

1-1-2008

Cranial anatomy and taxonomy of *Dolichorhynchops bonneri* new combination, a polycotyloid (Sauropterygia: Plesiosauria) from the Pierre Shale of Wyoming and South Dakota

F. Robin O'Keefe

Marshall University, okeefef@marshall.edu

Follow this and additional works at: http://mds.marshall.edu/bio_sciences_faculty



Part of the [Animal Sciences Commons](#), and the [Ecology and Evolutionary Biology Commons](#)

Recommended Citation

O'Keefe, F. R. (2008). Cranial anatomy and taxonomy of *Dolichorhynchops bonneri* new combination, a polycotyloid (Sauropterygia: Plesiosauria) from the Pierre Shale of Wyoming and South Dakota. *Journal of Vertebrate Paleontology*, 28(3), 664-676.

This Article is brought to you for free and open access by the Biological Sciences at Marshall Digital Scholar. It has been accepted for inclusion in Biological Sciences Faculty Research by an authorized administrator of Marshall Digital Scholar. For more information, please contact zhangj@marshall.edu.

CRANIAL ANATOMY AND TAXONOMY OF *DOLICHORHYNCHOPS BONNERI*
NEW COMBINATION, A POLYCOTYLID (SAUROPTERYGIA: PLESIOSAURIA)
FROM THE PIERRE SHALE OF WYOMING AND SOUTH DAKOTA

F. ROBIN O'KEEFE

ABSTRACT

The taxonomic identity of two well-preserved polycotylid plesiosaur skeletons from the Pierre Shale of far northern Wyoming and southern South Dakota has been controversial since their discovery. Originally referred to *Dolichorhynchops osborni*, the material was almost immediately christened *Trinacromerum bonneri* Adams 1997; more recently the material has been referred to *Polycotylus*. Recent preparation of the well-preserved skull of one specimen permits detailed examination of the cranial morphology of this animal for the first time, and allows for its inclusion in a cladistic analysis of the Polycotylidae. This analysis reveals a stable sister-taxon relationship with *Dolichorhynchops osborni*. However, the taxon possesses a bewildering mosaic of character states, superficially resembling *Polycotylus* in overall size and tooth morphology and *Trinacromerum* in details of the palate and lower jaw, while sharing several critical synapomorphies with *Dolichorhynchops osborni*. This wide-ranging homoplasy among characters previously diagnostic among polycotylid genera challenges the alpha taxonomy of forms from the western interior seaway. The conservative taxonomic course of referring the species *T. bonneri* to *Dolichorhynchops* is followed here, but a species-level review is necessary. Lastly, material described here reveals important new information concerning the polycotylid orbital region and lower jaw, allowing confident reconstructions of these controversial regions for the first time.

INTRODUCTION

Our knowledge of the Polycotylidae has increased markedly in the last decade, from the discovery of many new taxa to a clearer understanding of their comparative anatomy, along with the first cladistic hypotheses of the phylogenetic relationships among clade members. Recent work on this family of Cretaceous shortnecked plesiosaurs suggests it is most closely related to the cryptocleidoid Plesiosauroidea rather than the true pliosaurs, and is central to the finding of polyphyly in the Plesiosauroidea, as traditionally defined (O'Keefe, 2001; 2004a; Druckenmiller and Russell, 2006 present a contrasting view). This controversial finding led to a reanalysis of the cranial morphology of well-known polycotylid taxa *Trinacromerum* and *Dolichorhynchops osborni*, and to the description of fragmentary cranial material of *Polycotylus* (O'Keefe, 2004b), work made possible by Carpenter's (1996) review and systematic revision of American Cretaceous short-necked plesiosaurs. Carpenter's study collected and rationalized over a century of polycotylid research stretching back to the efforts of E. D. Cope (1869), and postulated three valid polycotylid genera from the Western Interior Seaway (WIS) of North America (*Trinacromerum*, *Dolichorhynchops*, and *Polycotylus*). Reviews of the rather tortured taxonomic history of North American polycotylids can be found in Carpenter (1996) and Adams (1997).

Recent study of the Polycotylidae has also benefited greatly from the discovery and description of new material. Druckenmiller (2002) described an important new animal from the Lower Cretaceous of Montana that displays many plesiomorphic character states, while Sato and Storrs (2000) described other plesiomorphic material from Japan. Sato (2005) also described a

new species from Saskatchewan that is very similar to *Dolichorhynchops osborni*. Two rather enigmatic animals from Morocco have also been described and referred to the Polycotyliidae: *Thililua longicollis* (Bardet et al., 2003), and *Manemergus anguirostris* (Buchy et al., 2005). Most recently, diverse new polycotyliid material has been recovered from the Tropic Shale of Utah (Albright et al., 2007a), comprising the remains of at least three taxa and possibly more, two of which were previously unknown. This wealth of new material led Albright et al. (2007a) to posit an increased level of polycotyliid diversity in the Cretaceous. These authors also performed the first family-level cladistic analysis of the Polycotyliidae, resulting in the hypothesis of a basal split in the clade between small, gracile, long-snouted animals and a larger clade of more traditional polycotyliids. This paper reports on the cranial anatomy of another new polycotyliid taxon, and studies its impact on the phylogeny of the clade.

The material described here consists primarily of the remains of two animals residing in the Kansas University Museum of Natural History (KUPV 40001 and 40002). The holotype and paratype fossils were originally collected by Larry Martin and colleagues and were partially prepared in the 1990s. The taxonomic status of the skeletons has been contentious; a brief description and taxonomic assignment was first made by Carpenter (1996), who assigned them to *Dolichorhynchops osborni* Williston 1903. The material was then studied in more detail by Adams (1997), who christened it *Trinacromerum bonneri* Adams 1997. Most recently, Albright et al. (2007a) considered *T. bonneri* a junior synonym of a third taxon, *Polycotylus latippinus* Cope 1869. Given the taxonomic confusion surrounding them, it is fortunate that the two skeletons have now been prepared in their entirety to allow for molding and casting, permitting detailed study of their cranial anatomy for the first time. The skulls reveal a puzzling mosaic of character states unlike that of any previously known polycotyliid taxon, making the taxonomic identity of the material difficult to determine. The material is certainly not referable to *Polycotylus*, however. In a cladistic analysis, it forms a stable sistergroup relationship with *Dolichorhynchops osborni*. The conservative course of referring the species to the latter genus is followed here. Lastly, the lower jaw of KUPV 40001 is extremely well-preserved, and yields a wealth of new information concerning this poorly known part of the skull.

Despite the lack of agreement concerning the taxonomic identity of KUPV 40001 and 40002, all workers have considered the two skeletons representative of the same taxon. This interpretation is supported here, as the extensively overlapping material is virtually identical in all respects save a small size difference. All Kansas material was personally examined by the author, and photographed using an 8.6 megapixel Cannon digital camera. Line drawing interpretations were produced directly from photographs with close referral to the original material.

Importantly, Adams (1997) refers other Wallace Ranch material to her taxon *Trinacromerum bonneri*, including a complete adult skull listed as USNM 50144 and a young juvenile partial skeleton listed as USNM 55810. These specimens are actually from the University of Nebraska State Museum (UNSM), and their correct specimen numbers are UNSM 50133 (adult) and UNSM 55810 (juvenile). This material presently resides at the Field Museum of Natural History, and was examined by the author in the course of this study. Lastly, Adams lists TAMU 3001, a skeleton referred to *Trinacromerum* by Storrs in an unpublished Master's thesis (1981), to *Trinacromerum bonneri*. The validity of this referral has yet to be determined.

Institutional Abbreviations—AMNH, American Museum of Natural History, New York; FHSM, Fort Hays State University, Sternberg Museum of Natural History; KUVF, University of Kansas, Natural History Museum and Biodiversity Research Center; MCZ, Museum of Comparative Zoology, Harvard University; UCM, University of Colorado Museum; UMUT, University Museum, University of Tokyo; UNSM, University of Nebraska State Museum; USNM, United States National Museum (Smithsonian Institution); TAMU, Texas A & M University, Austin, Texas.

SYSTEMATIC PALEONTOLOGY

SAUROPTERYGIA Owen, 1860
PLESIOSAURIA de Blainville, 1835
PLESIOSAUROIDEA Welles, 1943
POLYCOTYLIDAE Williston 1908
Dolichorhynchops Williston 1903

Genotypic Species—*Dolichorhynchops osborni* Williston 1903.

Revised Diagnosis—polycotylid plesiosaurs possessing 19 or 20 cervical vertebrae; 18-20 teeth in mandibular symphysis; short and very high sagittal crest; vertical suspensorium; temporal fenestra short antero-posteriorly and broad; orbits relatively large and round; scapula with distinct posterior bend at midshaft; epipodials shorter than broad and lacking antibrachial foramen; coracoid with lateral spur; haemal arch facets confined mainly to the posterior centrum face.

Dolichorhynchops osborni Williston 1903

Holotype—KUVF 1300, essentially complete skeleton.

Stratigraphic Occurrence—*Hesperornis* zone, Smoky Hill Chalk Member, Niobrara Formation.

Referred Material—See Carpenter (1996) for descriptions of the following specimens: FHSM VP404, MCZ 1064, UCM 35059, AMNH 5834, UNSM 50133.

Age—Santonian-Campanian

Diagnosis—Relatively small polycotylid plesiosaur possessing the following unique combination of characters: angulars reach into symphysis but do not meet anterior to splenials; tooth crowns small and long relative to height; pineal foramen present; lateral plates of pterygoids wide with round lateral margins, ectopterygoid not carried on distinct pterygoid process, parasphenoid has well-developed anterior process projecting into anterior interpterygoid vacuity; anterior interpterygoid vacuity extends anteriorly between internal nares; dorsal vertebral centra not compressed; humerus sigmoid but long and gracile, with poorly defined facets for supernumerary ossifications; ilium with pointed proximal end, pubis possesses distinct lateral process.

Dolichorhynchops bonneri (Adams 1997), new combination

Holotype—KUVF 40002, complete postcranial skeleton and posterior skull fragments, including basioccipital and attached pterygoid fragments, and most of the left squamosal.

Paratype—KUVP 40001, partial skeleton consisting of complete skull with mandible, cervical vertebrae 1-3, both pubes, both ischia, left humerus and femur, dorsal vertebrae, and ribs.

Type Localities—Holotype: Wyoming, northern Niobrara County, Johnson Ranch; further described in Adams, 1997. Paratype: South Dakota, southern Fall River County, Wallace Ranch; further described by Adams, 1997 and Carpenter, 1996.

