

ON THE CRANIAL ANATOMY OF THE POLYCOTYLID PLESIOSAURS, INCLUDING NEW MATERIAL OF *POLYCOTYLUS LATIPINNIS*, COPE, FROM ALABAMA

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ABSTRACT—The cranial anatomy of plesiosaurs in the family Polycotylidae (Reptilia: Sauropterygia) has received renewed attention recently because various skull characters are thought to indicate plesiosauroid, rather than pliosauroid, affinities for this family. New data on the cranial anatomy of polycotylid plesiosaurs is presented, and is shown to compare closely to the structure of cryptocleidoid plesiosaurs. The morphology of known polycotylid taxa is reported and discussed, and a preliminary phylogenetic analysis is used to establish ingroup relationships of the Cryptocleidoidea. This study also presents new material referable to *Polycotylus latipinnis* from the Mooreville Chalk Formation of Alabama. This skeleton is largely complete, and although the skull is fragmentary it does preserve several regions not previously represented. The preserved portions demonstrate that the palate of *Polycotylus* is similar to that of *Trinacromerum* in the possession of robust epipterygoids, and similar to that of all other polycotylids in the possession of a large anterior interpterygoid vacuity. *Polycotylus* therefore displays the derived palate morphology common to all polycotylids, but also displays some plesiomorphic features. This impression is confirmed by the results of the cladistic analysis.

INTRODUCTION

The Polycotylidae (Reptilia, Sauropterygia) are an important family of short-necked plesiosaurs common in the Cretaceous epicontinental seaway of North America (Carpenter, 1996), and also occurring in other areas of the world (e.g., Japan: Sato and Storrs, 2000; Russia: Storrs et al., 2000; Australia: Persson, 1963; Long, 1998). For most of the twentieth century the polycotylids were classified as true pliosaurs, because they possessed short necks, large heads, and other proportional differences in common with Jurassic pliosauroids such as *Peloneustes* and *Liopleurodon* (O'Keefe, 2002; see O'Keefe, 2001 for taxonomic review). In 1997, however, Carpenter questioned the monophyly of the Pliosauroida as traditionally defined and instead posited a sister-group relationship between the Polycotylidae and the Elasmosauridae, a view also championed by Bakker (1993). O'Keefe (2001) performed a cladistic analysis of the clade Plesiosauria, and found that the traditionally-defined Pliosauroida were indeed polyphyletic, although a sister-group relationship with the Elasmosauridae was not supported. Instead, O'Keefe found that the Polycotylidae were a derived group of cryptocleidoid plesiosauroids, most closely related to Jurassic taxa such as *Tricleidus* and *Cryptoclidus*. O'Keefe marshaled both cranial and post-cranial evidence in support of this hypothesis.

The novel phylogenetic position of the Polycotylidae found by O'Keefe (2001) renders the Pliosauroida polyphyletic as traditionally defined. Therefore, the character evidence underlying this hypothesis is important and must be examined. Morphological data on the crania of three polycotylid taxa are therefore presented here, and interpreted in relation to the cryptocleidoid *Tricleidus*. *Tricleidus* is a generalized cryptocleidoid known from one essentially complete skeleton from the Oxford Clay of Peterborough, England (Late Jurassic; Callovian; Andrews, 1910). *Tricleidus* was found by O'Keefe (2001) to reside in a polychotomy with the cryptocleidoid families Cimoliasauridae and Polycotylidae, and is not specialized in characters such as neck length (O'Keefe, 2002). *Tricleidus* is therefore a sensible source for comparison with the more derived cryptocleidoids, including the Polycotylidae. The three polycotylid

genera discussed in this paper (*Dolichorhynchops*, *Trinacromerum*, *Polycotylus*) were reviewed extensively by Carpenter (1996); synonymies and comprehensive lists of referred material can be found in that publication. Storrs (1999) also discusses historical holotypes and taxonomic issues relating to the Niobrara taxa *Dolichorhynchops* and *Polycotylus*, and presents revised diagnoses.

The genus and species *Polycotylus latipinnis* was first erected by Cope (1869) in his description of fragmentary material from the Cretaceous Niobrara Formation of Kansas. *Polycotylus* is large for a polycotylid, and possesses a high count of cervical vertebrae (26) compared to other polycotylids. This character plus several primitive features of the humerus led to O'Keefe's (2001) finding that *Polycotylus* was the sister group of another primitive polycotylid, *Edgarosaurus* (Druckenmiller, 2002), and that this clade was the sister group of the more derived polycotylids *Trinacromerum* and *Dolichorhynchops*. Given the importance of *Polycotylus*, the state of the fragmentary type material is unfortunate; however, Williston (1906) referred another specimen to *Polycotylus latipinnis* (taxonomy reviewed in Carpenter, 1996) and this skeleton is an essentially complete post-cranium. The known cranial material of *Polycotylus* comprises only a few teeth and the posterior portions of two mandibles. New cranial material of *Polycotylus* from Alabama is described below.

MATERIAL AND DESCRIPTION

Dolichorhynchops orborni

Dolichorhynchops orborni is the best known of all polycotylids, and will be described and reconstructed first so that taxa known from poorer material may be compared to it. Three well-preserved skulls were examined in the course of this study: FHSM VP404, comprised of a complete skeleton with a well-preserved skull and lower jaw; the holotype, KUVVP 1300, another complete skeleton, the skull of which is crushed laterally (figured in Storrs, 1999); and MCZ 1064, the skull of a juvenile specimen which preserves the skull roof well (Fig. 3; for repository information see Table 1). FHSM VP404 and KUVVP 1300 were collected from the *Hesperornis* zone of the Smoky

TABLE 1. Repositories and abbreviations for material discussed in this study.

Institution	Abbreviation	Material
Sternberg Museum of Natural History, Fort Hays, Kansas	FHSM	FHSM VP 404
Kansas Museum of Natural History, Lawrence, Kansas	KUVP	KUVP 1300, KUVP 5070
Museum of Comparative Zoology, Harvard, Massachusetts	MCZ	MCZ 1064
Field Museum of Natural History, Chicago, Illinois	FMNH, PR	PR 187, PR 1629
Smithsonian Institution, Washington, D.C.	USNM	USNM 27678, USNM 10945, USNM 10946
Yale Peabody Museum, New Haven, Connecticut	YPM	YPM 1125
The Natural History Museum, London, England	BMNH	BMNH R.3539
American Museum of Natural History, New York	AMNH	AMNH 2321

Hill Chalk Member, Niobrara Formation (early Campanian), Logan County, Kansas by C. Sternberg (Carpenter, 1996). MCZ 1064 is also a Sternberg specimen, and probably also comes from the Logan County Niobrara; however, a search of Sternberg's documentation by M. Everhart at the Smithsonian was unable to establish an exact locality for this specimen. The style of preservation of this skull is identical to other Niobrara fossils.

Palate—The palate of *Dolichorhynchops* is illustrated here by FHSM VP404 (Fig. 1, reconstructed in Fig. 2; also illustrated by O'Keefe, 2001:fig. 17, and Carpenter, 1996). The palate lacks pterygoid flanges or other processes that would break the ventral plane of the palate. The palate surface is highly fenestrate, possessing large sub-orbital and sub-temporal fenestrae, prominent anterior and posterior interpterygoid vacuities, and the choanae. The long, narrow snout of this taxon is composed primarily of premaxilla and maxilla; the premaxilla forms the snout tip and usually contains five finely striated teeth (tooth count contra Williston, 1903; see Carpenter, 1996). The suture between premaxilla and maxilla crosses the tooth row obliquely toward the midline, and disappears beneath the vomer antero-medially. The alveolar row of premaxilla and maxilla is carried on a raised ridge, giving the snout an inverted U-shape in transverse section. The vomer extends almost to the tip of the snout, is fused at the midline anteriorly and paired posteriorly. The

maxilla is large and carries most of the tooth row. The exact number of maxillary teeth varies ontogenetically and among specimens; twenty-one teeth is a typical number (FHSM VP404 has 25, KUVP 1300 has approx. 20), although the juvenile skull MCZ 1064 possesses only 13 or 14 maxillary teeth. The maxilla extends along the edge of the skull beneath the orbit as a broad boss, and sutures posteriorly with the squamosal.

On the midline, the vomers are divided posteriorly by an anterior extension of the pterygoids. The vomers continue posteriorly to the internal nares, and the vomer forms the anterior half of the medial margin of this structure, while the posterior half is formed by the pterygoid. The lateral, anterior, and posterior margins of the internal naris are formed by the palatine. The palatine is a very thin bone, contacting the pterygoid and vomer medially and the maxilla laterally. The posterior extent of the palatine is broken in FHSM VP404 and the exact nature of its relationships to the ectopterygoid and sub-orbital fenestra are impossible to determine; the finished bone on the medial aspect of the maxilla in this region does seem to indicate that a narrow sub-orbital fenestra was present. This region is reconstructed in Figure 2 as similar to the condition of *Trinacromerum* (see below).

The pterygoid in *Dolichorhynchops* is a large and complex bone comprising most of the posterior palate surface. The pterygoid consists of a kidney-shaped central plate of bone lying

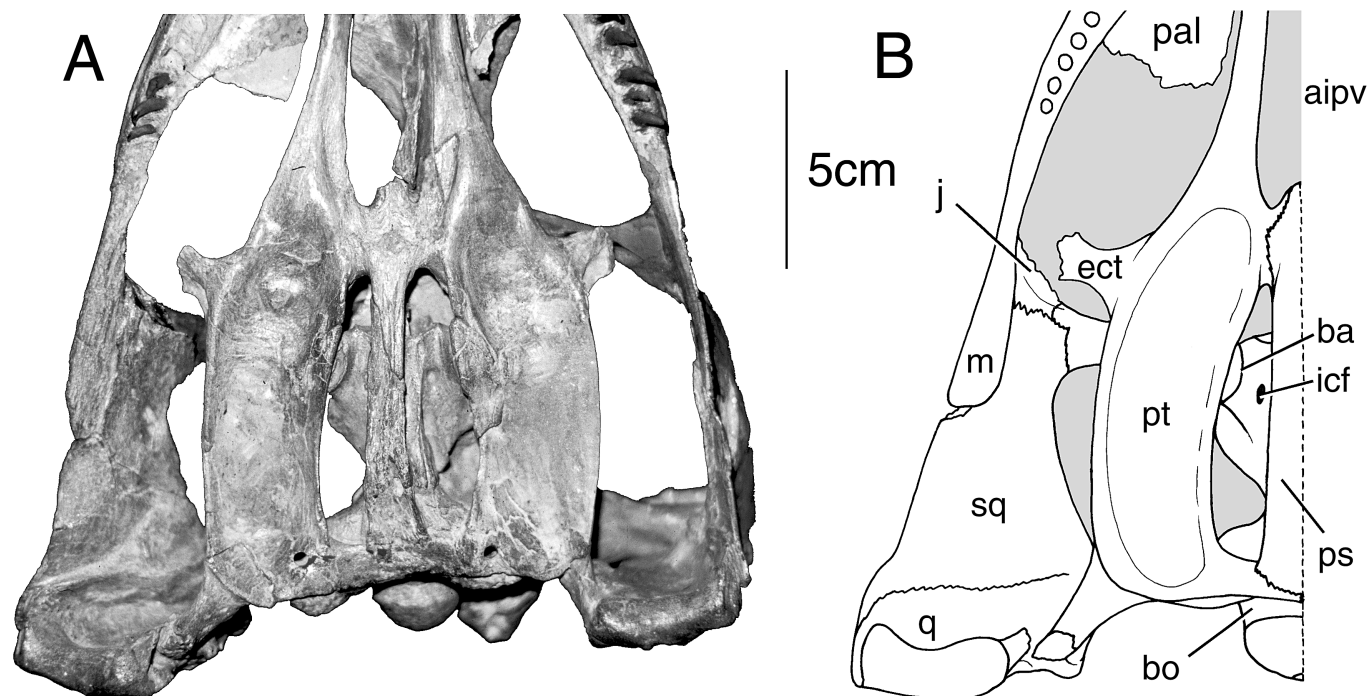


FIGURE 1. Palate of *Dolichorhynchops osborni*, FHSM VP404; photograph (A) with interpretive drawing (B). For anatomical abbreviations see Appendix 1.

