid ramus of the quadrate, and with the quadratojugal laterally. The dorsoventrally flattened dorsal ramus of the quadrate projects posterodorsally from the shaft at an angle of approximately 140°.

**Braincase.**—The occiput is low and broad (Fig. 9). The occipital surface projects strongly backward and the occipital elements are tightly fused. An inverted Y-shaped nuchal crest on the supraoccipital overhangs the dorsal lip of the foramen magnum. Its dorsal extension is delimited by the dermal plate on the upper portion of the occiput. A pair of circular depressions lateral to the sagittal ridge of the nuchal crest were probably for the cranial attachment of the rectus capitis posterior muscle. Lateral to the depression, there is a small subcircular posttemporal foramen. Distinct notches for articulation with the proatlas are present on each side of the foramen magnum. The foramen magnum is suboval in outline with a transverse diameter of 25 mm and a vertical diameter of 21 mm.

The coossified exoccipital and opisthotic form the lateral margin of the foramen magnum and extends laterally as a paroccipital process. It curves caudally and ventrally, especially at its distal tip, forming a prominent projection along the occipital margin of the skull. It is fused with the head of the quadrate ventrally and the squamosal dorsally. A suture along the contact with the basioccipital runs anteriorly from the ventrolateral margin of the foramen magnum (Fig. 10). Three foramina occur along the line of this suture and pass medially via canals into the braincase. The anterior foramen, for cranial nerves IX to XI, is just posterior to the crista tuberalis. Confluent with it

posteriorly, the jugular foramen, (which transmitted the internal jugular vein), exits the bone. Cranial nerve XII appears to exit from the posterior area of the cranium through a single large foramen, while in *Euoplocephalus* (AMNH 5337) it emerges via three foramina (Coombs, 1971). The anteroventral surface of the opisthotic is well marked by the crista prootica, which strongly projects caudolaterally. The auditory foramen is divided into the fenestra ovalis dorsally and the fenestra rotunda ventrally by a narrow crista interfenestralis.

The basioccipital forms the occipital condyle and the prominent basioccipital tubera. It articulates with exoccipitals and opisthotics dorsally and the basisphenoid anteriorly. The occipital condyle, formed exclusively by the basioccipital, is massive and circular in cross section except for a slight depression on the superior surface. It angles approximately 50° from the line of the maxillary tooth row, suggesting that in life the skull was carried at a downward angle from the neck (Coombs, 1978a).

The prootic is a crescent-shaped massive bone contacting the laterosphenoid anteriorly, the opisthotic posteriorly, and the basisphenoid ventrally. There is a prominent exit for the trigeminal nerve (V) at the anterior margin of the prootic. Anteriorly the canal for the three major branches of the trigeminal nerve (V) divides into two grooves. One of the grooves extends dorsally, and allowed for the passage of the deep ramus profundus (ophthalmicus) (V<sub>1</sub>). The ventral groove was probably for the passage of the ramus mandibularis (V<sub>3</sub>) and the ramus maxillaris (V<sub>2</sub>). In *Euoplocephalus* these nerves do not share a common canal (Coombs, 1971). The foramen for the facial nerve (VII) lies posterior to the trigeminal foramen. Two well-defined grooves extend posteriorly from the facial foramen, but do not pass over the crista prootica of the prootic. The dorsal groove shows the path of the ramus hyomandibularis and the lower accommodated the ramus palatinus of the facial nerve (VII). At the junction of the prootic with the laterosphenoid and basisphenoid, there is a large foramen which is divided into two separate openings by a narrow bony bridge. Posteriorly the foramen for the abducens nerve (VI) is situated. The foramen for the oculomotor nerve (III) is indicated anteriorly by a groove in the posterior wall of the laterosphenoid.

The laterosphenoid borders the prootic at the trigeminal foramen posteriorly and forms a narrow lateral wall of the braincase. Dorsally, it contacts the skull roof to produce a massive body. The lateral wing of the laterosphenoid is continuous ventrally with the basisphenoid. The anterior portion of the later-