Stratigraphic Occurrence—Sharon Springs Member, Pierre Shale, very near the Ardmore Bentonite.

Referred Material—TAMU 3001, Taylor Marl of McLennan County, Texas.

Age—Lower Campanian

Diagnosis—Relatively large polycotyloid plesiosaur possessing the following unique combination of diagnostic characters: Angulars reach forward to meet on the midline on the ventral surface of the mandible; teeth crowns large and broad relative to height; symphysis long; supra-orbital mass present; anterior interpterygoid vacuity terminates posterior to internal nares; parasphenoid without anterior process projecting into anterior interpterygoid vacuity; pterygoid with lateral process carrying the ectopterygoid; lateral pterygoid plates narrow and not curved; dorsal vertebrae strongly compressed; humerus sigmoid but short and robust, with clear facets for supernumary ossifications; tongue-and-groove articulations between phalanges; ilium with a straight shaft and blunt proximal end; pubis lacks distinct lateral process.

Systematic Notes—Recent work has established that the genus name *Palmula* is pre-occupied by a foraminifer; Albright et al. (2007b) have therefore renamed the taxon *Palmulasaurus*, and have also changed the name of the subfamily “Palmulainae” to Palmulasaurinae.

DESCRIPTION

The following description is concerned almost entirely with the complete paratype skull, KUVP 40001; comparisons were made with the holotype in the few preserved regions, and no differences were found. The postcranium of the holotype, KUVP 40002, is well figured by Adams (1997), and is therefore not reproduced here save for codings in the cladistic matrix (Appendices 1, 2) and a figure of the humerus below. All postcranial data were taken from the actual fossils and checked against Adams’ figures, which were found to be largely accurate; Adams does misidentify the fore- and hindlimbs, however; for a brief discussion of postcranial characters see below.

Skull Roof

The skull of KUVP 40001 is 98 cm long (measured along the mandible; the cranium is about 94 cm long from tip of snout to quadrate), large by polycotyloid standards. The skull is crushed flat at an oblique angle; the left and medial skull roof is exposed on one side (Fig. 1), and the palate and associated structures are visible on the reverse (Fig. 2). The skull is broken into anterior and posterior sections through the orbit. Despite various cracks and some distortion, especially to the right squamosal arch, the bone surface and sutures are well preserved.

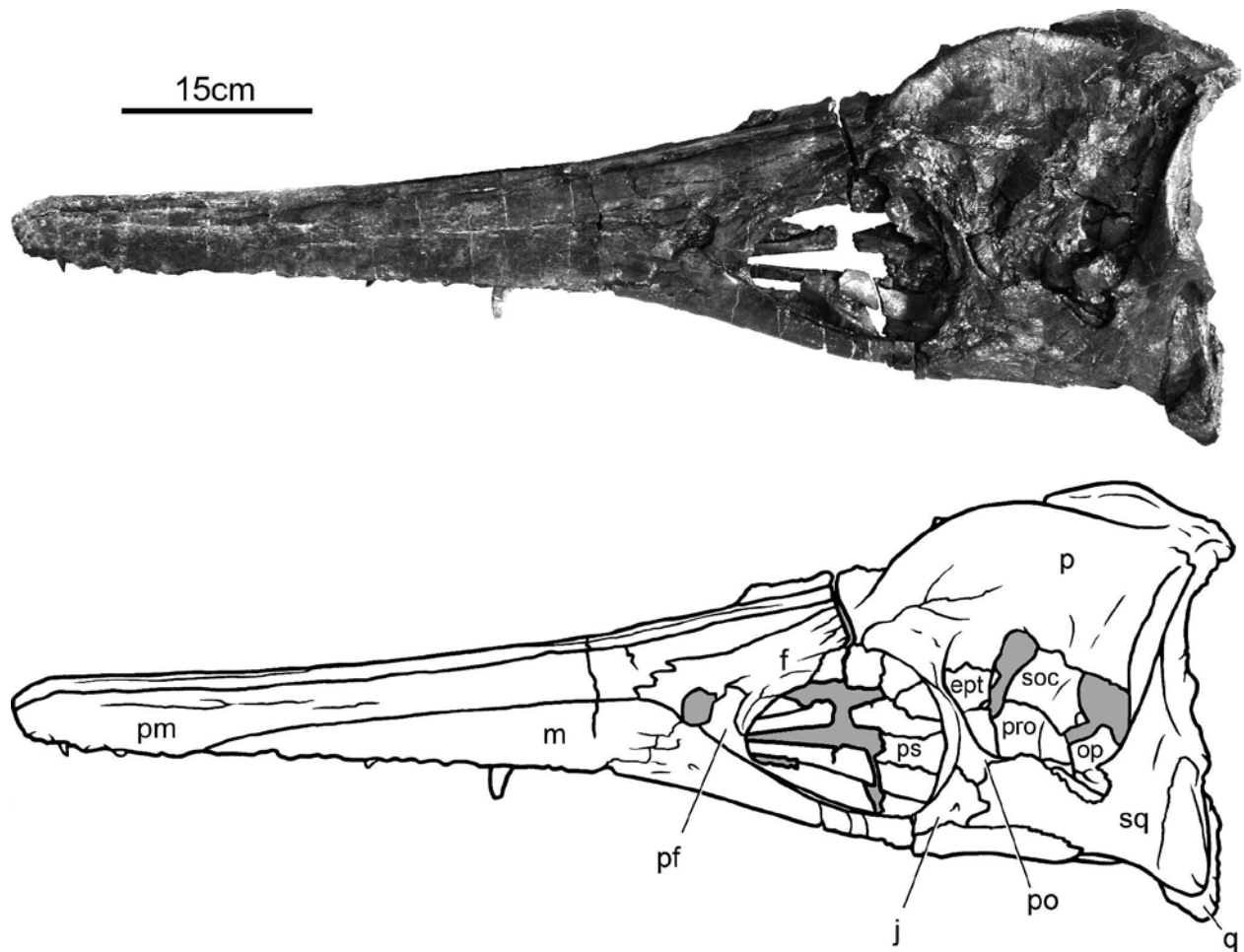


FIGURE 1. Photograph and interpretation of the left skull roof of *Dolichorhynchops bonneri*, new combination, KUVV 40001. **Abbreviations:** **ept**, epipterygoid; **f**, frontal; **j**, jugal; **m**, maxilla; **op**, opisthotic; **p**, parietal; **pf**, prefrontal; **pm**, premaxilla; **po**, postorbital; **pro**, prootic; **ps**, parasphenoid; **q**, quadrate; **soc**, supraoccipital; **sq**, squamosal.

The preorbital region of the skull is much longer than the postorbital region (Fig. 1). The greatly elongated snout consists of anterior extensions of both the premaxillae and maxillae. The premaxillae continue caudally on the midline as a pair of posterior processes that contact the parietal, separating the frontals on the skull roof; this condition is typical of polycotyliids except *Edgarosaurus* (Druckenmiller, 2002). The left premaxilla is the better preserved of the two and clearly shows five alveoli for large teeth. The left maxilla begins just behind the fifth tooth position and extends caudally beneath the external naris, under the orbit and the jugal, and then expands to form a robust attachment to the squamosal. This posterior extension of the maxilla is a typical polycotyliid feature (O’Keefe, 2004b). Near its midpoint, the maxilla extends dorsally to meet the anterior end of the frontal, and forms the ventral margin of the external naris just posterior to this region. This condition resembles that in *Dolichorhynchops osborni* more than the reconstruction of *Trinacromerum* offered by Carpenter (1996); however, my interpretation of the latter (KUVV 5070) differs from Carpenter’s; all taxa are very similar.

The prefrontal forms both the posterior margin of the external naris and the anterior margin of the orbit, a trait common to polycotylyds and elasmosaurs (Carpenter, 1997). The frontal forms the anterior and dorsal margins of the external naris and continues anteriorly to suture with the maxilla. The sutures in the region just anterior to the external naris are unclear due to crushing, and the interpretation, which differs from that of Adams (1997), is less sure than in other areas. There is no evidence of a frontal foramen. The frontal clearly forms a large portion of the dorsal orbit rim, although much of the latter is broken away; the suture between the frontal and parietal is also obscured due to a large break. The orbit is relatively large and round as is typical for polycotylyds. A prominent excrescence of rugose bone, located on the postero-dorsal rim of the orbit, is probably composed of parietal and postfrontal. However, no sutures could be identified and the possibility remains that the bone is a neomorphic ossification. This feature was first noted and named the supraorbital by Williston (1903) and is alluded to by Carpenter (1996), who described a supraorbital bone in *Dolichorhynchops osborni*. O'Keefe (2001; 2004a, b) erroneously dismissed this feature, as it is delicate and poorly developed in *Dolichorhynchops osborni*, and is broken away in the smaller specimens (MCZ 1064, FHSM VP404) on which the skull roof reconstruction in O'Keefe 2004b was based. However this feature is well developed in *Dolichorhynchops bonneri*, and subsequent reexamination of *Trinacromerum* (KUV 5070) revealed that it is certainly present in that skull as well. The supraorbital bone is therefore present in at least three derived polycotylyd taxa (*Dolichorhynchops osborni*, *D. bonneri*, and *Trinacromerum*), but is certainly absent in the archaic *Edgarosaurus*, and therefore evolved at some point within the clade. The homology of the supraorbital bone is unclear, although its posterior end certainly includes the postorbital. Anteriorly, it may be formed by an extension of the frontal, a neomorphic ossification, or both. Its anterior end extends ventrally and superficially over the rear of the prefrontal in both *Trinacromerum* and *D. bonneri* (Fig. 2). The best preserved of these structures is found in the Kansas skull of *Trinacromerum* (KUV 5070); a photograph of the orbital region of this skull appears in Figure 3, along with an attempted reconstruction of the region.

The remainder of the skull roof of *Dolichorhynchops bonneri* is very similar to that in other polycotylyds. The jugal is a small, squarish bone restricted to the posterior orbit margin, and contacts the antero-ventral edge of the postorbital. Behind this region the postorbital sutures to the anterior end of the squamosal ventrally, and forms the anterior edge of the temporal fenestra more dorsally. Neither the dorsal extent of the postorbital, nor the presence of the postfrontal, could be determined, as the supraorbital mass obscures this area. More posteriorly, the wide, straight temporal bar is formed by the anterior process of the squamosal. The ventral process of the squamosal covers the quadrate laterally almost to the jaw articulation, another typical feature of polycotylyds and other plesiosauroid taxa. The arched squamosal forms the posterior margin of the temporal fenestra and meets its neighbor on the midline, although the sutures between the two squamosals, and between them and the posterior end of the parietals, are not visible due to fusion. The suspensorium is vertical as in *Dolichorhynchops osborni*, rather than angled anteriorly as in *Trinacromerum*. The parietal possesses a highly keeled sagittal crest very similar to that in *Dolichorhynchops osborni* and unlike the low crest seen in *Trinacromerum* and *Polycotylus* (Carpenter, 1996; O'Keefe, 2004b).