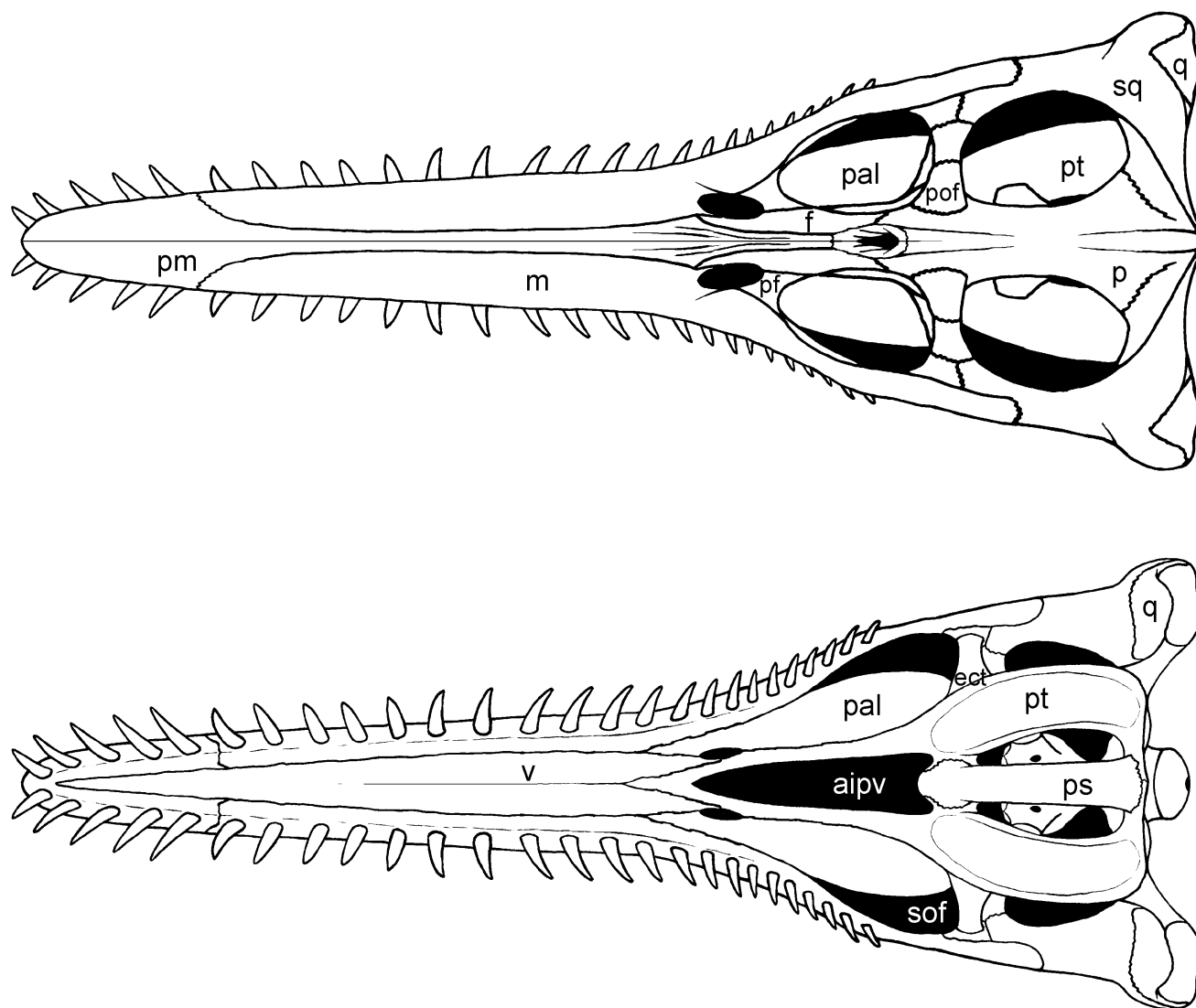


FIGURE 2. Dorsal and ventral reconstructions of the skull of *Dolichorhynchops osborni*, based primarily on FHSM VP 404, with additional information from KUVF 1300 and MCZ 1064.

laterally to the posterior interpterygoid vacuity; from this plate, four processes (two anterior, two posterior) radiate across the palate surface. The central plate is dish-shaped, bearing a broad, shallow fossa circled by a raised rim. Anteriorly, the central plate of the pterygoid narrows into a long, narrow process that trends anteriorly, forming the lateral margin of the large anterior interpterygoid vacuity, then participating in the medial margin of the internal naris, before joining the anterior process of the other pterygoid to form a triangular process dividing the vomers on the midline. The anterior medial process of the pterygoid is a short boss contacting the antero-lateral aspect of the parasphenoid in an interdigitating suture; this union divides the anterior and posterior interpterygoid vacuities. The posterior lateral process of the pterygoid is the quadrate flange. This gracile, cylindrical process trends from the postero-lateral corner of the central plate and contacts the quadrate near the jaw articulation. Unlike *Trinacromerum*, there is no flange of the central plate underlying the quadrate flange. The posterior medial process of the pterygoid arises from the postero-medial corner of the central plate and projects to the midline, where it sutures with its opposite. The area of the midline suture is covered almost en-

tirely by the parasphenoid. The basioccipital tuber articulates with the pterygoid on this bone's dorsal surface, at the juncture between the central plate and the posterior medial process. The pterygoid central plate also articulates with the ectopterygoid laterally. The suture between pterygoid and ectopterygoid is not visible in FHSM VP404. The ectopterygoid is a gracile flange of bone that trends dorso-laterally out of the plane of the palate to contact the postorbital bar, where it contacts the medial surface of the jugal and, possibly, the postorbital.

The ventral aspect of the braincase is visible within the posterior interpterygoid vacuities. The two vacuities are divided on the midline by the parasphenoid, a robust bone that sutures with the pterygoid both anteriorly and posteriorly. The anterior end of the parasphenoid is expanded and ends in a blunt tip; the tip extends a short distance into the anterior interpterygoid vacuity, and the anterior medial processes of the pterygoids suture with an expanded region just behind the tip. The posterior end of the parasphenoid trends ventral to the basioccipital and overrides the posterior medial processes of the pterygoids. The ventral surface of the basisphenoid is visible on either side of the parasphenoid. The basisphenoid is large and well ossified, bear-

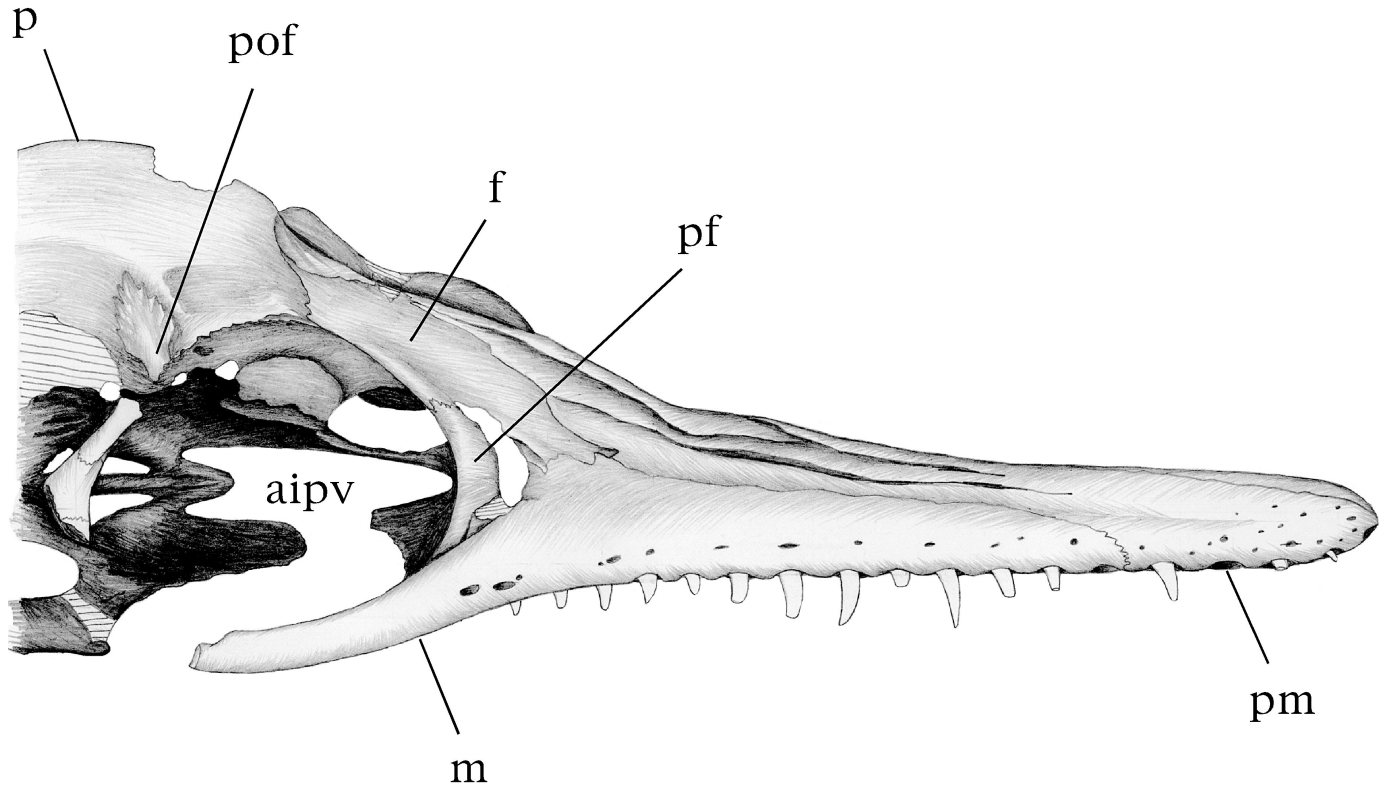


FIGURE 3. Skull roof of *Dolichorhynchops osborni*, MCZ 1064.

ing a prominent, cupped boss that forms the basal articulation with the pterygoid. The pterygoid carries on its dorsal surface a short, blunt process that articulates with this boss. A foramen for the passage of the internal carotid artery penetrates the body of the basisphenoid just posterior to the basal articulation; this condition is very similar to that in the basal plesiosaur *Thalassiodracon* (O'Keefe, in press). The region of contact between the basisphenoid and basioccipital is covered ventrally by the parasphenoid. The hemispherical occipital condyle bears a well-defined articular surface with a notochordal pit, and is set off from the body of the basioccipital by a short pedestal. The body of the basioccipital is shorter antero-posteriorly than in other plesiosaurs, the basioccipital tubers are reduced, and their pterygoid articulations appear to be confluent with the basisphenoid articulation. *Dolichorhynchops* shares these basioccipital features with other polycotylids, as well as with some cryptocleiods.