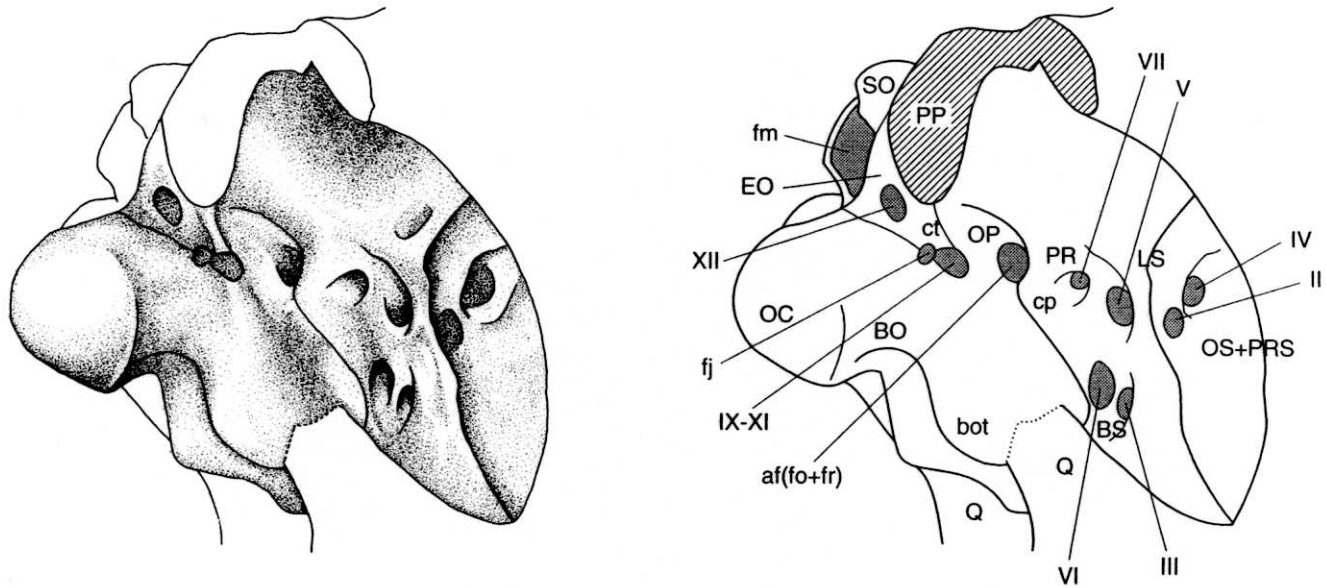


FIGURE 10. Brainscase of *Pawpawsaurus campbelli* (SMU 73203) in lateral view with foramina for cranial nerves II, III, IV, V, VI, VII, IX–XI, and XII. Abbreviations as in Figures 4, 5, 8 and 9 plus: cp, crista prootica; ct, crista tuberalis; EO, exoccipital; LS, laterosphenoid; OP, opisthotic; OS+PRS, orbito-presphenoid complex; PR, prootic.

osphenoid is folded medially to produce a prolongation of the postocular shelf.

The orbito-presphenoid complex forms the anterior limit of the ossified brainscase. It extends forward to the ossification of the anterior wall of the orbital cavity and meets the transverse wall of the palatine. An ovoid opening for the trochlear nerve (IV) pierces the orbitosphenoid dorsal to the foramen for the optic nerve (II), passing laterally and slightly anteriorly through the wall of the cranium. Dorsomedially there is a narrow canal which accommodated the olfactory nerve (I). This canal is bounded by the presphenoid, the ventral surface of the skull roof, and the palatine. Thus, the passage of the olfactory nerve from the brainscase is completely separated from the orbital cavity.

As in other thyreophoroideans the basisphenoid is much shorter in length than the basioccipital (Serenio, 1986). Anteriorly, the suture with the parasphenoid is not visible. The basipterygoid process and the pterygoid are firmly fused together. The internal carotid artery opens into the vidian canal through a foramen positioned dorsolateral to the basipterygoid process.

**Dentition**—There are four premaxillary and fourteen maxillary tooth sockets in the *Pawpawsaurus* specimen. An intervening ridge connects premaxillary and maxillary tooth rows, which is one of the unique features of nodosaurids. A round pit for the eruption of successive replacement teeth lies above the medial aspect of each alveolus as in most archosaurs. Replacement teeth do not interlock with functional teeth.

The posterior portion of the left premaxillary tooth row in the *Pawpawsaurus* skull is incomplete, but four tooth sockets are visible in the right premaxillary tooth row. Only the first premaxillary tooth is preserved in situ. Although not fully erupted, it is easily distinguished from the maxillary teeth by its small size, subconical shape, and crown flanks. The crown is slender and straight. In contrast to laterally compressed maxillary teeth, the premaxillary tooth is oriented with its greatest diameter (3.5 mm) perpendicular to the premaxillary tooth row. Whether such an extraordinary orientation is original or due to postmortem rotation cannot be determined with certainty. The labial margin exhibits two denticles, but the lingual margin has tiny round bumps instead of denticles. The anterior and poste-

rior surfaces of the crown are convex. There is no development of a cingulum at the base. In *Silvisaurus*, the premaxillary teeth curve slightly posteriorly, and four to six denticles occur on the anterior margin.

There are fourteen alveoli in each maxillary tooth row. Only one tooth is preserved in the left maxillary tooth row. It is small (6 mm in greatest diameter) and compressed labiolingually. The crown is subtriangular, but the apex and distal denticles are broken. The remaining denticles are sharply pointed, but the grooves separating them do not continue down to the cingulum. The cingulum is more expanded and undulated on the labial side, but better defined on the lingual side, which is almost straight and perpendicular to the tooth axis. Wear facets are very faint on this tooth. In other Ankylosauria, the maxillary tooth counts range between 16 and 30 (Coombs, 1978a).

NODOSAURID indet.

Fig. 11

**Referred Specimens**—SMU 73057, a right humerus, and both ilia; SMU 73494, a right scapulocoracoid; and SMU 72444 (a baby Nodosaurid; Jacobs et al., 1994).

**Horizon and Age**—All referred specimens are from the Paw Paw Formation (late Albian), Tarrant County, Texas; SMU 73057 (SMU locality 263), SMU 73494 (SMU locality 283), and SMU 72444 (SMU locality 241).

**Remarks**—Although referred specimens occur close to *Pawpawsaurus campbelli* geographically and stratigraphically, there are no common elements between them except for fragmentary skull pieces and isolated teeth. All referred specimens appear to pertain to a single taxon, but it is not possible to determine with certainty whether it is *Pawpawsaurus campbelli*. They are therefore regarded as nodosaurid indet.