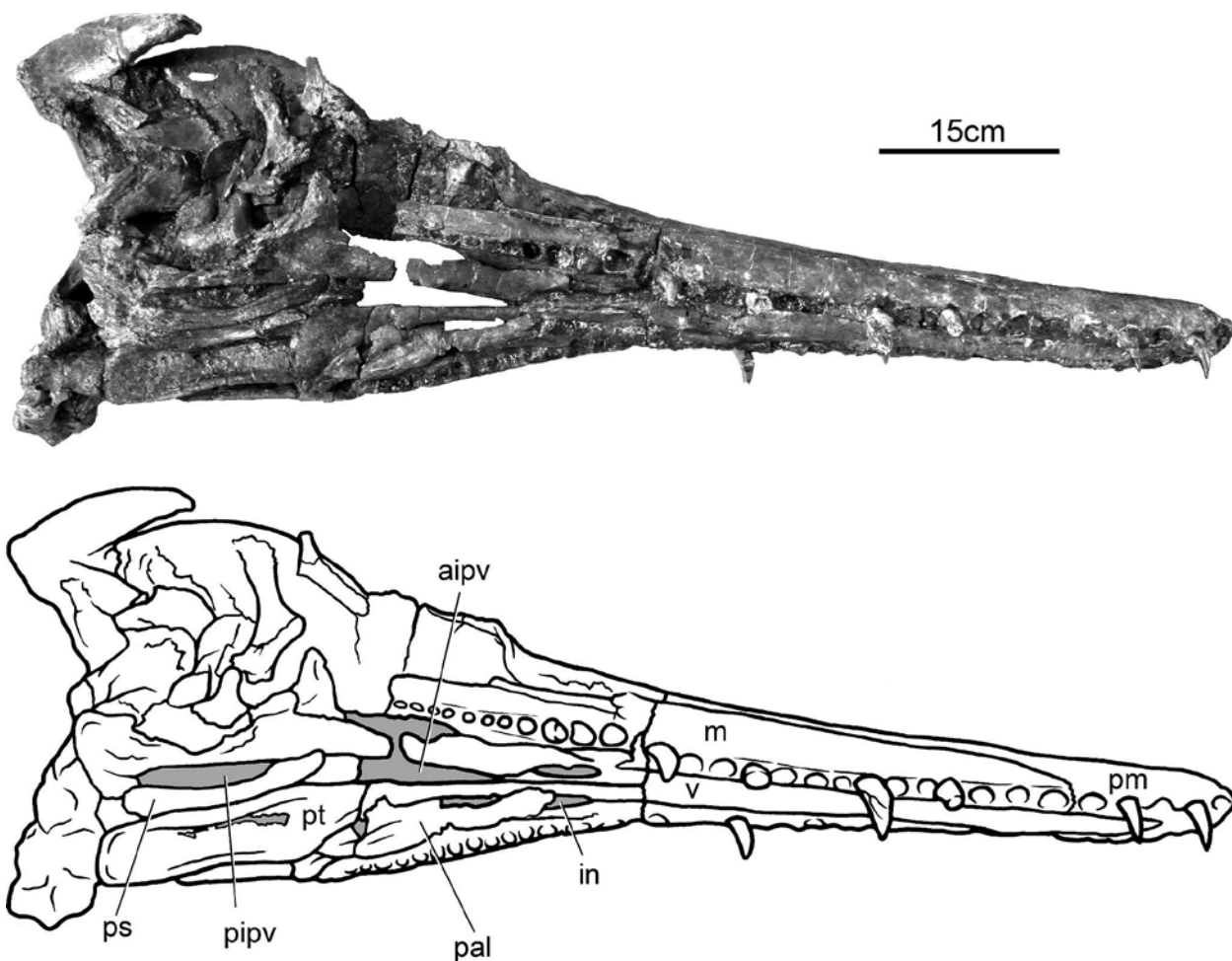


FIGURE 2. Photograph and interpretation of the palate of *Dolichorhynchops bonneri*, new combination, KUVV 40001. **Abbreviations:** **aipv**, anterior interpterygoid vacuity; **in**, internal naris; **m**, maxilla; **pal**, palatine; **pipv**, posterior interpterygoid vacuity; **pm**, premaxilla; **ps**, parasphenoid; **pt**, pterygoid.

Several elements of the braincase and associated structures are preserved in the left temporal opening. Just posterior to the postorbital bar, the broad epipterygoid reaches dorsally to the parietal and meets it in a prominent suture. Just caudal to the epipterygoid, the lateral aspects of the left supraoccipital, prootic, and opisthotic are visible. The supraoccipital is deep antero-posteriorly with a broad, curved suture to the prootic and fused exoccipital-opisthotic, the common condition in polycotylics and elasmosaurs (Carpenter, 1997); only the lateral aspect of the prootic is visible, and bears no remarkable features. The opisthotic carries the remains of the paraoccipital process, most of which is not preserved. However, enough remains to establish that the paraoccipital process was slender and relatively short.

Palate

The palate of KUVV 40001 is depicted in Figure 2. In this view, the right side of the skull roof is flattened obliquely so that it is flush with the palate; the palate itself is medio-laterally compressed as well. As a consequence, the bones on the right side of the palate are broken and

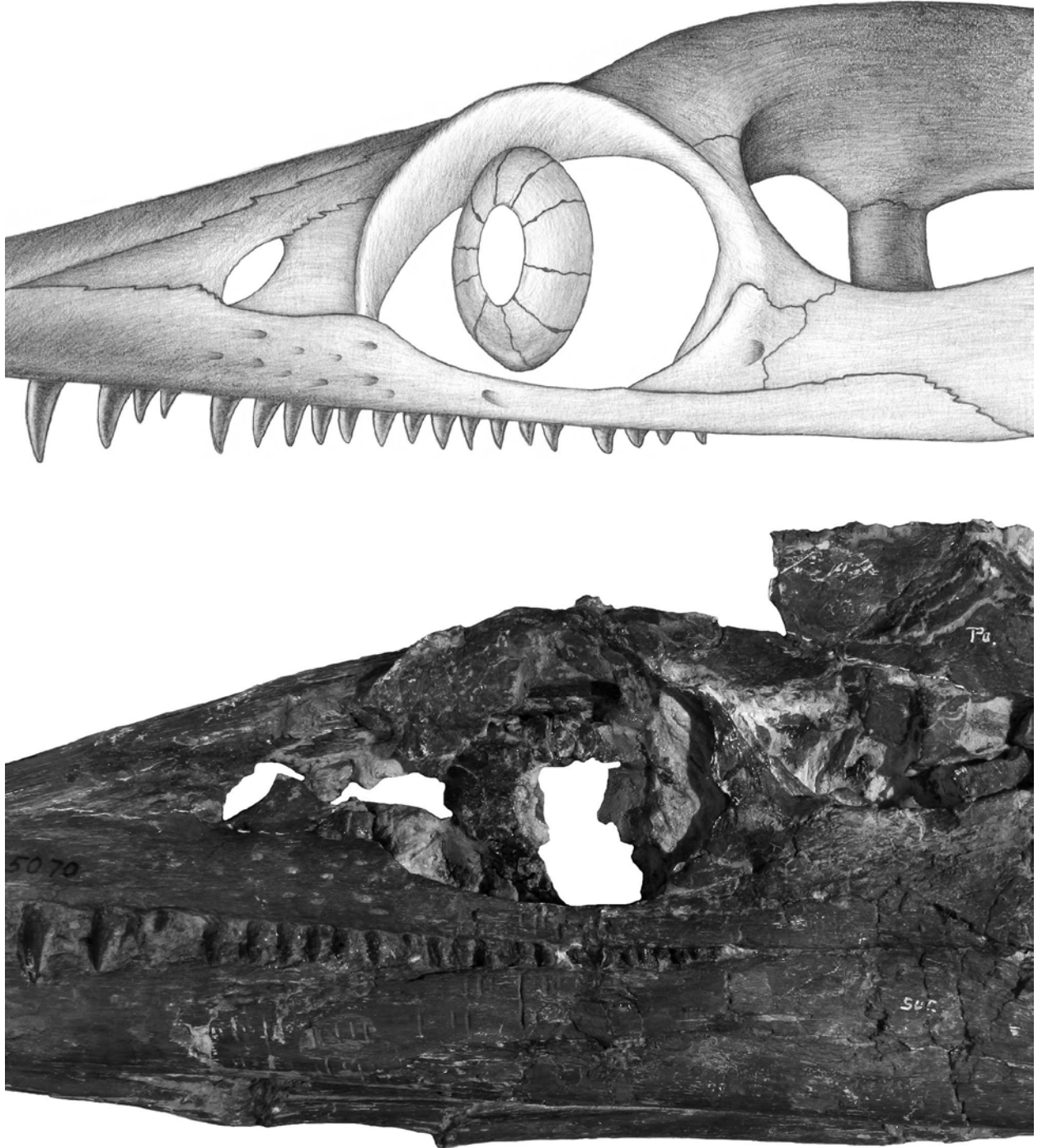


FIGURE 3. Photograph and interpretation of the left orbital region of KUVV 5070, *Trinacromerum Bentonianum*. The reconstruction above is based closely on the skull in the photograph, although an attempt has been made to reconstruct the three-dimensional geometry of the orbit, supraorbital bone, and sclerotic ring. The supraorbital bone expanded the diameter and lateral extent of the orbit, and may have had other functions. Length of illustrated portion approximately 32 cm.

their relations obscured; however, most of the left margin of the palate is visible back to the posterior margin of the pterygoid. The palate conforms very closely to the canonical polycotyloid pattern. The vomers are fused, forming a long element stretching from the third tooth position on the premaxilla to the region of the internal nares. The location of the suture between the vomers and the anterior ends of the pterygoids could not be determined. The vomer forms a ridge on the midline of the anterior palate that is separated from the raised tooth rows by deep grooves. The tooth row on the right maxilla extends to the front margin of the orbit, but contains only 26 tooth positions because the anterior teeth are quite large (Fig. 2). The maxillary dentition is quite different from that of dentition found in *Dolichorhynchops osborni* and *Trinacromerum*; the teeth are relatively larger, and the crowns are relatively wider and shorter. The alveoli are deeply thecodont and reside in a prominent, raised ridge in the premaxilla and maxilla. The dentition of *Dolichorhynchops bonneri* is almost identical to that of *Polycotylus*; the tooth crowns are stout and slightly recurved, and lightly striated on the lingual surface only (O'Keefe, 2004b). Tooth roots are much longer than crowns, and many of the roots swell to a greater diameter than the crown base. Stout, robust teeth have previously been treated as an autapomorphy of *olycotylus* within derived polycotylics (O'Keefe 2004b).