Skull Roof—The skull roof of *Dolichorhynchops* is depicted in Figure 3 (MCZ 1064), and reconstructed in Figure 4. Parts of the reconstruction and various anatomical details from the postorbital bar and jaw suspensorium are taken from the holotype skull, KUVF 1300 (figured by Carpenter, 1996, and Williston, 1903). The external naris is retracted to a position near the anterior margin of the orbit; the orbit is large and contains a prominent sclerotic ring in KUVF 1300 (not depicted in the reconstruction). Behind the orbit the skull is dominated by the large temporal fenestra. The medial margin of the fenestra consists of the parietal, which is developed into a thin, high, sagittal crest. The posterior and lateral margins of the temporal fenestra are formed by the squamosal, a large bone comprising the skull between the jugal and the quadrate. The squamosals meet on the midline posteriorly to form the 'squamosal arch' behind the sagittal crest. This feature is a stereotyped characteristic of all plesiosaurs (O'Keefe, 2001). The single temporal fenestra pre-

sent in *Dolichorhynchops* and all other plesiosaurs is thought to be homologous to the upper temporal fenestra of more basal diapsids (for discussion see Rieppel, 2000).

The premaxilla meets the maxilla in an interdigitating suture between the fifth and sixth teeth. This suture rises dorsally but also trends posteriorly until it parallels the midline. The premaxilla extends posteriorly as a long dorsal process along the midline until it contacts the parietal between the orbits. The possession of a dorsal process of the premaxilla contacting the parietal evolves convergently four times in the Plesiosauria, once in each of the three pliosauroform clades and once more within the Elasmosauridae (O'Keefe, 2001). The dorsal processes of the premaxillae separate the maxillae and frontals on the midline, although the frontals continue to have a midline suture beneath the premaxillae in *Peloneustes* (Andrews, 1911); the condition in *Dolichorhynchops* is currently unknown. The dorsal process of the premaxilla bears fine striations or sculpturing between the external nares.

The maxilla is a long bone carrying most of the tooth row and participates in a long parasagittal suture with the dorsal process of the premaxilla. The maxilla forms the ventral and anterior borders of the external naris, and has a small contact with the frontal above the external naris. The dorsal margin of the maxilla extends posteriorly from the external naris along the prefrontal and to the orbit, forms the ventral margin of the orbit, and then continues posteriorly beneath the jugal. The posterior end of the maxilla is an expanded flange that fits into a socket or excavation in the ventral edge of the squamosal, forming a solid connection between these two bones. The prefrontal is a small, triangular bone participating in the posterior border of the external naris anteriorly and in the anterior border of the orbit posteriorly. The frontal is relatively small, participating in the dorsal margin of the external naris and forming the antero-dorsal margin of the orbit. Medially, the frontal sutures with

the dorsal process of the premaxilla and with the parietal in the region of the parietal foramen. The frontal does not contact the postorbital.

The postorbital bar in polycotyliids is gracile and rarely preserved; Williston (1903) reconstructed *Dolichorhynchops* as lacking the postorbital entirely, with the postorbital bar composed solely of the postfrontal. However, the suture between the postorbital and postfrontal is visible in both MCZ 1064 and FHSM VP404, and the postorbital bar is reconstructed here as composed of both bones. The postorbital is a small, quadrangular bone articulating solely with the parietal medially and with the postfrontal laterally. The postfrontal is also quadrangular and articulates with the jugal and squamosal on its ventrolateral edge. The jugal forms the balance of the postorbital rim, and is also a small, quadrangular bone, articulating dorsally with the postfrontal, ventrally with the maxilla, and posteriorly with the squamosal.

The region of the skull posterior to the orbits is dominated by parietal and squamosal. The parietals form a high, sharply keeled sagittal crest separating the temporal fenestrae on the midline; the midline suture between the parietals is fused, except in the region of the pineal foramen. This foramen is located at the anterior margin of the parietals between the orbits. The anterior margin of the pineal foramen is formed by the parietals, however, rather than by the frontals as is the case in some elasmosaurs. The parietal around the pineal foramen bears several low ridges, and the pineal foramen faces antero-dorsally rather than dorsally. The sagittal crest itself is shaped like a pagoda roof with the parietals separating about halfway down the crest and trending ventro-laterally. The resulting triangular space between the parietals contains the articulation for the supraoccipital posteriorly. At the posterior margin of the skull roof the squamosals meet on the midline, and suture with the parietals within the temporal fenestrae. The squamosal is an L-shaped bone, with the upper leg forming the squamosal arch and the bottom leg forming the temporal bar. The temporal bar is robust and wide dorso-ventrally. The squamosal articulates anteriorly with the maxilla, jugal, and postfrontal. The squamosal bears a complex articulation for the quadrate. The quadrate rests in a shallow socket in the ventral face of the squamosal midway up the squamosal arch, and a thin, descending process of the squamosal covers almost the entire quadrate in lateral view.

The quadrate bears the jaw articulation ventrally. The mandibular condyle is long medio-laterally and much thinner in its center than at either end, giving the condyle a pulley-like appearance. This pulley articulates with a sharp ridge on the articular in the lower jaw. Dorsally the quadrate contacts the squamosal; medially the quadrate bears a shallow fossa that accepts the quadrate flange of the pterygoid. Just above this fossa in KUV 1300 is another that would accept the paraoccipital process of the opisthotic. In more basal sauropterygians (e.g., *Corosaurus* and *Cymatosaurus*) possessing an open occiput, the paraoccipital process articulates with the squamosal (Rieppel and Werneburg, 1998), and this condition is preserved in most plesiosaurs. Movement of the articulation from the squamosal to the quadrate is a feature shared by the polycotyliids and some other cryptocleidoids (O'Keefe, 2001). The nature of the quadrate articulation for the paraoccipital process indicates that the paraoccipital process was gracile, unlike the condition in all true plesiosaurs, and further that the paraoccipital process trended ventrally to a position level with or beyond the bottom of the occipital condyle (as illustrated by Williston, 1903). As is the case in all plesiosaurs, the opisthotic is restricted to the paraoccipital process and a small flange fused to the ventro-dorsal aspect of the exoccipital (O'Keefe, in press). Williston illustrates the supraoccipital as bifid; however, this condition has not withstood closer examination (Carpenter,

1996, 1997), and the supraoccipital in *Dolichorhynchops* is unpaired and deep antero-posteriorly. This condition is closely similar to that observed in elasmosaurs (Carpenter, 1997).

Mandible—The lower jaw of *Dolichorhynchops* is figured by Williston (1903), Carpenter (1996, 1997), and O'Keefe (2001), and is reconstructed here in Figure 4. The morphology of the lower jaw in cryptocleidoids is controversial, with some authors maintaining that the coronoid and prearticular are lost in cryptocleidoids (cryptocleidids sensu Cruickshank and Fordyce, 2002; Cruickshank, 1994; see also Brown, 1993). O'Keefe (2001) maintained that the coronoid was present in all plesiosaurs represented by adequate material save *Kimmerosaurus*, whereas the prearticular was found in all adequately-preserved taxa. The presence of both bones in the Polycotyliidae is not in doubt (Williston, 1903; Carpenter, 1997; O'Keefe, 2001); however the morphology of the posterior jaw is still problematical.

The lower jaw of FHSM VP404 is well preserved and forms the basis for the reconstruction in Figure 4 (the posterior portion of the left ramus is also illustrated in O'Keefe, 2001:fig. 19). In ventral view, the mandible is shaped like an isosceles triangle, with a long, narrow rostral portion matching the long rostrum of the skull. The symphysis is correspondingly long, extending for approximately 12–14 tooth positions. The dentary forms the anterior portion of the mandible and carries the entire tooth row. The teeth are largest at the anterior end of the snout and gradually decrease in size caudally. The splenial is included in the symphysis; this bone trends from the lingual surface of the jaw posteriorly to the ventral surface anteriorly and extends for about five tooth positions anterior to the point where the two rami join. A well-defined median suture separates the dentaries and splenials along the entire length of the symphysis. On the lingual surface of the jaw the splenial roofs the Meckelian canal, which is defined dorsally and laterally by the dentary and ventrally and laterally by the angular. The splenial is very thin over the Meckelian canal and liable to breakage, as is the case in many other plesiosaurs (O'Keefe, 2001). The angular forms the ventral margin of the jaw from the symphysis to the retroarticular process. In *Dolichorhynchops*, the angular separates the splenial and the dentary as far as the symphysis. In *Trinacromerum*, the angular extends anterior to the symphysis (Fig. 6) but is otherwise similar.

The conformation of the bones around the coronoid eminence is debated. Both Williston (1903) and Carpenter (1996, 1997) reconstruct the latero-posterior of the lower jaw as similar to the condition in other plesiosaurs (and in more basal sauropterygians; Rieppel, 2001); the angular forms the ventral margin of the jaw and the surangular forms the dorsal margin anterior to the articular. The coronoid is not exposed on the lateral jaw surface. O'Keefe's description (2001:fig. 19) is at variance with this interpretation. In my view, based on FHSM VP 404, the large bone forming the coronoid eminence is not the surangular but the coronoid, and the surangular is limited to a low, thin strap of bone covering the area between coronoid and angular. This condition is similar in some respects to that reported for *Muraenosaurus* by Andrews (1910), although that author misidentified the bone exposed on the coronoid eminence as the splenial. However, the holotype skull (KUV 1300) also preserves the lower jaw well, and there is no evidence of the strap-like surangular described for FHSM VP404 in this specimen. Several possibilities may explain this observation, including loss of the surangular in KUV 1300, fusion of the surangular with the coronoid in KUV 1300, or incorrect interpretation of FHSM VP 404. The posterior ramus fragments of *Polycotylus* (YPM 1125) also show a faint suture in this area. The reconstruction offered here is thought to be correct at this time, but more research is necessary on this difficult area.