USNM 337987 includes a piece of frontal, two teeth, and postcranial remains. The frontal is too fragmentary to be of taxonomic value. Isolated teeth are similar to those of the *Pawpawsaurus* skull, but they are of little taxonomic value beyond Nodosauridae (Coombs, 1990). In addition, the Smithsonian specimen is different from SMU 73494 in terms of the direction of the scapular spine. In USNM 337987, the scapular spine is



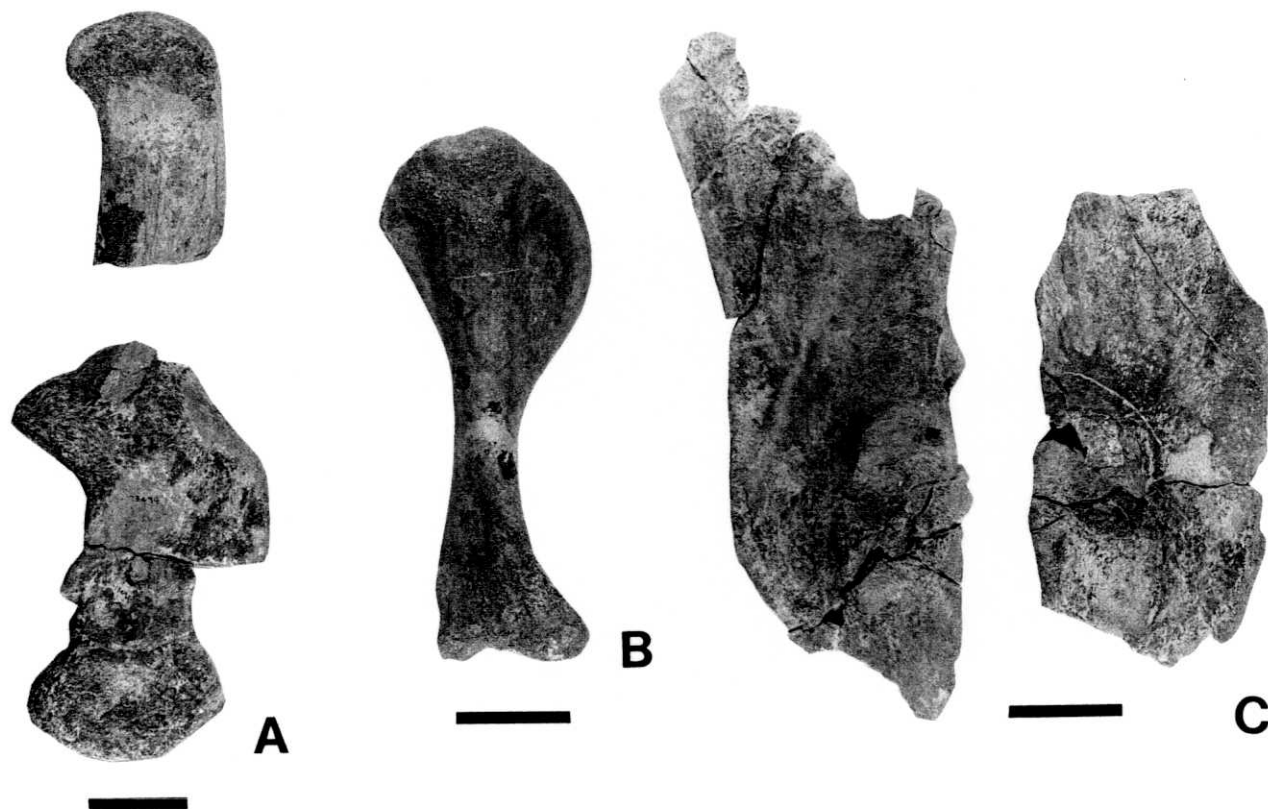


FIGURE 11. Nodosaurid indet. A right scapulocoracoid (SMU 73494) in lateral view (A); a right humerus (SMU 73057) in posterior view (B); ilia (SMU 73057) in ventral view (C). Scales equal 50 mm.

directed toward the innermost extent of the glenoid. This is regarded as an intermediate morphological character between the transverse blade-like scapular spine of primitive taxa and the displacement of the scapular spine toward the central area of the glenoid as seen in more derived taxa (Coombs, pers. comm.). In SMU 73494, however, the spine is directed posteriorly toward the upper lip of the glenoid as in *Sauropelta* and *Panoplosaurus* (ROM 1215).

**Description**—A right scapulocoracoid (SMU 73494) consists of a short, narrow, slightly curved scapula and a large coracoid. They are completely fused and massive at the glenoid. The upper lip of the glenoid opens posteriorly at approximately  $110^\circ$  to the lower lip. The scapular blade arises from the medial side of the glenoid fossa. It is thin and slightly expanded dorsally. The posterior margin of the blade is sharper than the anterior, and forms a round corner at the distal end. Only the base of the scapular spine is preserved. It projects ventrally, but not close to the upper lip of the glenoid as in *Sauropelta*. The width of the spine is constant, as far as preserved, indicating no knob-like projection as in *Sauropelta* and *Panoplosaurus*. The proximal portion of the spine is missing. The size of the prespinous fossa cannot be estimated in this specimen. Below the lower lip of the glenoid there is a deep oval depression for the coracobrachialis (Coombs, 1978b). It is bounded medially by a ridge that extends from the glenoid, but is somewhat open laterally. The coracoid foramen is large and oval in shape. Medially, a broad, shallow subcoracoid fossa is situated on the anteroventral surface of the coracoid.