Medial to the tooth row and posterior to the vomer, the anterior extensions of the pterygoids are clearly split by a midline suture. The anterior interpterygoid vacuity is a large, triangular opening with a broad base on the parasphenoid and a narrow apex, and posteriorly separates the pterygoids on the midline. The tip of the anterior interpterygoid vacuity does not extend forward between the internal nares, unlike the condition in *Dolichorhynchops osborni*. The anterior extensions of the pterygoids are bordered laterally by well-developed palatine bones, which form the lateral margins of the internal nares but do not reach anterior to them, and suture laterally with the maxillae. Suborbital fenestrae were probably present but have been obscured due to lateral compression of the palate; the lateral edge of the right palatine is finished bone and has no indication of articulation with another element.

The posterior end of the palatine rests on a lateral process of the pterygoid bone (O'Keefe, 2004b for this character). This lateral process supports the ectopterygoid, which is directed toward the skull roof. The exact lateral articulation of the ectopterygoid could not be determined because of crushing, but it probably contacted the jugal and postorbital bar, as is the case in other polycotylics and elasmosaurs (Carpenter, 1997; O'Keefe, 2004b). A distinct lateral process on the pterygoid carrying the ectopterygoid is also present in *Trinacromerum*, but absent in *Dolicho-rhynchops osborni*. The relatively narrow pterygoid plates just lateral to the posterior interpterygoid vacuities resemble those in *Trinacromerum*, but are unlike the wide, rounded plates in *Dolichorhynchops osborni*. The parasphenoid is long and sutures with the pterygoids laterally at its anterior end; it lacks an anterior process extending into the anterior interpterygoid vacuity. The posterior end of the parasphenoid continues ventrally and posteriorly, partially covering the union of the pterygoids on the midline behind the posterior interpterygoid vacuity, as in other derived polycotylics (O'Keefe, 2004b). The basioccipital is poorly preserved in KUV 40001; the condyle is crushed and the body of the bone is obscured by other elements. However, the occipital condyle shows no features differentiating it from other polycotylics, and enough of the body of the basioccipital is preserved to demonstrate that the basioccipital tubers are reduced and confluent with the anterior face of the basioccipital, as is the case in other polycotylics. The occiput of KUV 40001 is heavily disrupted by crushing, and the relations of

the quadrate flange of the pterygoid, the paraoccipital process, and the posttemporal fenestra could not be determined. Knowledge of the suspensorium is limited to what is visible on the left side of the skull roof, described above.

Mandible

The mandible of *Dolichorhynchops bonneri* is well-preserved, and shows a wealth of detail (Figs. 4, 5). A fortuitous break just anterior to the coronoid process of the left posterior jaw ramus affords a cross-sectional view of the jaw, and sutures visible within this cross section provide much additional information (Fig. 5). This excellent material allows a new and more detailed interpretation of the osteology of this region.

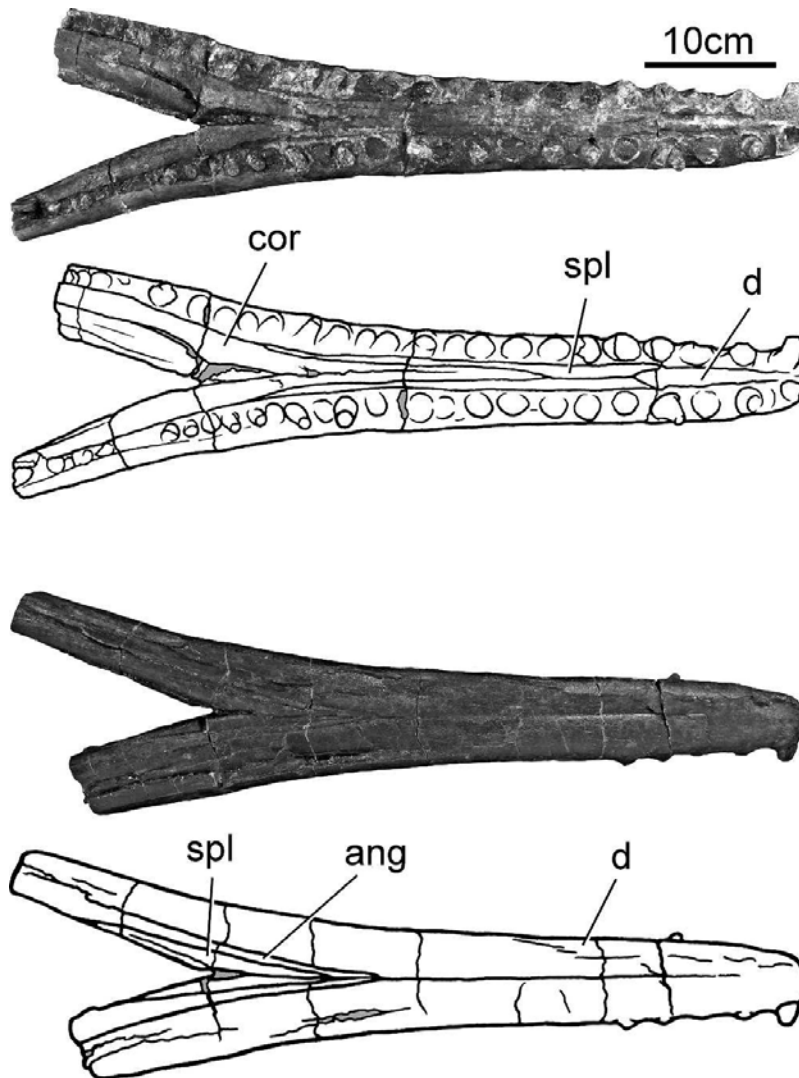


FIGURE 4. Photographs and interpretations of the mandibular symphysis of *Dolichorhynchops bonneri*, new combination, KUV 40001. Top is dorsal view, bottom is ventral view. **Abbreviations:** ang, angular; cor, coronoid; d, dentary; spl, splenial.

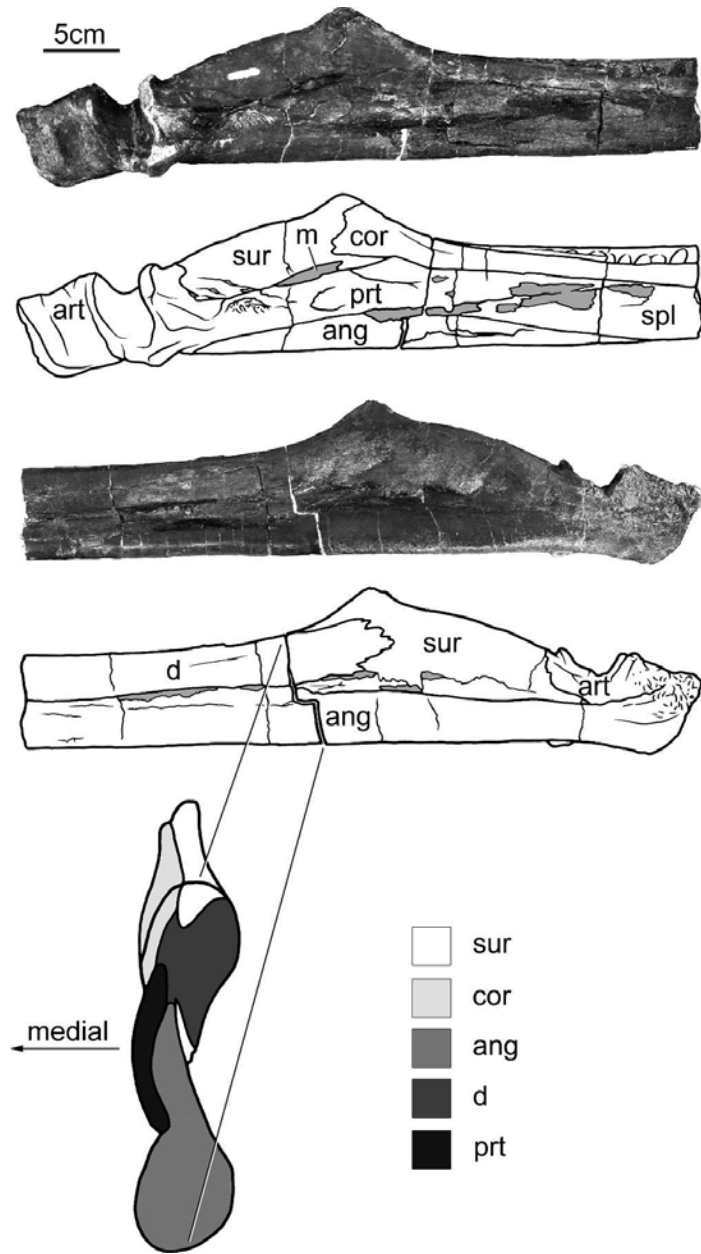


FIGURE 5. Photographs and interpretation of posterior fragments of left mandibular ramus of *Dolichorhynchops bonneri*, new combination, KUVVP 40001. Top photograph is lingual view, bottom photograph is lateral view. At bottom is a schematic interpretation of the cross section of the mandibular ramus at the level of the break between the two fragments, viewed on the edge of the posterior fragment.

Abbreviations: **ang**, angular; **art**, articular; **cor**, coronoid; **d**, dentary; **prt**, prearticular; **spl**, splenial; **sur**, surangular.

The mandibular symphysis is quite long in *Dolichorhynchops bonneri* (Fig. 4), comprising 19 tooth positions, similar to the 18-19 in *Dolichorhynchops osborni* (Carpenter, 1996) but greater than the 14 or 15 in *Eopolycotylus* (Albright et al., 2007a) or the 10-12 in *Trinacromerum* (Carpenter, 1996). The dentary teeth are robust, especially in the anterior of the jaw, and the

symphysis is relatively longer than in *D. osborni* to accommodate them. There are no caniniform teeth. On the ventral surface of the jaw symphysis, the sutures between dentary, splenial, and angular are clearly evident. The angular extends into the symphysis for a long distance, resembling *Trinacromerum* more in this regard than *Dolichorhynchops osborni* or *Eopolycotylus*.