The lingual surface of the coronoid eminence is formed by

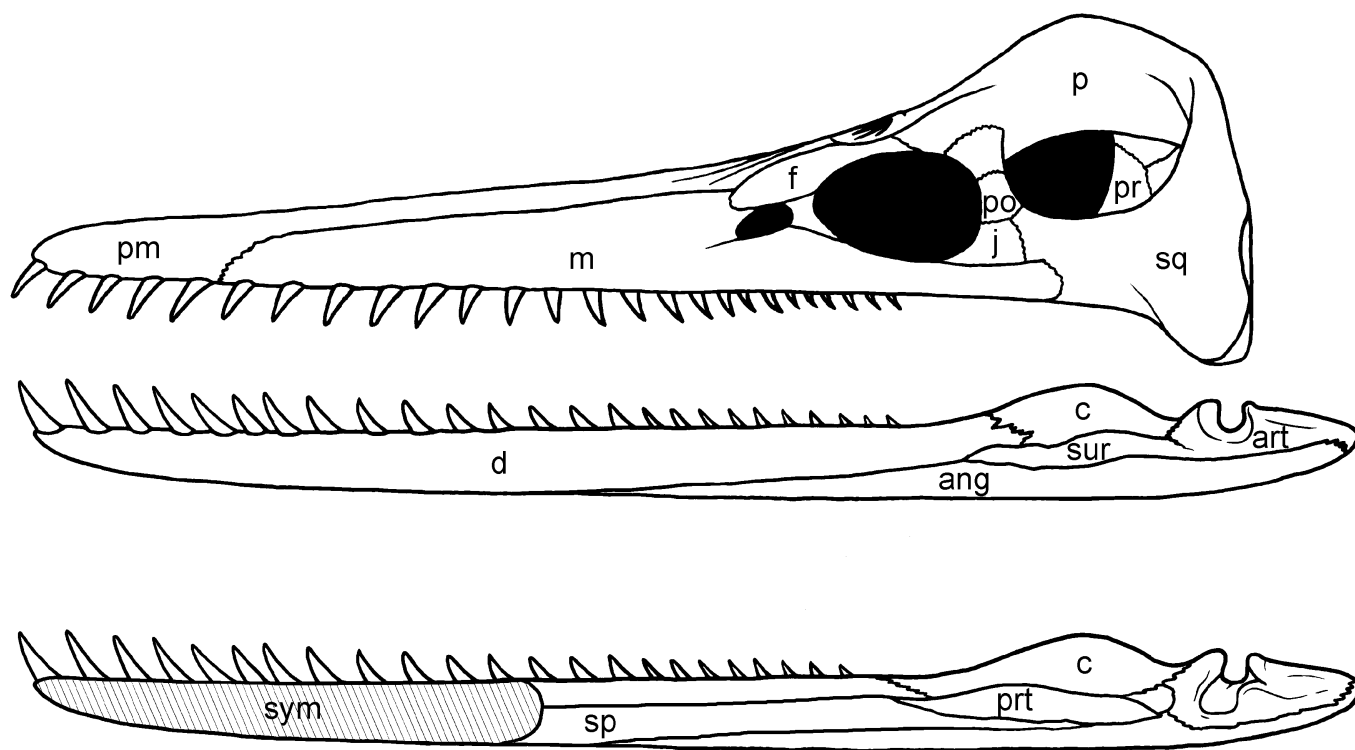


FIGURE 4. Lateral skull and lower jaw reconstruction of *Dolichorhynchops osborni*, based primarily on FHSM VP 404, with additional information from KUVF 1300 and MCZ 1064.

the coronoid bone dorsally and the angular ventrally. The splenial separates these bones and reaches posteriorly almost to the articular. The prearticular forms a shelf below the posterior portion of the Meckelian canal; this shelf is similar to those seen in other cryptocleidooids such as *Muraenosaurus* (Andrews, 1910). The opening of the Meckelian canal could not be identified with certainty.

Trinacromerum bentonianum

The holotype (USNM 10945) and paratype (USNM 10946) skulls of *Trinacromerum bentonianum* were examined in the course of this study, as well as the referred specimen KUVF 5070. The morphology of this taxon is very similar to that of *Dolichorhynchops*, and this description will therefore highlight areas of difference with that taxon and complementary material, rather than comprehensively redescribing the entire skull. A cranial reconstruction of *Trinacromerum* can be found in Carpenter (1996). *Trinacromerum* is also larger in terms of raw body size, and the skull is proportionally longer ($Trinacromerum = 1.54 \times Dolichorhynchops$; data from O'Keefe, 2002), although the proportions of the skull are similar. The cranial material of the holotype (Fig. 7) comprises the posterior portion of a skull that has been sectioned parasagittally (apparently during collection from the quarry where it was found; K. Carpenter, pers. comm.); this fortunate breakage allows study of the inside of the basicranium. The paratype skull is more complete but battered, missing most of the skull roof, and is broken into three fragments. The posterior palate (Fig. 5) is well preserved, however, as is the snout in the area of the mandibular symphysis (Fig. 6). The holotype and paratype skulls were found in the Fencepost Limestone, Pfeiffer Shale Member of the Greenhorn Limestone, Osborne County, Kansas, and are middle Turonian in age, and originally described by Cragin (1888). The specimen KUVF 5070 was found in the Jetmore Chalk, Hartland

Shale Member of the Greenhorn Formation, Cloud County, Kansas, and is lower Turonian in age.

Palate—The palate of USNM 10946 (Fig. 5) resembles that of *Dolichorhynchops* closely, being planar and highly fenestrate, possessing suborbital fenestrae, subtemporal fenestrae, and anterior and posterior interpterygoid vacuities. The central plate of the pterygoid is in an identical position to that in *Dolichorhynchops*; however, it is longer and narrower in *Trinacromerum*. The central plate is dished and surrounded by a raised rim. The rim of this fossa extends ventral to the quadrate flange of the pterygoid where it originates from the central plate. The possession of this squared lappet of the pterygoid is shared with some rhomaleosaurs, but not with *Dolichorhynchops*. The posterior interpterygoid vacuity is divided on the midline by the parasphenoid, which is much longer and narrower than the corresponding bone in *Dolichorhynchops*, and displays a faint midline suture posteriorly. Anteriorly the parasphenoid expands laterally to suture with the anterior medial process of the pterygoid, and comprises the posterior margin of the anterior interpterygoid vacuity. The anterior end of the parasphenoid lacks the blunt process projecting into the anterior interpterygoid vacuity observed in *Dolichorhynchops*. The matrix has not been fully cleared from the basicranium within the posterior interpterygoid vacuities, and the basisphenoid is therefore not identifiable, although small fragments of bone are preserved in this area. The body of the basioccipital is visible beneath the union of the pterygoids just anterior to the position of the occipital condyle. The occipital condyle is not preserved, however, and while the basioccipital tubers are not visible, the narrowness of the pterygoid here indicates that the tubers were reduced as in *Dolichorhynchops*.

The relations of the ectopterygoid and palatine differ significantly in *Trinacromerum*. In this taxon the central plate of the pterygoid gives rise to an anterior, lateral process or boss that

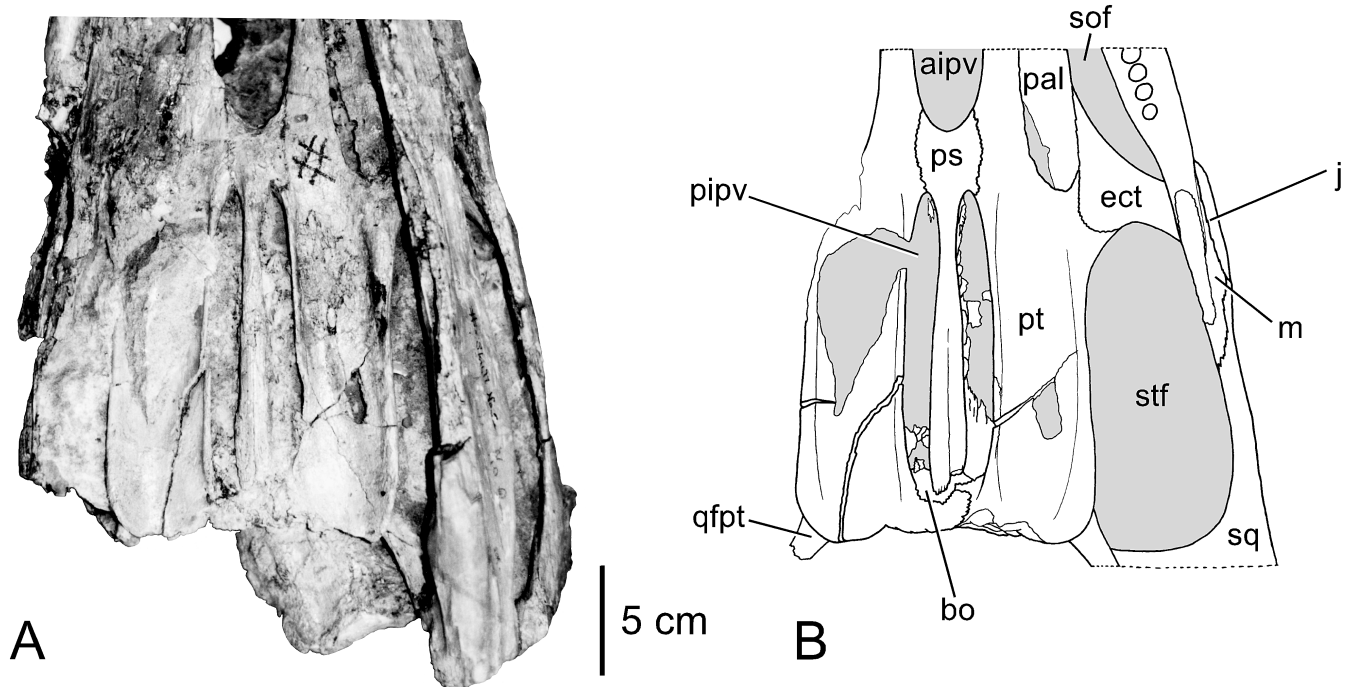


FIGURE 5. Paratype skull of *Trinacromerum bentonianum*, USNM 10946; photograph (A) with interpretive drawing (B); mandible is omitted in drawing.

meets the ectopterygoid in a curved suture. The ectopterygoid is more robust than is the case in *Dolichorhynchops* and trends postero-laterally rather than laterally. It does, however, rise dorsally out of the plane of the palate to suture with the postorbital bar, as is the case in *Dolichorhynchops*. The ectopterygoid also narrows to an anterior process extending anteriorly along the lateral edge of the palatine and defining the posterior margin of the suborbital fenestra. This condition is quite different than that in *Dolichorhynchops*. The more anterior relations of the palate are not visible, as preservation of the paratype skull is

poor in this area, and the mandible is closely applied to the anterior snout fragment (Fig. 6; see reconstruction in Williston, 1908:717). The teeth of *Trinacromerum* are more robust and heavily striated than those of *Dolichorhynchops*, as noted by Carpenter (1996). However, the teeth of both *Polycotylus* and *Edgarosaurus* are more robust than either of the former taxa.