A right humerus (SMU 73057) is rather elongate with a subspherical head projecting posteriorly well behind the shaft and wrapping around onto the medial process. The proximal portion is greatly expanded by a strong deltopectoral crest laterally and

by a medial process, producing a shallow concave anterior surface. The deltopectoral crest begins at the humeral head and extends down the shaft to a point just proximal to the mid-length. It projects anterolaterally at approximately  $70^\circ$  with respect to the distal end. The moderately expanded medial process is aligned in the same plane as the distal end. The shaft is straight and strongly convex posteriorly, forming a triangular cross section. The distal end is rotated with respect to the proximal end at an angle of approximately  $45^\circ$ . Both distal condyles are developed; the ectepicondyle being the larger of the two. The prominent spherical capitulum lies adjacent to the ectepicondyle, and together they form a broad ectepicondylar fossa on the anterior surface of the humerus. The medial portion of the entepicondyle is not preserved so the trochlea and entepicondylar fossa are poorly defined in this specimen.

The ilium (SMU 73494) is greatly expanded laterally by enlarged preacetabular and short postacetabular processes. The long, narrow, and thin preacetabulum diverges laterally from the midline, and tapers anteriorly. It is gently convex dorsally. Toward the anterior extremity, it curves to face ventromedially, in an inclined plane  $40^\circ$  from the horizontal. The horizontal postacetabulum is short and smoothly confluent with the ventral surface of the acetabulum. The acetabulum is a closed shallow oblong socket situated on the ventral surface of the ilium. It is bounded anteriorly by a massive, ventrally projecting process. The articulation facets for the sacral vertebrae are not preserved in this specimen.

## DISCUSSION

The discovery of a nearly complete skull of *Pawpawsaurus campbelli* in the Paw Paw Formation, Texas, permits a revised

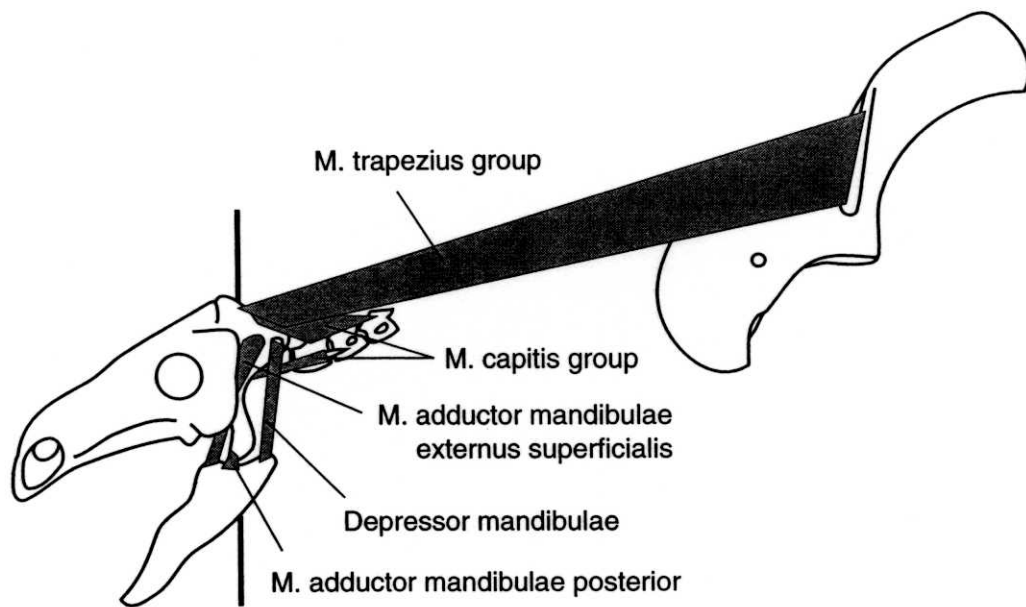


FIGURE 12. The reconstruction of muscles related to the skull orientation of the Nodosauridae based on *Pawpawsaurus* (skull and scapulocoracoid) and *Sauropelta* (mandible).

diagnosis to be made for the Nodosauridae. Nodosaurids are unambiguously united by six cranial synapomorphies including three new characters (see characters 8–13 in Appendix), which are closely related to the downward orientation of the nodosaurid head in life. Three cranial characters previously proposed as nodosaurid synapomorphies (Sereno, 1986; Coombs and Maryanska, 1990) are rejected here. These are (1) dorsoventrally low skull, (2) basiptyergoid processes consisting of a pair of rounded, rugose stubs, and (3) dermal plate pattern on the skull roof.