However, unlike the condition in all known polycotylids, the angular reaches forward to the anterior end of the splenial, and meets its neighbor on the midline just anterior to the tip of the splenial. In all other known polycotylids the tip of the angular is posterior to the tip of the splenial. The anterior extent of the angular is an autapomorphy of *Dolichorhynchops bonneri*.

The dorsal surface of the symphysis closely resembles the condition reported in *Eopolycotylus* reported by Albright et al. (2007a), contrary to previously published reconstructions (O'Keefe, 2001; O'Keefe, 2004b). The posterior end of the coronoid forms the antero-medial portion of the coronoid process; the bone then continues anteriorly just medial to the tooth row, forming the medial wall of the groove in which the alveoli are located. The coronoids make contact as they enter the symphysis at the 15th or 16th tooth position, and then extend anteriorly to the seventh tooth position. This long anterior process of the united coronoids is a novel feature and is probably an autapomorphy of the Polycotylidae. In *Edgarosaurus*, the coronoid is certainly long anteriorly but its relationship to the symphysis is unknown due to fusion of sutures (Druckenmiller, 2002). In true pliosaurs, the coronoid reaches the symphysis but does not continue into it (O'Keefe, 2001).

Anterior to the end of the tip of the coronoids is an obvious midline suture that separates two additional splints of bone (Fig. 4). These bones, also noted in *Eopolycotylus* by Albright et al. (2007a) and clearly present in *Dolichorhynchops bonneri* as well, are hypothesized here to be the anterior ends of the splenials. The splenials have a long suture with the inferior edges of the coronoids, traveling forward to the symphysis and covering the Meckelian grooves. The splenials enter the symphysis below the coronoids, and travel a significant way into it, underlying the coronoids within the symphysis. If the splenials continued past the anterior tips of the coronoids and trended dorsally, they would produce the observed morphology. This anterior exposure of the splenials on the dorsal surface of the symphysis is a highly derived condition, and is probably another autapomorphy of the Polycotylidae.

The posterior part of the left jaw ramus is preserved (Fig. 5). Laterally it displays the general plesiosaurian pattern, with the dentary prominently exposed dorsally, and underlain by the angular. A long, straight suture joins the two bones, and the dentary lacks the posterior process below this suture characteristic of true pliosaurs (O'Keefe 2001). Contrary to the condition in *Dolichorhynchops osborni* reported by O'Keefe (2001; 2004b), the surangular forms almost the entire lateral aspect of the coronoid process, just posterior to the end of the dentary. The suture between the dentary and angular continues posteriorly as the suture between the angular and surangular. The surangular overlaps the angular as a thin flange of bone, and most of this flange is broken away, giving the suture a cracked and ragged appearance. This thin, descending lateral flange of the surangular is probably the source of much of the confusion surrounding the polycotylid coronoid process, as it is easily crushed in or broken away. Therefore it sometimes gives the illusion of a separate ossification, and sometimes is gone entirely. Posterior to the coronoid process lies the jaw articulation, which is formed by the articular bone. It is warped inward due to crushing, but is otherwise unremarkable. The angular underlies the articular and

the entire retroarticular process. The latter is a well-developed, robust block of bone behind the jaw articulation, and bears a rugose area on its dorsal surface marking the area of attachment for the m. depressor mandibulae.

On the lingual surface of the left jaw ramus, the coronoid forms the antero-medial region of the coronoid process, extending posteriorly to a point just anterior to the tip of the process. The remainder of coronoid process is formed by the surangular; the surangular continues posteriorly behind this process to suture with the anterior edge of the articular. The inferior edge of the surangular contains a small but well-defined opening for the Meckelian canal. Beneath this foramen, the splint-like prearticular extends from the articular posteriorly to the splenial anteriorly. The suture between the articular and prearticular could not be identified. The oblique suture between the prearticular and splenial is almost parallel to the tooth row. The prearticular forms a distinct shelf that stands away medially from the rest of the jaw; this shelf is similar to that reported in *Dolichorhynchops osborni* by O'Keefe (2004b). The posterior end of this shelf carries a raised, rugose muscle attachment, probably for the m. pterygoideus.

In cross-section, the left jaw ramus reveals a complex pattern of bone contacts. The Meckelian canal is not visible, either due to post-mortem crushing or because it was not open this far anteriorly in life. The angular does seem tightly fused to the splenial, implying that the latter is the case. The sutures in this region are heavily interdigitated. The surangular continues anteriorly as two long processes encompassing the superior and inferior margins of the dentary. The inferior, split-like process of the surangular is extremely thin, both where it protrudes from beneath the dentary, and posterior to the posterior tip of the dentary. The inferior margin of the surangular is therefore extremely thin and delicate, and fractures of this margin make it difficult to interpret this region. The angular extends far dorsally, sending a narrow flange superiorly between the inferior process of the surangular laterally and the splenial medially. Three bones therefore contact the inferior edge of the dentary: the splenial, the angular, and the surangular. The robust superior process of the surangular resides in a deep notch in the dorsal surface of the dentary. Medially to this notch, the coronoid contacts the medial faces of the surangular, dentary, and splenial, being the most lingual of these bones.

Referred Material

The referred Wallace Ranch material is also relevant here given that these specimens are from the same formation and geographic area as the holotype and paratype of *Dolichorhynchops bonneri*, and are smaller than the holotype and paratype. They therefore may illuminate the extent of ontogenetic variation in diagnostic characters. The adult skull is about 2/3 the size of the *D. bonneri* paratype skull (approximately 65 cm). An exact measurement of the length of the poorly ossified, juvenile skull is not possible, but it is certainly shorter than 30 cm. The two referred Wallace Ranch specimens demonstrate that variation of most taxonomically relevant characters is not ontogenetic in character.

The adult skull (UNSM 50133) is crushed dorso-ventrally and not as well preserved or prepared as the *D. bonneri* material. Currently the skull is in several large pieces and many small ones. The jaws are preserved in a closed position and this makes tooth counts difficult, although

the premaxillary tooth count is certainly five, and the maxillary count is about 27. The mandibular and associated symphyseal counts are unknown.

Only the medial rims of the orbits are preserved undamaged, but the anterior roots of the supraorbital processes are clearly apparent, especially on the right side. These bones appear to be extensions of the frontal and not novel ossifications in this specimen, although cracks prevent certainty. The remainder of the skull roof is poorly preserved except on the midline, and only the major sutures are easily identified, such as the midline suture and those between the parietals and premaxillary processes. However, there is certainly a small pineal foramen. This structure is slit-like rather than round, and is surrounded by a thin ridge of bone. The pineal foramen is in the exact location and of the same morphology as that in the MCZ specimen of *D. osborni* illustrated by O'Keefe (2004b), and the retention of this feature appears to be an autapomorphy of *D. osborni*. The premaxillary and maxillary teeth are narrow and high-crowned, and much more gracile than those of *D. bonneri*, and the snout is relatively shorter even though the maxillary tooth count is similar.

The location of the internal nares cannot be determined with certainty, although the anterior interpterygoid vacuity does reach far anteriorly (i.e. anterior to the anterior margin of the orbit). This implies that the anterior interpterygoid vacuity reaches beyond the level of the internal nares, as in *D. osborni* but not *D. bonneri*. Laterally, the posterior pterygoid plates are curved and broad rather than long and narrow, and there is no pterygoid process for the ectopterygoid; in both of these features the skull resembles *D. osborni*, not *D. bonneri*. The anterior process of the parasphenoid possesses a well-developed anterior process projecting into the posterior part of the anterior interpterygoid vacuity. This is another feature diagnostic for *D. osborni*, as is the anterior extent of the angulars into the ventral surface of the mandibular symphysis. The angulars do not approach the end of the paired splenials, or reach past them anteriorly to meet on the midline. In summary, the adult Wallace Ranch skull shares many features with *D. osborni* to the exclusion of the *D. bonneri* material, and is referred to the former species. A differential diagnosis for each of the two currently valid species of *Dolichorhynchops* is given in the SYSTEMATIC PALEONTOLOGY section of this paper.

The Wallace Ranch juvenile skeleton (UNSM 55810) is an extremely juvenile polycotyloid plesiosaur comprising a fragmentary skull and most appendicular elements. Although the pectoral girdle elements are very poorly ossified, the propodials are surprisingly well-ossified and relatively large. The premaxillae are almost complete, missing only the end of the posterior process. Other cranial material includes the body of the left maxilla, the dorsal process of the left squamosal in articulation with most of the parietal crest, and a large fragment of palate and basicranium comprising both pterygoids, right ectopterygoid, para- and basisphenoid (although no basioccipital), and fragments of the left quadrate. Portions of the left palatine and maxilla are also preserved. Almost the entire left hemimandible is preserved, although much of the lingual surface is broken away. The posterior half of the right hemimandible is also preserved, although not as well as the left. There are also many unidentifiable bone fragments and isolated tooth crowns.

The juvenile skull is interesting in many respects and deserves close study; this description is limited to diagnostic characters. The lack of an obvious mandibular symphysis probably

indicates that the contact between the hemimandibles was still cartilaginous at death. The teeth have relatively low and robust crowns, more comparable to those of *D. bonneri* than *D. osborni*. There are only five teeth preserved in the anterior portion of the left hemimandible, and three others are preserved on the maxillary fragment. Tooth counts are not possible given the fragmentary nature of the material. The lateral plates of the pterygoids are long and narrow laterally, as in *D. bonneri*. The ectopterygoid is also carried on a distinct process, again as in *D. bonneri*. Fragments of the anterior palate demonstrate that the internal nares were anterior to the end of the pterygoids, once more as in *D. bonneri*. However, the parasphenoid has an anterior process extending into the anterior interpterygoid vacuity, as in *D. osborni*. Unfortunately these are the only diagnostic features in the skeleton; the lack of a preserved mandibular symphysis and tooth counts precludes use of these characters, and the postcranial elements are too poorly ossified to establish definitive character states. However, in three of four traits—tooth morphology, lateral pterygoid plate shape, and ectopterygoid process presence—the juvenile skull resembles *D. bonneri*. This demonstrates that these characters are not ontogenetic in nature. However, the anterior process of the parasphenoid does resemble *D. osborni*, and this may or may not be an ontogenetically variable feature. On balance the juvenile resembles *D. bonneri* and may be referable to that taxon, but given the lack of more diagnostic characters the conservative course of referring the material to Polycotylidae *incertae cedis* is followed here.