Skull Roof—The skull roof of *Trinacromerum* is poorly preserved in the paratype skull and absent in the holotype; the referred specimen KUV 5070 preserves the skull roof relatively well (Carpenter, 1996:fig. 16). The paratype does preserve the ventral orbit margin. As in *Dolichorhynchops*, this margin is formed by a posterior extension of the maxilla, and this process extends posterior to the orbit to contact the squamosal in a flange-and-socket articulation. Just dorsal to this area is the jugal, a crescent-shaped bone defining the postero-lateral corner of the orbit, and articulating with the postorbital along its dorsal margin. In this area and in other osteological details the skull roof of *Trinacromerum* is closely similar to that of *Dolichorhynchops* described above. As noted by Carpenter (1996), differences between the two taxa include the relatively lower and longer sagittal crest in *Trinacromerum*, as well as the anterior tilt of the suspensorium. This tilt continues as a posterior projection of the quadrates, so that the jaw articulation is relatively far behind the braincase. Additionally, the prefrontal of *Trinacromerum* extends below the external naris in a narrow triangular process. The symphysis of the lower jaw is illustrated in Figure 6. The morphology here is similar to that in *Dolichorhynchops*; the splenials are included in the symphysis and separate the dentaries for a short distance anterior to the symphysis, whereas the angulars extend between the splenials and dentaries to a point anterior to the symphysis.

Basicranium—The holotype skull of *Trinacromerum* (USNM 10945; Fig. 7) consists of a large fragment of the left pterygoid ventrally, comprised of the central plate, the posterior medial process extending to the midline, and most of the quadrate flange. The anterior end of the central plate is broken away

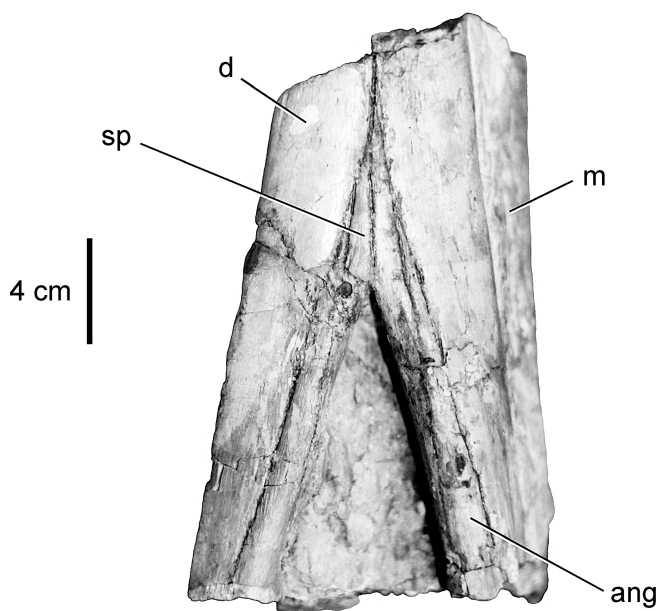


FIGURE 6. Snout fragment from the paratype skull of *Trinacromerum bentonianum*, USNM 10946.

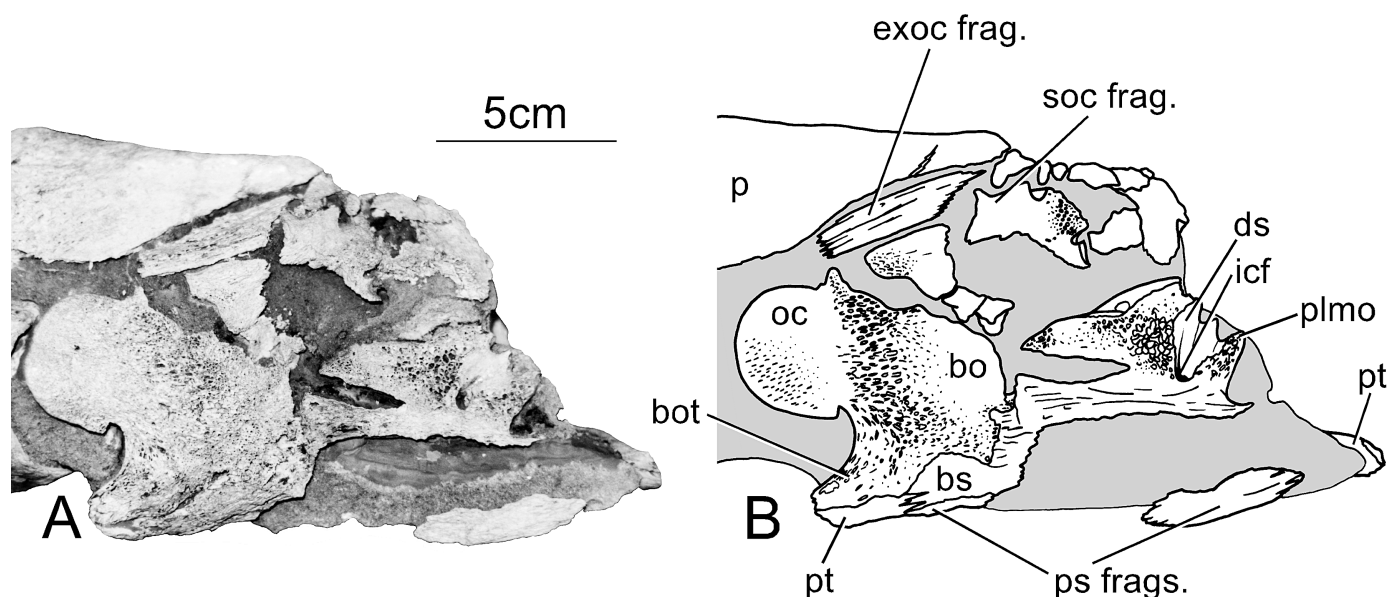


FIGURE 7. Holotype skull of *Trinacromerum bentonianum*, USNM 10945; photograph (A) with interpretive drawing (B).

near the region of the ectopterygoid articulation and anterior medial process, so that the left posterior interpterygoid vacuity is largely preserved. The anterior medial process reaches the midline at the extreme anterior end of the skull fragment. At the anterior end of the fragment, the left epipterygoid arises from the dorsal surface of the central plate of the pterygoid and trends dorsally and posteriorly towards the parietal. The epipterygoid is robust with a wide root and articulates in a clear suture with a broad, low boss on the pterygoid. The dorsal end of the epipterygoid is broken away, but seems to have articulated with the parietal in a condition similar to that displayed by *Brachauchenius* and other true pliosauroids (Carpenter, 1996:fig. 1). The epipterygoid also continues medially as a sheet of bone, but this area is fragmented and the relations here are unclear.

The medial view of the holotype skull was reconstructed schematically by Williston (1908) and presented in a photograph by Carpenter (1996). In medial view, the skull is fractured in an almost flat plane. The plane passes through the midline ventrally, and passes through the braincase at an angle of about 20 degrees to a true sagittal plane, angled toward the anatomically left side of the skull. The braincase section in Figure 7 therefore begins on the midline but passes through the basioccipital and basisphenoid to the left of the midline. The basioccipital carries the hemispherical occipital condyle set off from the basioccipital body by a constriction that is deeper ventrally than dorsally. The basioccipital tuber is reduced and has a poorly-defined articulation with the pterygoid. The body of the basioccipital is also rather abbreviated and the articulation with the basisphenoid is probably confluent with the pterygoid facet of the basioccipital tuber, as is the case in many other cryptocleidoids (i.e., *Morturneria*; Chatterjee and Small, 1989). The articulation for the left exoccipital is evident in the dorsal surface of the basioccipital body, and the base of this exoccipital is preserved near life position above this articulation. The more dorsal portion of the exoccipital is not preserved, nor are the hypoglossal and jugular foramina that presumably perforated this area, and no trace exists of the paraoccipital process. A fragment of the supraoccipital is preserved near life position, and includes portions of the bony labyrinth, although the exact identity of the preserved features could not be established. The

supraoccipital is certainly deep antero-posteriorly, however, as is the case in *Dolichorhynchops* and in elasmosaurs. Above these braincase elements lies the sagittal crest. Posteriorly the crest is complete, but it breaks up into fragments anteriorly.

A small fragment of the parasphenoid is preserved on the midline, in life position on the medial margin of the left posterior interpterygoid vacuity. This fragment contains a midline suture and is identical to the parasphenoid in the paratype skull. Posteriorly, another small parasphenoid fragment underlies the posterior flange of the basisphenoid and underlaps the posterior medial process of the pterygoid, again as in the paratype skull. The basisphenoid is a complex bone; posteriorly, a ventral flange of this bone underlies the anterior body of the basioccipital and articulates with the pterygoid. This articulation is underlain in turn by the parasphenoid. This posterior ventral flange of the basisphenoid is a common feature in primitive plesiosaurs, being present in *Plesiosaurus*, *Thalassiodracon*, and *Eurycleidus* (O'Keefe, in press), whereas it is absent in derived pliosauroids (O'Keefe, 2001). The body of the basisphenoid contacts the basioccipital in a broad contact, and then narrows to a plate of bone beneath the dorsum sellae and sella turcica. The ventral edges of this plate appear to be fractured, however, and the body of the basisphenoid may have been deeper dorso-ventrally than the fossil would indicate. The body of the basisphenoid is elaborated into a broad shelf posterior to the dorsum sellae, another feature common in more primitive plesiosaurs. The dorsum sellae is relatively high for a plesiosaur. A prominent foramen at its base provided passage for the internal carotid artery. The conformation of the sella turcica, dorsum sellae, and internal carotid foramina is very similar to that displayed by a well-preserved braincase of *Muraenosaurus* (LEICS G18.1996, Leicester, England; Evans, 1999), and by *Tricleidus* (Andrews, 1910). Anterior to the sella turcica is a knob of bone, probably the root of the pilla metoptica.