The low skull configuration is also present in ankylosaurids. It duplicates a synapomorphy of Ankylosauria, “rectangular skull in occipital view; long axis horizontal” (Sereno, 1986:

241) and “cranium low and flat, rear of skull wider than high” (Coombs and Maryanska, 1990:456). As for the second character, basiptyergoid processes of Ankylosauria are relatively short and blunt compared to other ornithischians except for a single polacanthid skull (CEU 184v.237, sensu Kirkland, 1993, pers. comm.), which has very long basiptyergoid processes. The basiptyergoid processes generally project more ventrolaterally in Nodosauridae (SMU 72444, YPM 5529) than Ankylosauridae. Although a broken base of a basiptyergoid process is preserved in an isolated basicranium of *Sauropelta* (YPM 5529), it is highly distorted. The intact basiptyergoid processes are visible in a baby specimen (SMU 72444). They consist of a pair of short, blunt bones, projecting ventrolaterally (Jacobs et al., 1994:fig. 22.3A). In most adult nodosaurids, however, they are completely fused with the pterygoids so it is not possible to trace the contact. Thus, the anterior portion of the pterygoid process is concealed from view, leaving a flat posterior surface. In most Ankylosauridae, pterygoid processes are short, and blunt as in the Nodosauridae. Therefore, this character should be reevaluated in Ankylosauria with respect to the polacanthid skull CEU 184v.237. Adult skulls of Ankylosauria are heavily armored with dermal plates. However, there is no universally consistent dermal pattern present in all nodosaurid skulls (see characters 20–22 in Appendix). The pattern may be depend on ontogeny (Coombs and Maryanska, 1990) or on individual variation (cf. NMC 2759 and ROM 1215), or both. Dermal plates may be a secondary accretion deposited directly from overlying keratin scutes (Coombs, 1971). The detailed pattern of dermal plates cannot be shown to be diagnostic of the Nodosauridae.

Although detailed discussion of the phylogeny of the Ankylosauria is beyond the scope of this study, some supposed cranial synapomorphies of the Ankylosauria ought to be reexamined. These are 1, a bony median septum extending from the ventral surface of the skull roof onto the palate; 2, pterygoid closing the space between the palate and the braincase, and 3, quadrate slants rostroventrally from the underside of the squamosal (Coombs and Maryanska, 1990). The first two characters are not supported by *Pawpawsaurus*, and the third appears to be a synapomorphy of the Nodosauridae (for details, see char-

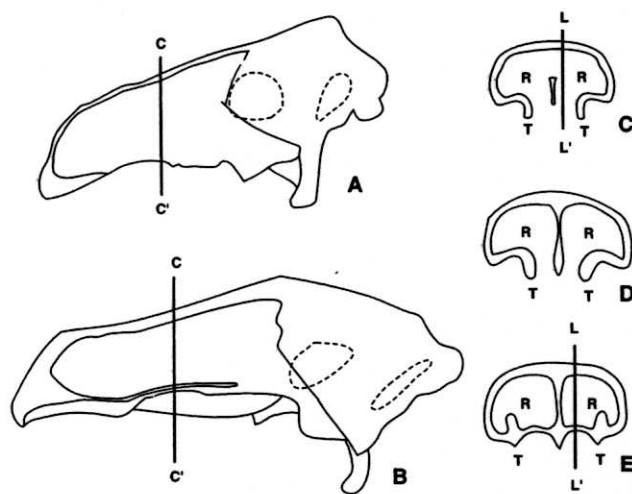


FIGURE 13. Diagrammatic parasagittal sections through the skull of *Pawpawsaurus* (A) and *Edmontonia* (AMNH 3076, from Coombs, 1978a) (B). Cross sections through the snout of *Pawpawsaurus* (C), *Sauropelta* (AMNH 3035) (D), and *Edmontonia* (E) (from Coombs, 1978a). Abbreviations: C-C', level of cross section shown in C, D, and E; L-L', level of parasagittal section shown in A and B; R, respiratory tract; T, tooth row.

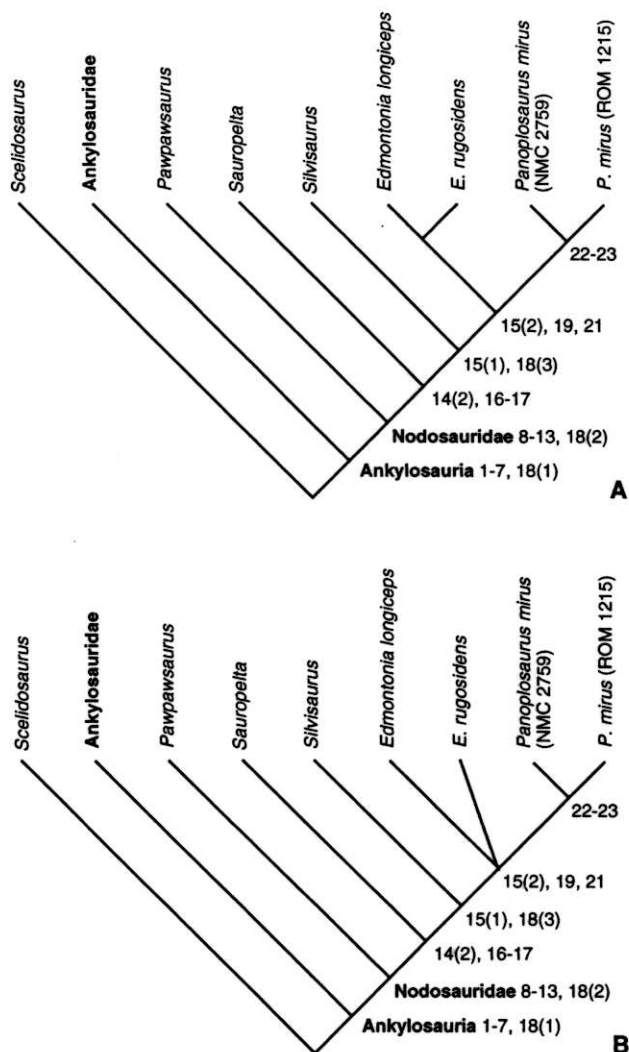


FIGURE 14. Two equally parsimonious trees from an exhaustive search of PAUP 3.1.1 on the matrix in the appendix, showing relationships of the Nodosauridae, based on analysis of 25 cranial characters. These trees have a length of 34 steps and a consistency index of 0.882. Character numbers show position of apomorphic states on the parsimonious trees. See the appendix for details regarding the character distribution.