Comments on the Postcranium

In general, Adams (1997) figures the postcranium of *D. bonneri* well, obviating the need for a complete postcranial redescription. However, some comments on taxonomically relevant postcranial characters are given here. In the axial skeleton, *D. bonneri* possesses about 20 cervical vertebrae. Adams (1997) counted only 19, while the present author counts 21; given that the transition from cervical to pectoral vertebrae is somewhat arbitrary in plesiosaurs, this discrepancy is understandable given the flattened preservation of the cervical series. The cervical centra are closely similar to those of other polycotylids, being much shorter than broad, and with poorly ossified articular surfaces. The dorsal vertebrae in *D. bonneri* are markedly compressed, a trait the taxon shares with *Polycotylus*, while the chevrons are carried wholly by the anterior centra in the caudal series. This trait is diagnostic for the genus *Dolichorhynchops*.

Regarding the appendicular skeleton, Adams (1997) does misidentify the fore- and hindlimbs, and given the importance of humeral morphology to polycotylid systematics it seems wise to refigure the humerus here (Fig. 6). The humerus is similar to that of other polycotylids, possessing a marked sigmoid curvature, a wide posterior margin with a thin posterior process, and facets for four ossifications on the distal margin (radius, ulna, and two supernumerary ossifications). The humerus of *D. bonneri* differs from the autapomorphic humerus of *Polycotylus* in lacking a constricted midshaft and in being relatively shorter and wider. In both distal limbs, the tongue-and-groove articulations between phalangeal rows noted by Adams is obviously present, and must have made the flipper quite stiff while in motion.

In terms of other appendicular characters, the ilium of the *D. bonneri* has a straight shaft with a blunt proximal end, and both of these characters are diagnostic for the clade *Trinacromerum* (*Dolichorhynchops*). The dorsal process of the scapula is also angled at midshaft, another character diagnostic for the same clade. Lastly, the ischia are longer than the pubes in a sagittal plane; this is a common trait among polycotylids (and among plesiosauromorphs in

general, O’Keefe and Carrano 2005). However the ischia exhibit the same relative proportions as in other polycotylids, and are not elongated as in *Polycotylus*.

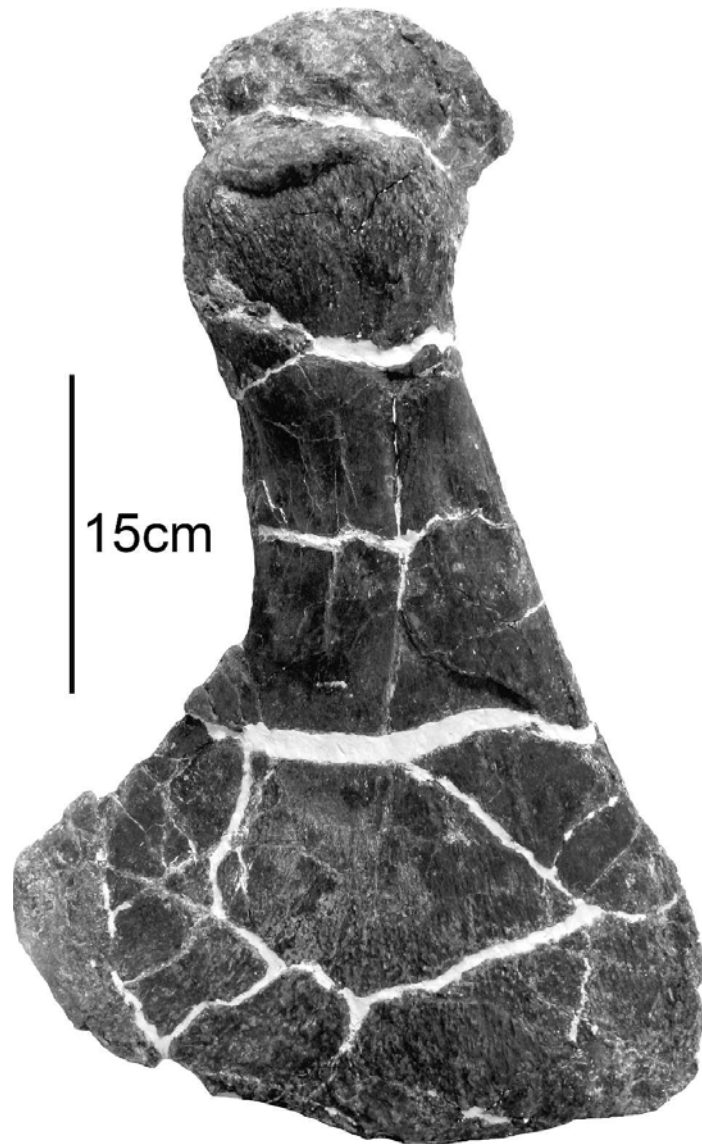


FIGURE 6. Dorsal surface of the right humerus of *D. bonneri*, KUV 40002. This humerus shares features with those of other polycotylids but is not identical to any; the shaft is sigmoid as in *Polycotylus* but is more broad, while the distal end is extremely expanded antero-posteriorly. Four clear facets for radius, ulna, and two supernumerary ossifications are evident.

PHYLOGENETIC ANALYSIS

Given the confusion about the generic identity of “*Trinacromerum*” *bonneri* Adams 1997, a phylogenetic analysis of the Polycotylidae was performed to investigate the relationships of the animal. The matrix used here is an extensively modified version of that published by

Albright et al. (2007a), and differed from that matrix in two major ways. The first was the removal of data originating from KUVV 40001 and 40002 from the scoring for *Polycotylus*; this taxon is now scored only from the historical material plus that referred to the genus in O'Keefe (2004b; for taxonomic history see Carpenter, 1996; Storrs, 1999). Secondly, several new taxa and characters were added to the matrix, described in Appendices 1 and 2. Holotype and referred material of the taxa *Polycotylus*, *Dolichorhynchops osborni*, *Dolichorhynchops bonneri*, *Trinacromerum*, *Tricleidus*, and *Plesiosaurus* were examined personally by the author; the other taxa were scored from the literature.

The cladistic matrix contains 12 taxa scored for 44 characters. *Plesiosaurus* and *Tricleidus* comprised the outgroup taxa, and constrained to be paraphyletic with respect to the ingroup, although results are identical without this constraint. Parsimony analysis was performed in PAUP* 4.0 (Swofford, 2001). Nine of the characters were parsimony-uninformative, leaving 35 for the determination of relationships. The branch-and-bound algorithm was used, and the shortest trees found had a length of 80 steps. The search returned 20 most-parsimonious trees (MPTs); the strict consensus of these is reported as Figure 7A. The Consistency Index of these trees was 0.74, the Rescaled Consistency Index was 0.48, and the Retention Index was 0.66. As might be expected given the number of trees, the strict consensus tree has little resolution, giving only three secure nodes: that at the base of Polycotylidae, the sister-group relationship between *Eopolycotylus* and *Polycotylus*, and a sister-group relationship between *Manemergus* and *Thililua*. To further investigate the phylogenetic structure in the data matrix, a reduced analysis was also run. The unnamed taxon UMUT MV 19965 has 74% missing data, and inspection of the unpruned MPTs showed that this OTU was acting as a wildcard taxon. The matrix was therefore rerun with this taxon excluded, and the search returned five MPTs of length 79 (RCI 0.50, RI 0.67), whose strict consensus is reported in Figure 7B. This result is more stable, but differs significantly from that reported by Albright et al. (2007a). A grouping of *Trinacromerum*, *Dolichorhynchops bonneri*, and *Dolichorhynchops osborni* is reasonably well-supported, with *Dolichorhynchops bonneri* as the sister taxon of *Dolichorhynchops osborni*. *Eopolycotylus* and *Polycotylus* again form a clade, as do *Thililua* and *Manemergus*. These groupings are all parts of a polytomy also containing *Palmulasaurus* and then *Edgarosaurus* within a monophyletic Polycotylidae.

Lastly, Figure 7C presents the results of a matrix with another taxon, *Palmulasaurus*, also deleted. This taxon contains 39% missing data, and its relationships are unstable in both of the above analyses. This final analysis returns 3 MPTs with a tree length of 76, an RCI of 0.50, and an RI of 0.67. The strict consensus of these trees does not differ from the above except for the omission of *Palmulasaurus*; *Edgarosaurus* and a clade of the Moroccan taxa still reside in a polytomy with a clade comprised of the other polycotylids. This result is significant, however, because it demonstrates our poor understanding of the position of the Moroccan taxa. They are part of the polycotylid ingroup in the current analysis, but neither these taxa nor *Edgarosaurus* are known from complete material, and the critical palate region in *Edgarosaurus* is crushed and open to interpretation. The Moroccan taxa are also poorly known, and my attempts to score them from the literature are of course suspect. However, both taxa are superficially similar to a new taxon of leptocleidid under description by Druckenmiller and Russell (2006). Confident assignment of the Moroccan animals to the Polycotylidae requires more complete material and a more detailed description, as well as a cladistic analysis of wider scope.