Polycotylus latipinnis

Material of three *Polycotylus latipinnis* specimens was examined in the course of this study; one of these is a new referral. The holotype material of *Polycotylus latipinnis* consists of vertebrae, an ilium, and metapodials housed at the Smith-



FIGURE 8. Left humerus of the FMNH specimen of *Polycotylus latipinnis*, PR 187, in dorsal aspect. Epipodial bones distal to humerus are, from top to bottom, radius, ulna, and first supernumerary ossification.

sonian (USNM 27678), as well as more vertebrae and assorted phalanges housed at the American Museum of Natural History (AMNH 1735). The AMNH material also includes a badly weathered bone interpreted here as a basioccipital; the basioccipital tubers on this specimen are reduced and their articulations with the pterygoid are confluent with the basisphenoid articulation, a character common to other polycotylids (O'Keefe, 2001). The vertebrae are of broadly polycotylid type, amphiceolous and antero-posteriorly compressed.

The paratype of *Polycotylus latipinnis* was referred by Williston in 1906, and consists of a well-preserved skeleton consisting of a vertebral column, limb girdles, propodials, other limb elements, and the posterior portions of both mandibles (YPM 1125). This specimen comes from the *Hesperornis* zone of the Smoky Hill Chalk Member, Niobrara Formation (Santonian–Campanian). The specimen was collected from along the Smoky Hill River, 22.5 km east of Fort Wallace in Logan County, Kansas (Carpenter, 1996). As described by Carpenter, *Polycotylus* has 26 cervical vertebrae; the vertebrae are compressed antero-posteriorly, being much wider than long. The articular facet of each cervical vertebra displays the scalloped or sigmoid margin common to all polycotylids as well as the more basal cryptocleidooids *Kimmerosaurus* and *Colymbosaurus* (Brown et al., 1986; O'Keefe, 2001). The number of cervical vertebrae is less than the 30–32 that is plesiomorphic for all plesiosaurs (Brown, 1981) but greater than the number seen in more derived polycotylids (20 in *Dolichorhynchops*, 19 in *Trinacromerum*; O'Keefe, 2002). The cervical neural spines also display the anterior flange common to many cryptocleidooids (Williston, 1908; O'Keefe, 2001).

Polycotylus also has several derived features in the appendicular skeleton. The ischia are very long, longer relatively than in any other plesiosaur, although the other polycotylids (and pliosauromorphs in general) also have relatively long ischia (Carpenter, 1996; O'Keefe, 2002). The humerus of *Polycotylus* is autapomorphic for this genus. As illustrated by Williston (1903, 1908; Fig. 8), the humeral shaft is sigmoidally curved; the humeral head faces a bit anteriorly, while the distal faces for the propodials are angled posteriorly. This sigmoid curve is weakly expressed in the humeri of *Trinacromerum* and *Dolichorhynchops*, but not to the degree displayed by *Polycotylus*. The humerus of the latter taxon is also unique among plesiosaurs in the possession of four discrete, deep facets on the distal margin for articulation of radius, ulna, and two supernumerary ossifications in the epipodial row. Well-preserved paddles of *Dolichorhynchops* also display two ossifications in the epipodial row (Williston, 1903); however, the humeral facets for the epipodials are poorly developed and there are no discrete facets for the supernumerary ossifications. The humeri of *Trinacromerum*

are similar. The possession of two distinct articular facets for the epipodials is a feature common to many cryptocleidooids. However, the four distinct, deep facets and the strongly sigmoid humeral shaft are diagnostic for *Polycotylus*.

The lower jaw fragments found with the paratype skeleton were figured and discussed by Williston (1908), and are very similar those of *Dolichorhynchops* (Fig. 4). The prearticular forms a discrete trough that articulates with the rest of the lingual surface of the lower jaw; the posterior extent of the splenial is unknown. Unfortunately, the sutures on the lateral surface of both lower jaw fragments are unclear, and the rami of *Polycotylus* shed little additional light on this difficult area.

A new, nearly complete specimen referable to *Polycotylus latipinnis* from the Mooreville Chalk Formation of western Alabama (see Chiappe et al., 2002, and Kiernan, 2002, for references) resides in the Field Museum of Natural History (PR 187, PR 1629). According to field notes with the specimen, the fossil was collected May 22, 1949 by J. A. Robbins from a "deep gully in an old field, 1.25 miles west and 0.75 miles north west of West Green, Alabama," from the "Mooreville Member of the Selma Formation." This note is interpreted to mean the Mooreville Chalk Formation of the Selma Group. The Mooreville Chalk Formation consists of two members, the upper Arcola Limestone and a lower, unnamed member (Raymond et al., 1988). This lower member contains alternating horizons of oxic sediments rich in invertebrate fossils and dysoxic horizons containing vertebrate fossils (Chiappe et al., 2002; Kiernan, 2002). Without a detailed examination of the locality it is impossible to know from what level the present specimen originates, although it seems probable that it was found in one of the dysoxic horizons of the unnamed lower member of the Mooreville Chalk Formation. The lower member is late Santonian to early Campanian in age (Puckett, 1996), and therefore is contemporaneous with the Niobrara Formation.

PR 187 is comprised of a complete vertebral column, all elements of both girdles save the left scapula (the elements are fragmentary, however, and completed in plaster), all four propodials, and many disarticulated paddle elements including epipodials, metapodials, and phalanges. The specimen also includes fragments of the skull (see below; the sagittal crest is given its own number [PR 1629] although no explanation is given for this in the field notes). The bones in general are not as well preserved as is common in the Niobrara Formation, although the chalky matrix is very similar; the bones display some erosion not due to recent weathering. The neck contains 26 cervical vertebrae and the ischia are very long, as is the case in *Polycotylus*. The left humerus is illustrated here in Figure 8. Although eroded, it is identical to the humerus of *Polycotylus*, displaying the strong sigmoid curvature of the shaft and the four distinct epipodial facets on the distal end. This specimen is therefore referred to the taxon *Polycotylus latipinnis*.

The preserved cranial elements of PR 187 are illustrated in Figures 9 and 10. The following elements are represented: fragments of both pterygoids with attached epipterygoids, sagittal crest, supraoccipital, basioccipital, several small maxillary fragments, the posterior rami of both mandibles, and many teeth. The mandibular fragments are poorly preserved and duplicate the better Yale material, and will not be discussed further. The teeth (Fig. 9c) are also very similar to those in the Yale specimen, possessing stout, curved crowns that are heavily striated all around and possessing long, curved roots.

The sagittal crest (Fig. 9a) is long and low, unlike the high, arched crest found in *Dolichorhynchops* and, to a lesser extent, *Trinacromerum* (Carpenter, 1996). The anterior margin of the fragment does not show any lateral expansion that would indicate the beginnings of the anterior margin of the temporal fenestrae. Posteriorly, however, the fragment flares laterally and splits on its ventral surface. In this region of the skull the pa-

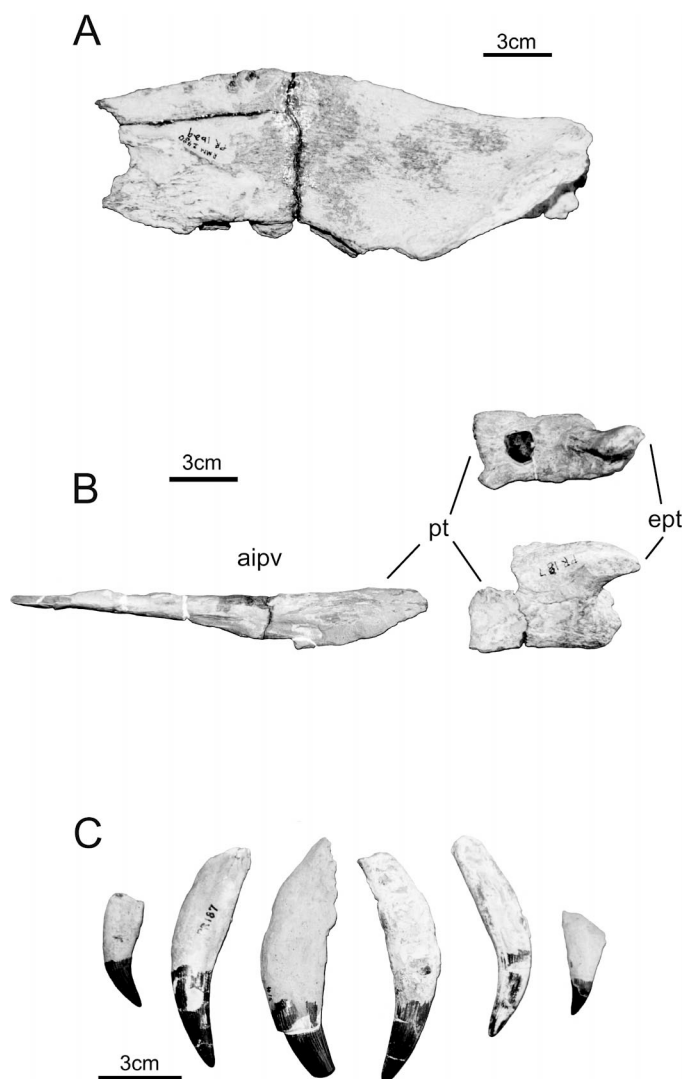


FIGURE 9. Cranial fragments of the FMNH specimen of *Polycotylus latipinnis*, PR 1629 and PR 187. Sagittal crest shown in A, pterygoids and epipterygoids in dorsal aspect shown in B, teeth shown in C.

rietyals trend laterally to participate in the posterior border of the temporal fenestrae, and form long sutures with the squamosal arch.

The pterygoids are represented by three fragments (Fig. 9B). The two posterior fragments also preserve the roots of the epipterygoids, which trend dorsally and posteriorly from the pterygoids toward the skull roof. The right fragment preserves a small part of the medial process that forms the articulation with the anterior parasphenoid in polycotyliids (O'Keefe, 2001); the basisphenoid and parasphenoid would sit between the two posterior pterygoid fragments. The suture between the epipterygoid and pterygoid is not visible in either fragment. This suture is visible in the type material of *Trinacromerum bentonianum* (USNM 10945), which preserves this area well. The morphology of *Polycotylus* and *Trinacromerum* is extremely similar in this region. The anterior fragment of the left pterygoid is a slender blade of bone that preserves the articulation for the ectopterygoid on its lateral edge; the medial edge is finished bone and would have formed the lateral margin of a large anterior interpterygoid vacuity, as is the case in other polycotyliids. The pterygoid in this region is relatively narrow, however, and



FIGURE 10. Braincase elements of the FMNH specimen of *Polycotylus latipinnis*, PR 187. Top, supraoccipital in ventral aspect. Bottom, basioccipital in lateral aspect.

this is the only way that *Polycotylus* differs from other members of the group.