acters 14, 17, and 10 in Appendix). Therefore, they are not accepted as synapomorphies of Ankylosauria in this paper.

The cladogram for phylogenetic relationships of the Nodosauridae (Fig. 14) shows that *Pawpawsaurus* has the most primitive nodosaurid skull with an incomplete septum and no secondary palate. The derived nodosaurid respiratory structure was achieved through the progressive development of the sagittal septum and the secondary palate. In nodosaurids, the postorbital dermal plates appear to be a plesiomorphic condition and absent in derived forms. In contrast, ankylosaurids developed various prominent postorbital "horns."

This study indicates that *Pawpawsaurus*, while geologically younger, is more primitive than *Sauropelta* from the Cloverly Formation, Montana and Wyoming (late Aptian to Albian, Jacobs et al., 1991). Faunal differences are known between the Trinity Group of Texas and the Cloverly (Kirkland, 1987; Winkler et al., 1990). During the late Albian, there was a progressive incursion of the northern and southern arms of the Western Interior Seaway (Kauffman, 1984). Later, this seaway estab-

lished a biogeographic barrier (Winkler et al., 1989) during the deposition of the Washita Group. Therefore, *Pawpawsaurus* appears to be part of an endemic fauna isolated from the Rocky Mountains by the Western Interior Seaway during the Albian.

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# APPENDIX

This cladistic analysis is based only on cranial features of *Panoplosaurus mirus* (NMC 2759, Lambe, 1919; ROM 1215, Russell, 1940), *Edmontonia longiceps* (NMC 8531, Sternberg, 1928), *Edmontonia rugosidens* (USNM 11868, Gilmore, 1930; AMNH 5665, Carpenter, 1990; fig. 21.5), *Silvisaurus condrayi* (KU 10296, Eaton, 1960), *Sauropelta edwardsi* (YPM 5499, 5529, Ostrom, 1970), and *Pawpawsaurus campbelli* (SMU 73203). *Nodosaurus textilis* (Marsh, 1889) and *Hoplitosaurus marshi* (Lucas, 1902; Gilmore, 1914) were excluded from this analysis because they comprise fragmentary postcranial remains without the cranium. Character polarity was established using the Ankylosauridae and *Scelidosaurus harrisonii* (BMNH R1111, Owen, 1861) as successive outgroups (Sereno, 1992). Character states for 25 cranial characters are discussed below, including diagnostic characters of the Ankylosauria and the Nodosauridae proposed by Coombs and Maryanska (1990). The synapomorphies of the Ankylosauridae were not considered. Characters were given equal weight and treated as unordered. Character state distributions are shown in a taxon/character matrix, with lack of preservation scored as ?. The resulting matrix was analyzed using the exhaustive search algorithm in PAUP version 3.1.1 (Swofford, 1993). Two equally parsimonious trees were found, each with a tree-length of 34 steps, a consistency index (C.I.) of 0.882, a homoplasy index (H.I.) of 0.118, and a retention index (R.I.) of 0.907. The two trees (Fig. 14) produced consistent results for pre-Campanian nodosaurid taxa. Lack of resolution is mainly restricted to the interrelationships of *Edmontonia* and *Panoplosaurus*. Their relationships may be better resolved by using postcranial characters (Carpenter, 1990).

TABLE

Taxa	Characters				
	1	11	21		
<i>Scelidosaurus</i>	00000	00000	00000	??000	00000
Ankylosauridae	11111	11000	00013	00110	00000
<i>Pawpawsaurus</i>	11111	11111	11100	00201	00010
<i>Sauropelta</i>	11111	11111	11120	?1200	00000
<i>Silvisaurus</i>	11111	11111	11121	11300	0?000
<i>Edmontonia longiceps</i>	11111	11111	11122	11310	10001
<i>E. rugosidens</i>	11111	11111	11122	11310	10001
<i>Panoplosaurus mirus</i> (NMC 2759)	11111	11111	11122	11311	11?01
<i>P. mirus</i> (ROM 1215)	11111	11111	11122	11311	11110

1. "Cranium low and flat, rear of skull wider than high" (Coombs and Maryanska, 1990:456): absent (0), present (1).
2. "Antorbital and supratemporal fenestrae" (Coombs and Maryanska, 1990:456): open (0), closed (1).
3. "Sutures between cranial bones of the skull roof obliterated in adults" (Coombs and Maryanska, 1990:456): absent (0), present (1).
4. "Maxilla with deep, dorsally arched cheek emargination" (Coombs and Maryanska, 1990:456): absent (0), present (1).
5. "Accessory antorbital ossification(s) and postocular shelf partially or completely enclose orbital cavity" (Coombs and Maryanska, 1990:456): absent (0), present (1). In *Pawpawsaurus*, a round open-