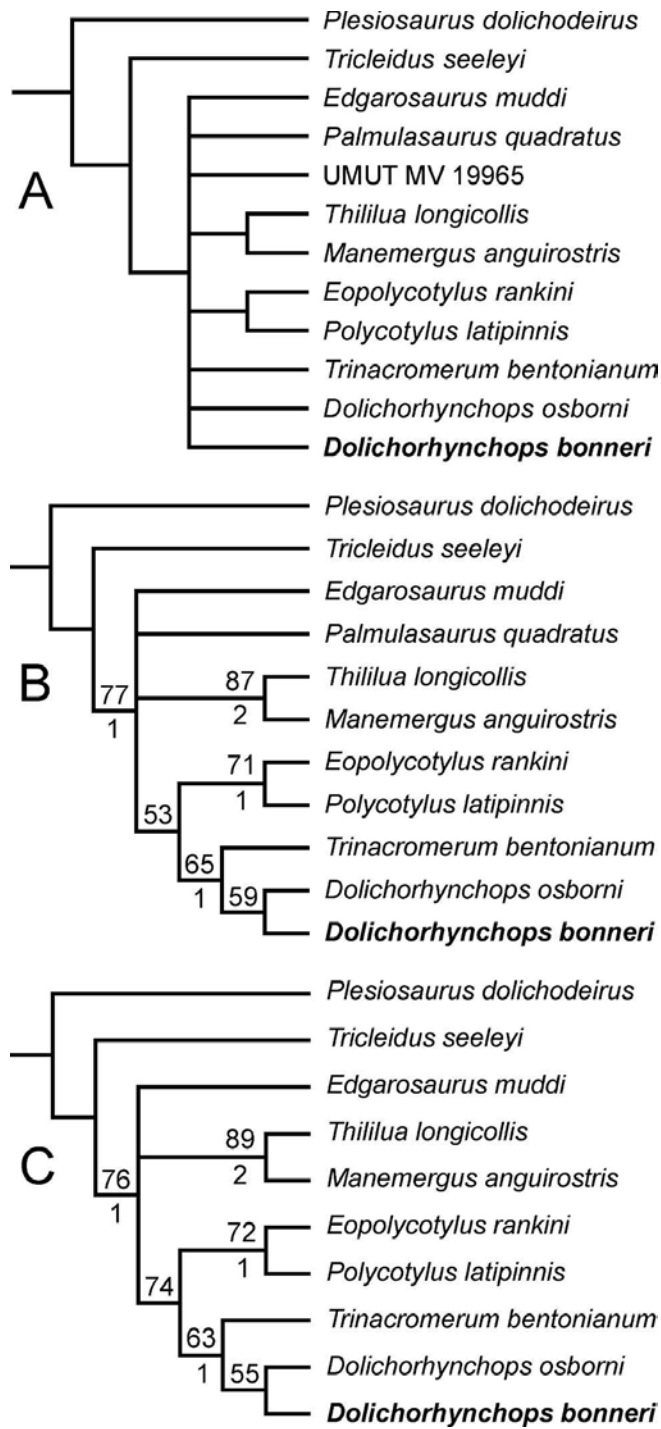


FIGURE 7. Summary of cladistic analyses of the Polycotylidae described in the text. **A**, the strict consensus of 20 MPTs resulting from the original analysis is tree A. **B**, tree B is the strict consensus of five MPTs resulting from an analysis with UMUT MV 19965 omitted. **C**, tree C is the strict consensus of three trees resulting from an analysis with both UMUT MV 19965 and *Palmulasaurus* removed. Numbers above each node are bootstrap values (1000 replicates); numbers below are decay indices. For tree statistics see text.

DISCUSSION

Two taxonomic issues arise from the phylogenetic analysis performed above. The first concerns the taxonomic validity of “*Trinacromerum bonneri* Adams 1997, while the second is a larger question concerning the recently-erected subfamilies of the Polycotylidae. *Dolichorhynchops bonneri* resides in a sistertaxon relationship with *Dolichorhynchops osborni*, which is a bit surprising given the large size of *Dolichorhynchops bonneri*, and its robust teeth. However, closer inspection shows that *Dolichorhynchops bonneri* shares several synapo-morphies with *Dolichorhynchops osborni*, including the derived condition of the chevron facets, the high, arched sagittal crest, the vertical suspensorium, and the bent dorsal scapular process. These characters link *Dolichorhynchops bonneri* with *Dolichorhynchops osborni* to the exclusion of *Trinacromerum*, even though *Trinacromerum* and *Dolichorhynchops osborni* are superficially more similar in body size and some details of the palate. The clado-gram above therefore supports the contention of Carpenter (1996) that the KUVF material is referable to *Dolichorhynchops*, contra Adams (1997). The contention of Albright et al. (2007a) that *Dolichorhynchops bonneri* is referable to *Polycotylus latippinus*—is not supported here. To investigate this possibility, the cladistic analysis was run again with *Dolichorhynchops bonneri* constrained to form a clade with *Polycotylus* and *Eopolycotylus*. Trees resulting from this analysis were three steps longer than the MPTs in both the full and pruned (minus UMUT MV 19965 and *Palmulasaurus*) matrices. This relationship is therefore unlikely, and the superficial resemblance in body size and tooth robusticity between *Dolichorhynchops bonneri* and *Polycotylus* is yet another example of morphotype convergence in plesiosaurs (see O’Keefe and Carrano, 2005 for a review of this common phenomenon).

Trinacromerum and *Dolichorhynchops osborni* have always been viewed as very similar animals; Williston (1903, 1906, 1908) was content to treat all concerned species as a single genus. However, Carpenter (1996) thought the species involved belonged to separate genera, a conclusion accepted (2001) and then supported by O’Keefe (2004a,b). Other recent authors have generally accepted this conclusion (i.e. Albright et al., 2007a). The splitting of the sister-taxon relationship between these two taxa by *Dolichorhynchops bonneri* also supports this view, as all three taxa would have to be congeneric if *Dolichorhynchops osborni* was equivalent to *Trinacromerum*. This idea—that all three taxa above might be congeneric—is worthy of consideration. *Dolichorhynchops bonneri* exhibits many character states thought to be autapomorphic for other polycotylid taxa. Its large, robust teeth, large body size, and compressed dorsal vertebrae link it to *Polycotylus*, although it lacks the autapomorphic humerus morphology of that taxon. Cranially, the suspensorium and sagittal crest are like *Dolichorhynchops osborni*; however, the palate is more reminiscent of *Trinacromerum*, possessing straight-edged lateral pterygoid plates with a distinct ectopterygoid process, and lacking an anterior parasphenoid process. Given this mosaic of character states, one might postulate that the characters traditionally used in polycotylid taxonomy are highly labile and variable among individuals, or at least species, or are obscured by ontogenetic variation. This could be used as a justification for combining all three taxa into the genus *Trinacromerum* Cragin 1888.

This course is not taken here for two reasons. The first is that at least three good autapomorphies exists for *Dolichorhynchops bonneri*: the angulars meet on the ventral midline of the mandibular symphysis; the dentition is significantly more robust, and carried in a long snout; and the dorsal vertebrae are strongly compressed. The first of these characters is otherwise unknown

in polycotyliids crownward of *Edgarosaurus*, while the later two are independently-evolved features in *Polycotylus* only. As for the other characters, their combination in a single taxon is unprecedented. *Dolichorhynchops osborni*, for example, is known from several complete skeletons with good skulls (Carpenter, 1996; O'Keefe, 2004b), all of which are homogenous with respect to diagnostic characters despite significant differences in size (see above). The characters that diagnose this taxon are stable; the same holds true for *Trinacromerum*, and for *Polycotylus* for the characters that are known. Given that existing polycotyliid taxonomy seems to be founded on stable characters, their novel combination in *Dolichorhynchops bonneri* should be autapomorphic, justifying the new combination. One might also argue that erection of a new genus for the Kansas material is also warranted. This course is not followed due to the general similarity of the taxa involved and the rampant homoplasy in diagnostic characters. This is especially true of body size, which appears to be unreliable as a taxonomic character within polycotyliids.

The second taxonomic issue raised by the phylogenetic analysis is the failure to recover the two polycotyliid subfamilies erected by Albright et al. (2007a), the Palmulasaurinae and the Polycotyliinae. This failure results from the large amount of missing data for UMUT MV 19965 and *Palmulasaurus*. Both taxa are so poorly known that many different positions are equally parsimonious. UMUT MV 19965 fails to cluster only with *Palmulasaurus*, as well as destroying the resolution of the tree in general. *Palmulasaurus* is a somewhat better known, but still lacks most diagnostic characters of ingroup polycotyliids. As these two taxa are the only ones presently comprising the Palmulasaurinae, the present analysis does not support the existence of the subfamily, reflecting the poor state of current knowledge regarding it. More complete description of UMUT MV 19965 and *Palmulasaurus* will hopefully clarify this area of the cladogram. The subfamily was originally founded on at least one good character (Albright et al., 2007a), so the conservative course is to leave the subfamilial taxonomy unchanged at this time.

In summary, detailed examination of the cranium of "*Trinacromerum*" *bonneri*, and its inclusion in a cladistic analysis of the Polycotyliidae using cranial and postcranial characters, support Carpenter's (1996) original interpretation of an affinity with *Dolichorhynchops osborni*. Possession of an autapomorphic mandible and a novel combination of several other characters justifies the erection of a new combination, *Dolichorhynchops bonneri*. The new taxon shares significant characters with *Dolichorhynchops osborni*, *Trinacromerum*, and *Polycotylus*. The status of the subfamily Palmulasaurinae could not be determined due to missing data. Lastly, the anatomy of *Dolichorhynchops bonneri* is another example of the common pattern of convergence in plesiosaur body morphology.

ACKNOWLEDGMENTS

Special thanks are due to L. Martin for collection of the material described in this paper, and to D. Miao and L. Martin for specimen access and hospitality in Kansas. Reviews by A. Smith, T. Sato, R. Holmes, and an anonymous reviewer made substantive improvements to the manuscript. This study was supported by research funds from the College of Science, Marshall University.