Preserved braincase elements of PR 187 are illustrated in Figure 10. The supraoccipital is deep antero-posteriorly and possesses a sigmoid ventral margin. This morphology is again typical of polycotyliids (as well as elasmosaurs; Carpenter, 1997; O'Keefe, 2001), and the exoccipitals and prootics would have articulated here as is the case in other plesiosaurs (O'Keefe, in press). Both ventral edges of the supraoccipital preserve a fossa for the top of the posterior ampulla, and a channel for the posterior vertical semicircular canal. The basioccipital is very similar to the weathered bone in the *Polycotylus* type material, but preservation is better here. The basioccipital tubers are very reduced and their articulations with the pterygoids are confluent with the basisphenoid articulation; this morphology is common to other polycotyliids and to some cryptocleidiids as well (O'Keefe, 2001).

The cervical vertebrae of PR 187 are wider than long as in other *Polycotylus* material and in polycotyliids in general. The atlas/axis complex is preserved and is of polycotyliid type. The atlas and axis intercentra meet ventrally, excluding the atlas centrum from the ventral surface of the complex as in *Dolichorhynchops* (Williston, 1903). The atlas intercentrum and atlas neural spine are not preserved in PR 187, and the articular facets for these bones are well preserved on the atlas centrum. The neural spines of the remaining cervical vertebrae are generally poorly preserved, although several vertebrae preserve the anterior flange mentioned above. All vertebrae have strongly

scalloped articular margins, and in this and all other respects the cervical vertebrae are identical to those in the Yale specimen. A total of 68 vertebrae are preserved with the specimen. The transition from dorsal to caudal occurs at or near vertebra 57, although the exact location of the sacral vertebrae, and presence of heamal arches, was impossible to determine due to poor preservation.

Cladistic Analysis

A cladistic analysis was performed to establish a hypothesis of relationships for the Polycotylidae, and for the other members of the clade Cryptocleidoida (Williston, 1925, as revised in O'Keefe, 2001). All analyses were performed using PAUP* 4.0 (Swofford, 2001). The matrix is an edited version of that presented in O'Keefe, 2001 (see Appendices 2 and 3) and contains 95 characters, 62 of which are parsimony-informative, for 13 taxa. Autapomorphies were retained in the matrix to aid in the diagnosis of individual genera. Two of these taxa (*Plesiosaurus* and *Brancaosaurus*) comprise the outgroup; the outgroup was defined prior to parsimony analysis and constrained to be paraphyletic relative to the ingroup to reflect the topology in a larger analysis (O'Keefe, 2001), although the same clade topology is obtained with this constraint not in force. The taxa *Edgarosaurus* Drukenmiller, 2002, *Kaiwhekea* Cruickshank and Fordyce, 2002, and *Brancaosaurus* Wegner, 1914 were scored from the literature, while all other genera were scored from the fossils. Parsimony analysis was performed using the branch-and-bound algorithm and yielded four most-parsimonious trees (MPTs) having a tree length of 160, a consistency index (CI) excluding uninformative characters of 0.675, and a rescaled consistency index (RCI) of 0.532. A strict consensus tree of the four MPTs is presented in Figure 11. Bootstrap percentages based on 1,000 replicates, as well as decay indices, are presented next to the relevant node on the cladogram.

DISCUSSION

Phylogenetic Analysis

The results of the phylogenetic analysis indicate that, as found previously, the family Cryptocleididae is paraphyletic via the inclusion of the Polycotylidae. O'Keefe (2001) therefore redefined the Cryptocleididae as a taxon including only the genera *Muraenosaurus* and *Cryptocleidus*. In the present analysis, however, this clade is recovered in only two of the four MPTs, and the status of this new definition is therefore in doubt as well. The monophyly of the families Cimoliasauridae and Polycotylidae, however, was a well supported finding. The monophyly of the Polycotylidae is not seriously debated, and the node at the base of the clade is robust, with 95% bootstrap support and a decay index of five. The present analysis also recovers a clade of derived cryptocleidoids (Cimoliasauridae, redefined below) comprised of the Cretaceous austral taxa *Kaiwhekea* and *Morturneria* (and presumably *Aristonectes*, although this genus was not included in the analysis; see Cruickshank and Fordyce, 2002, for discussion). This clade also includes the Jurassic taxa *Kimmerosaurus* and *Tatenectes* from Wyoming, previously referred to *Tricleidus* by Mehl (1912). A preliminary description of the Wyoming taxon can be found in O'Keefe and Wahl (2003). This clade is also well supported, with 65% bootstrap support and a decay index of three.

Systematic Paleontology

In the present analysis, the genus *Kaiwhekea* falls outside the family Cimoliasauridae as defined by O'Keefe (2001). The definition of the family is therefore broadened here to accommodate this genus within the family.

CIMOLIASAURIDAE Delair, 1959

Revised Definition—A taxon including *Kimmerosaurus*, *Kaiwhekea*, their most recent common ancestor, and all descendants.

Revised Diagnosis—Rostrum long, unconstricted, and broad anteriorly; paraoccipital process articulating with squamosal only; teeth very small and needle-like; number of premaxillary teeth seven or greater; number of maxillary teeth greater than thirty.

POLYCOTYLIDAE Williston, 1908

Revised Definition—A taxon including *Polycotylus*, *Edgarosaurus*, *Dolichorhynchops*, *Trinacromerum*, their most recent common ancestor, and all descendants.

Revised Diagnosis—Neck length short, possessing a reduced number of cervical vertebrae; cervical vertebrae compressed antero-dorsally; ischium longer than pubis; maxillary/squamosal suture present and formed by posterior expansion of maxilla; pterygoids with distinct medial processes that meet behind posterior interpterygoid vacuities; pterygoid plate present and dish-shaped; mandibular symphysis scoop-like or long; splenial included in mandibular symphysis; longitudinal pectoral bar present and formed by clavicle and coracoid; supernumerary ossifications in podial and epipodial rows.

POLYCOTYLUS LATIPINNIS Cope, 1869

Holotype—USNM 27678, consisting of ilium, metapodial, vertebrae; AMNH 1735, phalanges, vertebrae, and basioccipital.

Type Locality and Horizon—*Hesperornis* zone of Stewart (1990), Smoky Hill Chalk Member, Niobrara Formation, Logan County, Kansas.

Referred Material—YPM 1125, mostly complete postcranial skeleton; PR 187, PR1629, mostly complete postcranial skeleton with fragmentary skeleton.

Revised Diagnosis—A relatively large polycotylid plesiosaur possessing 26 cervical vertebrae; ischia very long; humerus with pronounced sigmoid curvature and four distinct facets for articulation with ossification of epipodial row; robust, heavily-striated teeth; narrow central plate of pterygoid; low sagittal crest and robust epipterygoid; chevrons borne equally by adjacent caudal vertebrae; anterior edge of ilium posteriorly curved.

TRINACROMERUM BENTONIANUM Cragin, 1888

Holotype—USNM 10945, fragmentary skull and postcranial skeleton. Paratype: USNM 10946, skull and atlas/axis complex.

Type Locality and Horizon—Fencepost Limestone (Carpenter, 1996), Pfeiffer Shale Member of the Greenhorn Limestone, Osborne County, Kansas.

Referred Material—KUV 5070, partial skeleton and skull.

Revised Diagnosis—A medium-sized polycotylid plesiosaur possessing 20 cervical vertebrae; teeth less robust than those of *Polycotylus* but more robust than those of *Dolichorhynchops*; skull with anteriorly angled suspensorium; ectopterygoid with distinct anterior process enclosing lateral edge of palatine; squared lappet of pterygoid ventral to quadrate flange of pterygoid; parasphenoid lacking blunt anterior process and narrow posteriorly; vertebral centra lacking lateral and ventral constriction unlike other polycotylids.

DOLICHORHYNCHOPS OSBORNII Williston, 1903

Holotype—KUV 1300, complete skeleton.

Type Locality and Horizon—*Hesperornis* zone of Stewart

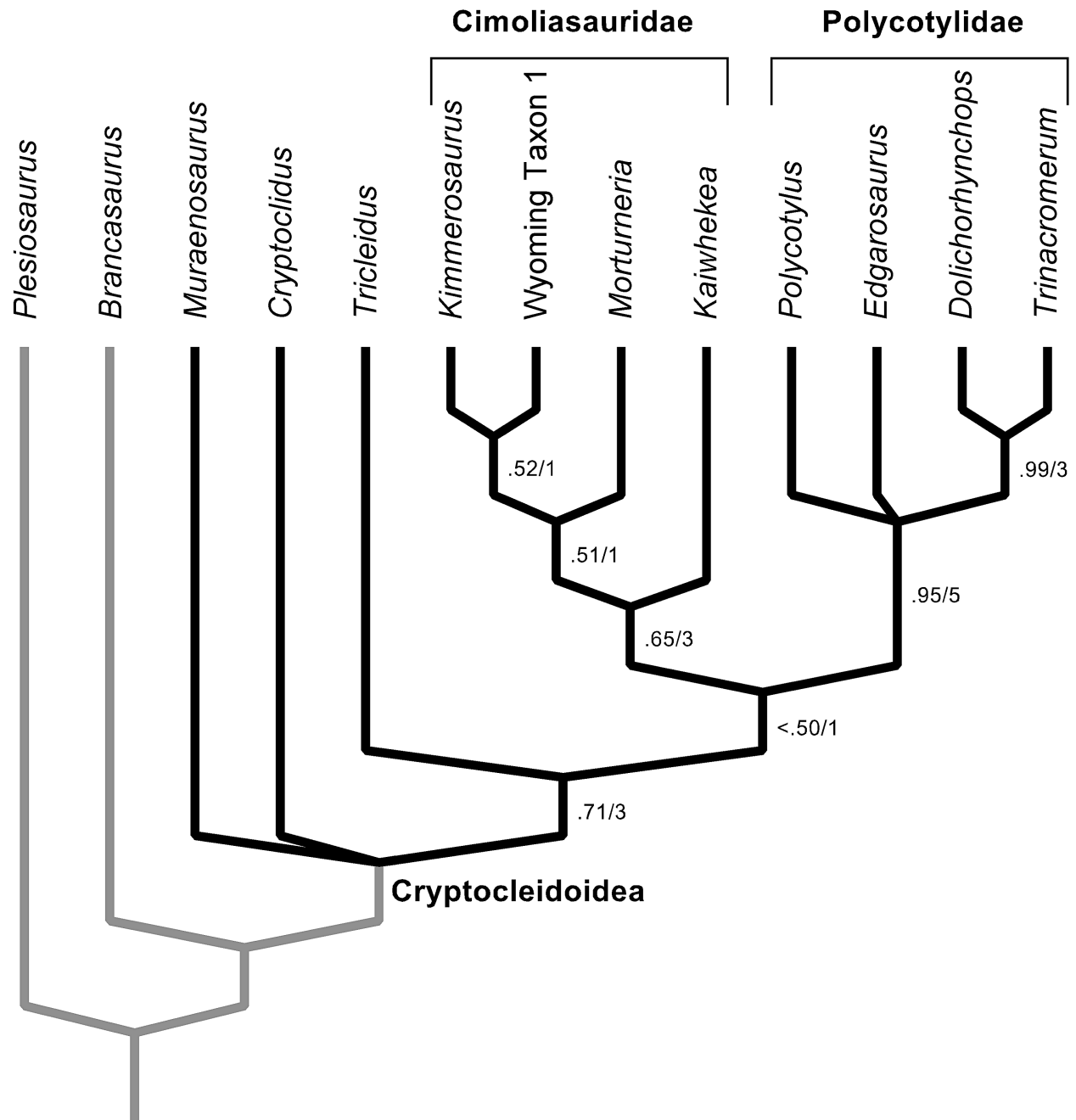


FIGURE 11. Cladogram of the Cryptocleidoidea. *Plesiosaurus* and *Brancasaurus* comprise the outgroup. Bootstrap percentages and decay indices are indicated beneath each ingroup node. For tree statistics and further discussion see text. 'Wyoming Taxon' refers to *Tatenectes laramiensis* O'Keefe and Wahl (2003) from the Sundance Formation of Wyoming.