- ing pierces the palatine dorsomedially so the orbital cavity opens into the air passage (Fig. 13A). In other nodosaurids, in contrast, the transverse wall of the palatine completely separates the orbital area from the respiratory passage (Coombs, 1971; Fig. 13B).
6. "Quadratojugal contacts postorbital" (Coombs and Maryanska, 1990:456): absent (0), present (1).
  7. "Dorsoventrally narrow pterygoid process of the quadrate" (Coombs and Maryanska, 1990:456): absent (0), present (1).
  8. "Hour-glass shaped palate" (Coombs and Maryanska, 1990:473): absent (0), present (1).
  9. "Hemispherical occipital condyle composed of basioccipital only, set off from braincase on a short neck and angled about 50° downward from line of maxillary tooth row" (Coombs and Maryanska, 1990:477): absent (0), present (1). One of the extraordinary features distinguishing the Nodosauridae from other groups is that nodosaurid heads were carried at a downward angle of approximately 50° to the neck, supported by a downwardly angled occipital condyle. This posture facilitated cropping low vegetation but required strong muscles to sustain the head posture (Fig. 12). This habit of nodosaurids is correlated with other skull modifications (see characters 10–13). The insertion of the trapezius muscle group from the posteriorly displaced occiput region was supported by the unique scapular spine. The neck was covered with prominent cervical spines in *Sauropelta* (Carpenter, 1984) or heavy ossicles (*Edmontonia*, AMNH 5665).
  10. "Quadrate angled rostroventrally" (Coombs and Maryanska, 1990:477): absent (0), present (1). The rostral inclination of the quadrate in the Nodosauridae is a modification that keeps the quadrate parallel to the vertical axis of the skull (Fig. 12). The dorsal end of the quadrate expands posterodorsally to contacts with the squamosal and the paroccipital process as in most ornithischians. The angle of the quadrate shaft in *Edmontonia rugosidens* (USNM 11868) is exaggerated due to dorsoventral postdepositional compression. In ankylosaurids, it ranges between almost vertical and a moderate inclination, but not as strong as those of nodosaurids (Coombs and Maryanska, 1990).
  11. Prominent W-shaped basioccipital tubera: absent (0), present (1). The short basisphenoid relative to the basioccipital is a feature of thyreophoroideans, which include *Scelidosaurus*, stegosaurs, and ankylosaurs (Sereno, 1986). Strong basioccipital tubera are clearly present in nodosaurids and stegosaurids, which were probably correlated with downwardly directed and long skulls, respectively. They are much larger than the basal tubera of the basisphenoid and extend slightly below the level of the occipital condyle. In nodosaurids, basioccipital tubera meet each other at the border with the basisphenoid, forming a W-shaped pair of tubercles whose apices point posteriorly. Their surfaces are smooth to very rugose. In the Stegosauria, they are separated by a median notch.
  12. Anteriorly concave and anteroposteriorly flattened quadrate: absent (0), present (1). To adduct the lower jaw, the nodosaurid adductor muscles were relatively strong. The occipital region is displaced posteriorly so that the line of action of the adduction is not perpendicular to the tooth row as in other ornithischians. The enlarged lateral temporal fenestra produced a larger attachment surface for the development of the adductor mandibulae externus superficialis muscle. The anteriorly concave quadrate surface provided increased space for the muscle contraction. In ankylosaurids, the quadrate is compressed anteroposteriorly as in nodosaurids, but not folded anteriorly.
  13. Transversely continuous and straight posterior margin of the pterygoid aligned with the quadrate shaft: absent (0), present (1). The posterior margin of the pterygoid ramus is in line with the ramus of the quadrate, producing a transversely straight palatal margin. Anteriorly, it meets a longitudinal ridge in the midline where a thick triangular junction is formed. Along with prominent basioccipital tubera, this distinct transverse ridge probably served as an origin for the strong neck muscles. In most ankylosaurids, the pterygoid does not meet its counterpart completely, leaving an anteriorly directed deep V-shaped fissure instead of a fused blunt junction. In other ornithischians, the pterygoid junction is positioned farther forward than the line of the mandibular condyle of the quadrate.
  14. Extension of the vomer septum: incomplete (0), to palatal shelves (1), or to skull (2). *Pawpawsaurus* lacks the bony sagittal septum, which has been regarded as a derived character in Ankylosauria (Sereno, 1986; Coombs and Maryanska, 1990), possibly related to the depressed shape of the skull. The vomer septum in *Pawpawsaurus*, as in *Scelidosaurus*, does not extend to the underside of the skull roof but lies above the level of the maxillary tooth row (Fig. 13C). In other nodosaurids (Fig. 13D, E), in contrast, a long bony sagittal septum extends from the skull roof to the level of the maxillary crowns dividing the respiratory passage into two separate canals in the snout. In ankylosaurids, the sagittal septum contacts the skull roof through palatal shelves (Coombs, 1978:fig. 5).