LITERATURE CITED

- Adams, D. A. 1997. *Trinacromerum bonneri*, new species, last and fastest plesiosaur of the Western Interior Seaway. *Texas Journal of Science* 49(3):179–198.
- Albright, B. A., D. D. Gillette, and A. Titus. 2007a. Plesiosaurs from the Upper Cretaceous (Cenomanian-Turonian) Tropic Shale of southern Utah, part 2: Polycotylidae. *Journal of Vertebrate Paleontology* 27(1):41–58.
- Albright, B. A., D. D. Gillette, and A. Titus. 2007b. Plesiosaurs from the Upper Cretaceous (Cenomanian-Turonian) Tropic Shale of southern Utah, part 2: Polycotylidae; replacement names for the preoccupied genus *Palmula* and the subfamily Palmulinae. *Journal of Vertebrate Paleontology* 27(4): 1051.
- Bardet, N., X. P. Suberbiola, and N.-E. Jalil. 2003. A new polycotylid plesiosaur from the Late Cretaceous (Turonian) of Morocco. *Comptes rendus Palévol* 2:307–315.
- Buchy, M.-C., F. Metayer, and E. Frey. 2005. Osteology of *Manemergus anguirostris* n. gen. et sp., a new plesiosaur (Reptilia, Sauropterygia) from the Upper Cretaceous of Morocco. *Palaeontographica Abteilung A-Palaeozoologie-Stratigraphie* 272(5–6):97–120.
- Carpenter, K. 1996. A review of short-necked plesiosaurs from the Cretaceous of the western interior, North America. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* 201(2):259–287.
- Carpenter, K. 1997. Comparative cranial anatomy of two American Cretaceous plesiosaurs; pp. 191–216 in J. M. Callaway and E. L. Nicholls (eds.), *Ancient Marine Reptiles*. Academic Press, San Diego.
- Cope, E. D. 1869. Synopsis of the extinct Batrachia, Reptilia and Aves of North America. *Transactions of the American Philosophical Society (new series)* 14:1–252.
- Cragin, F. 1888. Preliminary description of a new or little known saurian from the Benton of Kansas. *American Geologist* 2:404–407.
- de Blainville, H. D. 1835. Description de quelques espèces de reptiles de la Californie, precede de l'analyse d'un système general d'Erpetologie et d'Amphibiologie. *Nouvelles Annales du Muséum (National) d'History Naturelle*, Paris 4:233–296.
- Druckenmiller, P. S. 2002. Osteology of a new plesiosaur from the lower Cretaceous (Albian) Thermopolis Shale of Montana. *Journal of Vertebrate Paleontology* 22(1):29–42.
- Druckenmiller, P., and A. Russell. 2006. A phylogeny of the Plesiosauria (Sauropterygia), with emphasis on the systematic status of *Leptocleidus*, Andrews 1922. *Journal of Vertebrate Paleontology* 26(3) Supplement:57A.
- O'Keefe, F. R. 2001. A cladistic analysis and taxonomic revision of the Plesiosauria (Reptilia: Sauropterygia). *Acta Zoologica Fennica* 213: 1–63.
- O'Keefe, F. R. 2004a. Preliminary description and phylogenetic position of a new genus and species of plesiosaur (Reptilia: Sauropterygia) from the Toarcian of Holzmaden, Germany. *Journal of Paleontology* 78(5):973–988.
- O'Keefe, F. R. 2004b. Cranial anatomy of the polycotylid plesiosaurs, including new material of *Polycotylus latipinnis*, Cope, from Alabama. *Journal of Vertebrate Paleontology* 24(2):326–340.
- O'Keefe, F. R. and M. T. Carrano. 2005. Correlated trends in the evolution of the plesiosaur locomotor system. *Paleobiology* 31(4):656–675.
- O'Keefe, F. R. and W. Wahl. 2003. Preliminary report on the osteology and relationships of a new aberrant cryptocleidoid plesiosaur from the Sundance Formation, Wyoming.

- Paludicola 4(2):48–68.
- Owen, R. 1860. On the orders of fossil and Recent Reptilia, and their distribution through time. Report of the British Association for the Advancement of Science 29:153–166.
- Sato, T. A new polycotyloid plesiosaur (Reptilia, Sauropterygia) from the Upper Cretaceous Bearpaw Formation in Saskatchewan, Canada. Journal of Paleontology 79(5):969–980.
- Sato, T., and G. W. Storrs. 2000. An early polycotyloid plesiosaur (Reptilia: Sauropterygia) from the Cretaceous of Hokkaido, Japan. Journal of Paleontology 74:907–914.
- Storrs, G. W. 1981. A review of occurrences of the Plesiosauria (Reptilia: Sauropterygia) in Texas, with description of new material. Master's thesis, University of Texas, Austin.
- Storrs, G. W. 1999. An examination of Plesiosauria (Diapsida: Sauropterygia) from the Niobrara Chalk (Upper Cretaceous) of central North America. University of Kansas paleontological Contributions (New Series) 11:1–15.
- Swofford, D. L. 2001. PAUP*. Phylogenetic analysis using parsimony (*and other methods), v. 4. Sinauer Associates, Inc., Sunderland, Massachusetts.
- Welles, S. P. 1943. Elasmosaurid plesiosaurs with description of new material from California and Colorado. Memoirs of the University of California 13:125–254.
- Williston, S. W. 1903. North American plesiosaurs, Part 1. Field Columbian Museum Publication (Geology) 73(2):1–77.
- Williston, S. W. 1906. North American plesiosaurs: *Elasmosaurus*, *Cimoliasaurus*, and *Polycotylus*. American Journal of Science, Fourth Series 21(123):221–236.
- Williston, S. W. 1908. North American plesiosaurs: *Trinacromerum*. Journal of Geology 16(8):715–736.

APPENDIX 1. List of characters and states used in the cladistic analysis reported in this article.

Character	States	Citation	Notes
1 Premaxillary Teeth	0 5 or less 1 6 or more	Albright et al., 2007; previous authors	
2 Maxillary Teeth	0 20 or less 1 21-30 2 30 or more	ibid.	
3 Caniniform Teeth	0 absent 1 present	ibid.	Refers to large teeth on anterior maxilla; autapomorphy of <i>Edgarosaurus</i> in this matrix.
4 Dentary Teeth	0 20 or less 1 21-25 2 26-30 3 30 or more	ibid.	
5 Tooth Form	0 gracile 1 robust	ibid.	
6 Pineal Foramen	0 present 1 absent	ibid.	
7 Elongate Rostrum	0 absent 1 premax only 2 both max and premax	ibid.	State 1 is an autapomorphy of <i>Edgarosaurus</i> in this matrix.
8 Mandibular Symphysis	0 short 1 long	ibid.	
9 Splenial enters Symphysis	0 does not 1 does, but not angular 2 both do	ibid.	
10 Coronoid enters Symphysis	0 does not 1 does	ibid.	
11 Neck Length	0 primitive 1 long 2 intermediate 3 short	ibid.	
12 Cervical Vertebrae Proportion	0 length greater or equal to height 1 length less than height	ibid.	
13 Cervical Vertebrae Number	0 28-32 1 more than 32 2 less than 28	ibid.	
14 Dorsal Vertebrae Morphology	0 lateral walls constricted 1 lateral walls not constricted	ibid.	Autapomorphy of <i>Trinacromerum</i> .
15 Dorsal Vertebrae Compression	0 longer than wide 1 shorter than wide 2 much shorter than wide	ibid.	
16 Caudal Facets	0 anterior and posterior centrum face 1 mainly posterior 2 on ventral surface	ibid.	
17 Humerus Shaft	0 narrow 1 broad	ibid.	
18 Humerus Sigmoid	0 not 1 weakly 2 strongly	ibid.	
19 Supernumerary Facets, Humerus	0 absent 1 present	ibid.	
20 Supernumerary Ossifications	0 epipodial row 1 pro- and epipodial rows	ibid.	
21 Epipodial Dimensions	0 longer than wide 1 shorter than wide 2 equal	ibid.	
22 Interlocking Phalanges	0 absent 1 present	ibid.	
23 Antebrachial Foramen	0 present 1 absent	ibid.	
24 Interclavicle	0 present 1 absent	ibid.	
25 Anterior Coracoid Process	0 absent/short 1 intermediate	ibid.	Ordered

26	Posterior Extension, Coracoids	2 elongate 0 absent 1 present	ibid.	
27	Medial Coracoid Foramina	0 absent 1 present	ibid.	
28	Ilium Proximal End	0 blunt 1 tapered	ibid.	
29	Ilium Shaft	0 straight 1 curved	ibid.	
30	Relative Pubis/Ishium Length	0 pubis longer 1 pubis shorter	ibid.	
31	Ischium Length vs. Width	0 short 1 long 2 very long	ibid.	
32	Sagittal Crest Height	0 low and straight 1 high and arched	novel	Refers to a high, arched crest as shown my <i>Dolichorhynchops</i> .
33	Width Lateral Pterygoids	0 narrow 1 wide 2 wide with curved margin	novel	Ordered; the lateral pterygoid plates are narrow in <i>Tricleidus</i> , but are much wider in polycotyliids. All have straight margins save <i>Dolichorhynchops</i> .
34	Palpebral Process	0 absent 1 present	Modified from Carpenter, 1996	Refers to the rugose swelling of bone in the postero-dorsal corner of the orbit.
35	AIPV/Internal Nares	0 does not reach 1 reaches past	novel	Refers to the anterior extent of the anterior interpterygoid vacuity; autapomorphy of <i>Dolichorhynchops</i> .
36	Body Size	0 small 1 large	O'Keefe, 2001	<i>Polycotylus</i> , <i>Eopolycotylus</i> , and <i>D. bonneri</i> are significantly larger than other polycotyliids.
37	Scapula Dorsal Process	0 not bent 1 distinct bend	novel	Taxa with this character have a distinct, sharp bend of the dorsal scapular process near the body of the scapula.
38	Cervical margin	0 not poorly ossified 1 poorly ossified with raised centrum face/marked groove around articular surface	O'Keefe and Wahl, 2003b	
39	Curved dentary	0 not curved 1 curved	novel	Both Moroccan taxa appear to have a pronounced dorso-ventral bend in the anterior mandible.
40	Deep temporal bar	0 relatively narrow 1 deep	novel	Noted in <i>Manemergus</i> in Buchy et al., 2005; I also interpret this feature as present but crushed in <i>Thililua</i> .
41	Frontal foramina	0 absent 1 present	novel	Shared by <i>Manemergus</i> and <i>Thililua</i> .
42	Swollen premaxillary process	0 absent 1 present	novel	Shared by <i>Manemergus</i> and <i>Thililua</i> .
43	Parasphenoid morphology	0 flat 1 keeled	modified from O'Keefe, 2001	
44	Posterior pterygoid morphology	0 do not join behind pipv 1 broadly overlap behind pipv 2 join by narrow, novel process	modified from O'Keefe, 2001	

Most of these characters are identical in states and coding to those in Albright et al. 2007, who cite the history of each character; differences and novel characters as noted.

APPENDIX 2. Character-taxon matrix used in the cladistic analyses reported in this article.

Plesiosaurus dolichodeirus 0101000000 0010000000 0001000000 00?0000000 0000

Tricleidus seeleyi 0?0000000? 00000?1010 1?001100?? ?000?00100 0012

Edgarosaurus muddy 1113101021 2120??0?1? 110??????? ?01000?100 0001

Palmulasaurus quadratus 0?0?0?21?1 ?1?0120011 210??0?011 1????0?0? ????

UMUT MV 19965 ?????????? ?1?0?10?11 21??2?1??1 ?????????? ????

Thililua longicollis 01020?212? 21001????? ?????????? ?0?0?0?011 11??

Eopolycotylus rankini 0?0?1?2111 ?1?01?1111 1110201111 1????1010? ????

Polycotylus latipinnis ???1????? 2120200211 1110211111 200??101?? ??12

Dolichorhynchops osborni 1102012111 3120110101 1110201001 1121101100 0012

Trinacromerum bentonianum 0203012121 3121100111 1110201001 1011001100 0012

Dolichorhynchops bonneri 0103112121 3120210211 1110201001 1111011100 0012

Manemergus anguirostris 000000212? 20201????0 ???0000??1 0000?0?011 110?