(1990), Smoky Hill Chalk Member, Niobrara Formation, Logan County, Kansas.

Referred Material—FHSM VP404, complete skeleton; MCZ 1064, partial skeleton and skull.

Revised Diagnosis—A small polycotylid plesiosaur possessing 19 cervical vertebrae, gracile, lightly-striated teeth, short and very high sagittal crest; parasphenoid broad posteriorly, possessing blunt process projecting into anterior interpterygoid vacuity; ectopterygoid lacking anterior process and not enclosing lateral edge of palatine; suspensorium vertical; temporal fenestra short antero-posteriorly and broad; four bones present

in epipodial row; distal end of humerus lacking well-defined facets.

Polycotylus and Polycotylid Phylogeny

There seems to be little doubt that PR 187 is a skeleton of *Polycotylus latipinnis* given the presence of the diagnostic humerus morphology and other characters of *Polycotylus* (26 cervical vertebrae, very long ischia, robust teeth, overall large body size) and the lack of any autapomorphic character. The cranial material preserved with the specimen, though fragmen-

tary, is therefore a welcome addition to knowledge of this taxon. In general the cranial morphology of *Polycotylus* is closely comparable to better-known polycotyliids such as *Trinacromerum* and *Dolichorhynchops*; however, several characters are relatively primitive, and together contribute to the phylogenetic position of *Polycotylus*.

The teeth of *Polycotylus* are more robust and heavily striated than those of *Trinacromerum* or *Dolichorhynchops*, comparable to those of stratigraphically earlier and morphologically more primitive *Edgarosaurus* (Druckenmiller, 2002). The sagittal crest in *Polycotylus* is also low and rather long, again comparable to *Edgarosaurus* rather than other polycotyliids. Finally, the central plate of the pterygoid lateral to the anterior interpterygoid vacuity is narrow, and is closely comparable to the pterygoid in *Tricleidus* rather than other polycotyliids, including *Edgarosaurus*. This combination of cranial characters is relatively primitive. The postcranium of *Polycotylus* also possesses characters primitive for polycotyliids, such as the relatively large number of cervical vertebrae, the retention of a well-developed anterior flange on cervical neural spines, and the retention of well-developed articulations on the propodials for the epipodial bones.

Unfortunately, most of the postcranium of *Edgarosaurus* is unknown at present. The fragmentary humerus preserved with the holotype does possess well-developed facets for the radius and ulna, and is more similar in this regard to *Polycotylus* than the more derived polycotyliids. In the cladistic analysis presented here *Polycotylus* is the sister group to the rest of the polycotyliids in two of the four MPTs. In the other two MPTs *Polycotylus* and *Edgarosaurus* form a clade of primitive taxa to the exclusion of a clade comprising *Dolichorhynchops* and *Trinacromerum*. In sum, there is some evidence that *Polycotylus* is the sister taxon to all more derived polycotyliids; however, the relationships with *Edgarosaurus* are unclear at present. This lack of resolution is due at least partially to the lack of postcranial data for the latter taxon; a complete humerus and series of cervical vertebrae would help to clarify the relationships of these taxa. There is no doubt, however, that *Dolichorhynchops* and *Trinacromerum* are derived relative to other polycotyliids, and that they are closely related.

Trinacromerum and *Dolichorhynchops* are very similar, and were in fact synonymized (with *Trinacromerum* senior) by Williston (1908). However, Carpenter (1996) maintained that *Dolichorhynchops* is a valid genus based on various differences in the skull. This conclusion is also supported by this analysis. The morphology of the ectopterygoid and its relationships with the palatine and suborbital fenestra are very different between the two taxa. *Trinacromerum* also lacks the blunt anterior process of the parasphenoid present in *Dolichorhynchops*, while the former taxon possesses a squared lappet of the pterygoid ventral to the quadrate flange of the pterygoid. When combined with other autapomorphies of *Trinacromerum* noted by Carpenter (1996) (more robust teeth, larger body size, and slanted suspensorium) the taxa are easily diagnosable given adequate material, and one must conclude that both genera are valid.

Comparison with *Tricleidus*

The palate of *Tricleidus seeleyi* (BMNH R.3539) is illustrated here in Figure 12. Comparison with the taxa discussed in this paper demonstrates the many similarities between *Tricleidus*, and by extension other cryptocleidiids, and the polycotyliids. This character evidence is important because it is the basis for the finding that the Pliosauridae are polyphyletic as traditionally defined (Carpenter, 1996, 1997; O'Keefe, 2001). In a broad sense, the palate of *Tricleidus* is highly fenestrate, possessing prominent anterior and posterior interpterygoid vacuities as well as a large subtemporal fenestra. The parasphenoid

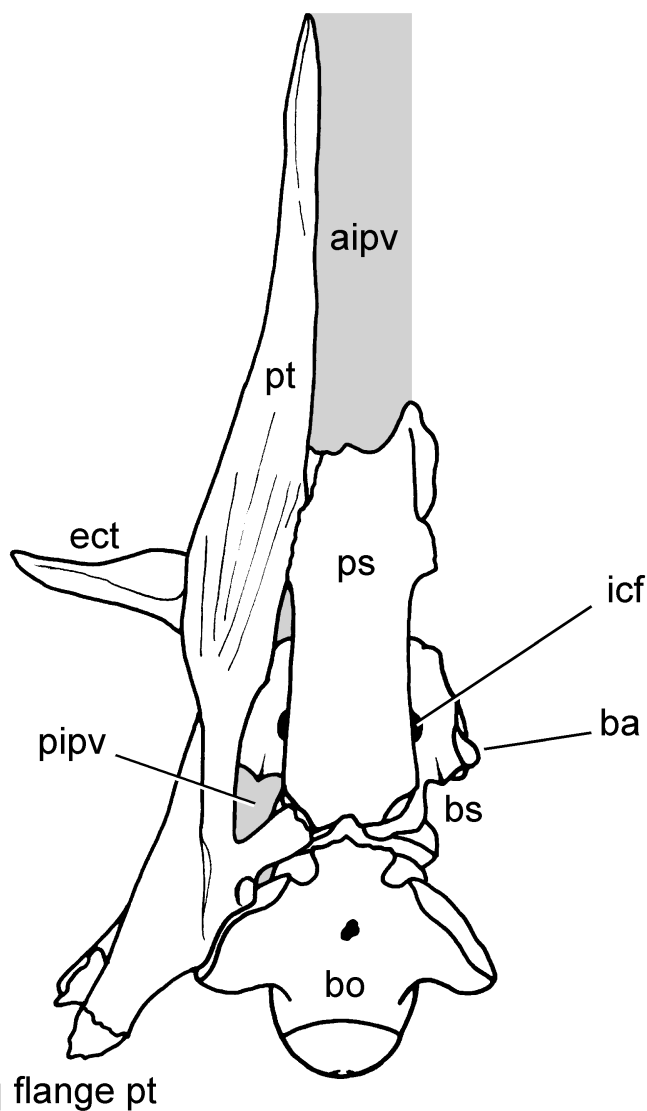


FIGURE 12. Basicranium of *Tricleidus seeleyi*, BMNH R. 3539.

is a large ossification extending posteriorly to the basioccipital, with which it has a small area of articulation. Anteriorly the parasphenoid is blunt, lacking a true cultriform process, and possessing novel articular facets for the medial edge of the pterygoid. This conformation of the parasphenoid is closely similar to that displayed by *Dolichorhynchops* and other cryptocleidiids, and very different than that in all other plesiosaurs. The basisphenoid is also well ossified and possesses clear foramina for the passage of the internal carotid artery, a plesiomorphic feature retained in cryptocleidiids but lost in all true plesiosaurs. The basioccipital is relatively short in *Tricleidus*, and the basioccipital tubers are confluent with the basisphenoid articulation, again as in the polycotyliids. Lastly, the pterygoid possesses a central plate in *Tricleidus*. This plate is not as wide as the plate in polycotyliids; however, it does articulate with the parasphenoid in the same manner, and possesses a posterior medial process articulating with the parasphenoid. The only other taxa known to possess this feature are the polycotyliids. In summary, the palate of *Dolichorhynchops* and other polycotyliids is very similar to that of *Tricleidus*, and radically different than the condition displayed by true plesiosaurs (O'Keefe, 2001, and references therein).

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APPENDIX 1
Abbreviations used in figures.

APPENDICES 2 and 3

Supplemental data available from SVP website: <http://www.vertpaleo.org/jvp/JVPcontents.html>.

aipv	anterior interpterygoid vacuity
ang	angular
ba	basal articulation
bo	basioccipital
bot	basioccipital tuber
c	coronoid
d	dentary
ds	dorsum sellae
ept	epipterygoid
ect	ectopterygoid
exoc	exoccipital
f	frontal
icf	internal carotid foramen
j	jugal
m	maxilla
oc	occipital condyle
p	parietal
pal	palatine
pf	prefrontal
pipv	posterior interpterygoid vacuity
plmo	pylla metoptica
pm	premaxilla
po	postorbital
pof	postfrontal
pr	prootic
prt	prearticular
ps	parasphenoid
pt	pterygoid
q	quadrate
sp	splenial
sq	squamosal
sur	surangular
sym	mandibular symphysis