  15. Secondary palate: absent (0), incomplete (1), complete (2), or complex (3). As in *Scelidosaurus*, *Pawpawsaurus* and *Sauropelta* lack a secondary palate. The secondary palate is formed laterally by the maxillary shelf and medially by the shelf from the vomer. In *Silvisaurus*, it is incomplete and open in an elongate cleft because of the lack of a lingual shelf of the maxilla (Eaton, 1960:fig. 3). The pterygoid bone of these primitive taxa extends well anterior to the maxillary tooth row. More derived nodosaurids, such as *Edmontonia* and *Panoplosaurus*, have a complete secondary palate forming a long air passage. Thus the pterygoid bone is positioned behind the internal nares, not reaching the maxillary tooth row anteriorly. In ankylosaurids, the secondary palate is complex and associated with two shelves for the respiratory passage and cranial sinuses (Coombs and Maryanska, 1990).
  16. Prevomer foramen: present (0), absent (1). *Pawpawsaurus* has a unique prevomer foramen which is not known in other nodosaurids. It is probably related to a similar, but more anteriorly placed foramen in *Ankylosaurus magniventris* (AMNH 5214). The function of these foramina is not known.
  17. Pterygoid and postpterygoid foramina: present (0), absent (1). In Ankylosauria the passage between the space above the palate and that below the braincase was closed by vertically oriented pterygoids (Sereno, 1986:241; Coombs and Maryanska, 1990:456). In *Pawpawsaurus*, however, a large pterygoid foramen opens at the middle of the bone into the space ventral to the braincase. This foramen is probably related to a similar, but smaller foramen at the base of the ectopterygoid in the ankylosaurids, *Pinacosaurus* (ZPAL MgD-II, Maryanska, 1977:fig. 2A2), *Saichania* (GI SPS 100/151, Maryanska, 1977:fig. 5A1), *Ankylosaurus* (AMNH 5214, Coombs, 1971:fig. 2), and a polacanthid skull (CEU 184v.237, *sensu* Kirkland, pers. comm.). The postpterygoid foramen of *Pawpawsaurus* is similar to that of the ankylosaurid, *Saichania* (GI SPS 100/151, Maryanska, 1977:fig. 4A2), but the functional significance of these foramina is unknown.
  18. Postorbital dermal plate: absent (0), strong (1), moderate (2), or weak (3). A pyramid-shaped dermal plate is developed behind the orbit in *Pawpawsaurus* and *Sauropelta* (YPM 5549), but not strong as in ankylosaurids. In ankylosaurids, postorbital dermal plates protrude much more, forming horn-like projections. In most derived nodosaurids, the caudolateral corners are smoothly rounded without distinct expansions.
  19. Premaxillary teeth: present (0), absent (1). Premaxillary teeth are absent in the derived nodosaurids, *Edmontonia*, *Panoplosaurus*, and ankylosaurids. Their presence appears to be a plesiomorphic condition within nodosaurids. *Pawpawsaurus* has two fewer premaxillary teeth than *Silvisaurus*, which is the only ankylosaurian taxon in which complete premaxillary teeth (6 in situ) are preserved. On the basis of a crushed skull (AMNH 3035) premaxillary teeth are known for *Sauropelta*, but the exact tooth count is uncertain.
  20. Posteriormost dermal plate: absent (0), present (1). The anteroposteriorly narrow posterior dermal plate along the posterior margin of the skull roof is distinct only in *Pawpawsaurus* and *Panoplosaurus*.
  21. A large subcircular dermal plate between the orbits: absent (0), present (1). Although a large subcircular scute between the orbits appears in *Panoplosaurus* and *Edmontonia*, it is not apparent in other nodosaurids and ankylosaurids. In *Pawpawsaurus*, the area of the posterior dermal plate consists of eight variously shaped small elements.
  22. Scutes on orbital roof: less than three (0), three (1). One scute is incorporated into the orbital roof between the prefrontal and post-orbital in *Scelidosaurus*, *Pawpawsaurus*, and possibly *Edmontonia*. In the middle portion of the dorsal orbital roof in *Pawpawsaurus*, one rhombic-shaped orbital dermal plate overlaps the anterior aspect of the postorbital dermal plate posteriorly. Thus, the orbital roof of *Pawpawsaurus* is covered with an orbital dermal plate and a part of the postorbital dermal plate, not with a series of three scutes. Three scutes on the orbital roof are found only in *Panoplosaurus* (NMC 2759, ROM 1215). In other nodosaurids, the presence of these dermal plates cannot be determined with certainty.
  23. Vomer shape: keeled (0), swollen (1). *Panoplosaurus* (ROM 1215) has distinct vomers with a depressed cylindrical form. The swollen ventral margin is divided by a canal-like longitudinal groove. This condition is distinguished from a sharp median ridge in other nodosaurids (Carpenter, 1990).
  24. Doming of the skull roof: absent (0), present (1). A pronounced dome-like swelling is developed dorsomedially on the skull of *Pan-*

*oplosaurus* (ROM 1215) and *Pawpawsaurus*. In *Pawpawsaurus*, it occurs more posteriorly than in ROM 1215. Noticeable doming on the skull roof is not found in other nodosaurids.

25. Beak shape: rounded (0), square (1). Most derived nodosaurids having no premaxillary teeth have rugose, pitted anterior corners ex-

ternal to the spoon-shaped premaxillary rim forming a square beak tip. *Panoplosaurus* (ROM 1215), in contrast, has a rounded beak as in primitive nodosaurids, *Pawpawsaurus*, *Sauropelta*, and *Silvisaurus*. Their premaxillae are smoothly rounded along the premaxillary tooth ridge.