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OSTEOLOGY OF THE CRYPTOCLEIDOID PLESIOSAUR TATENECTES LARAMIENSIS, WITH COMMENTS ON THE TAXONOMIC STATUS OF THE CIMOLIASAURIDAE

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ABSTRACT—Recent field work in the Bighorn Basin, Wyoming has recovered significant new material of the plesiosaur Tatenectes laramiensis. The majority of cryptocleidoid plesiosaurs have been recovered from Middle and Upper Jurassic units (Oxford and Kimmeridge Clays, respectively) in the United Kingdom, but Tatenectes laramiensis is one of at least two cryptocleidoids known from the Upper Sundance Member of the Sundance Formation (Oxfordian) of North America. Although poorly known, they bear directly on both the phylogeny and biogeography of the cryptocleidoid plesiosaurs. Here we describe new fossil material of Tatenectes, and reevaluate the phylogenetic position of this genus based on all known material. New material includes a partial skeleton comprising cranial elements, axial column, and a partial pectoral girdle, as well as an isolated humerus and vertebrae. The pectoral girdle closely resembles that of Muraenosaurus beloclis from the Oxford Clay, but is even shorter anteriorly. The cervical vertebrae are more compressed anteroposteriorly than in other Jurassic cryptocleidoids. The humerus is less derived, resembling that of Tricleidus seeleyi. Two most parsimonious trees were obtained, and the consensus tree solidifies the phylogenetic position of Tatenectes as being most closely related to the Oxford Clay taxon Kimmerosaurus.

INTRODUCTION

Plesiosaurs of the late Middle and early Upper Jurassic are relatively well known, as they occur commonly in the Oxford Clay (Callovian), one of the classic marine Lagerstätten of the Western Tethys. The marine reptiles of this deposit were treated extensively by Andrews (1910, 1913) in his classic two-part monograph, and cryptocleidoid plesiosaurs featured prominently, including well-known taxa such as Cryptoclidus and Muraenosaurus (Andrews, 1910). However, cryptocleidoid plesiosaurs of comparable age are poorly known outside the Western Tethys. Yet marine sediments of this age are actually common in the western United States, and one of these formations—the Sundance Formation—is quite fossiliferous. Marine reptiles were first described from the Sundance Formation of Wyoming by O. C. Marsh at the end of the 19th century (Marsh, 1891, 1893, 1895). The most common vertebrate fossils in the Sundance are ichthyosaurs ("Baptanodon," a junior synonym of Opthalmosaurus; Gilmore, 1906), but plesiosaur fossils representing at least two genera also occur.

The osteology and phylogenetic position of Sundance plesiosaurs are significant for two reasons. Both plesiosaurs known from the Sundance are cryptocleidoids (O'Keefe and Wahl, 2003a), and because the outlet of the Sundance Seaway was to the west, the fauna was presumeably isolated from the Oxford Clay fauna. As a consequence, the Sundance cryptocleidoids may illuminate the degree and character of cryptocleidoid morphological difference on a broad geographic scale. Additionally, O'Keefe (2001, 2002, 2004) postulated that the pliosauromorph Polycotylidae are nested within the Cryptocleidoidea. The Polycotylidae are a Cretaceous clade, thereby making the cryptocleidoids of the Late Jurassic especially significant, as the phylogenetic history of these taxa may shed light on the link between polycotylids and cryptocleidoids (O'Keefe and Wahl, 2003b). Lastly, the recent discovery of Opallionec demonstrates that the cimoliasaurid cryptocleidoids have a temporally deep origination, lending credence to the finding that the progenitors of this group are Jurassic (O'Keefe andWahl, 2003b). Here we report on significant new material of one genus, Tatenectes laramiensis Knight 1900, and investigate its impact on cryptocleidoid phylogeny.

Institutional Abbreviations—USNM, Smithsonian Institution, Washington, D.C.; UW, University of Wyoming Museum of Geology, Laramie, Wyoming.

GEOLOGICAL SETTING

The Sundance Seaway was a shallow, epicontinental marine incursion that covered most of Wyoming and parts of Montana, South Dakota, and Colorado during the Jurassic (Kvale et al., 2001). Its oceanic inlet was to the west, and was eventually closed off by uplift and sedimentation from the rising Rocky Mountains. The principal sediment source in the seaway was this uplifting tectonic high, and depositional composition and grain size were determined by the distance from this source: farthest west in the basin, a sand facies with wood fragments and large chert pebbles was deposited, indicating a short transit distance and a nearshore depositional environment. This facies transitions to a mud facies and then a carbonate-clay facies as one moves east. With increased erosion from the tectonic high, these facies shifted to the east over time. The last facies of the basin sequence is an extremely heterogeneous (both sequentially and laterally) group of bar, tidal, and possibly fluvial sandstones formed as deposition rates increased and inundation was insufficient to maintain the seaway, leading to the final regression (Brenner and Davies, 1974) and subsequent deposition of the terrestrial Morrison Formation.

The marine sediments of Jurassic age from southeastern Wyoming were originally named the "Shirley Stage" by Knight in 1900. The name Sundance Formation was in use by 1919, when Reeside published on the ammonites found in these sediments. The Sundance Formation was divided into several members based on ammonite biostratigraphy, erosional features, andtes (Kear, 2006) from the Aptian-Albian of Australia regional correlations (Pipiringos, 1957). The most extensive study was conducted by Imlay (1947), who split the Laramie Basin strata first into five and later into seven members; in the less-studied Bighorn Basin, the Sundance remained divided into Upper and Lower members (Wright, 1973). The most recent studies on the

Sundance Formation were conducted by Kvale et al. (2001) during their investigation of dinosaur megatracksites in the Bighorn Basin. These authors did not use the member names of Imlay (1947) as they do not have clear lateral equivalents between the basins, but rather referred to the "basal," "middle," or "upper" divisions of the Lower or Upper members of the Sundance Formation; this conservative terminology is followed here.

The Upper Member of the Sundance Formation (Kvale et al., 2001) is a thick, laterally heterogenous, glauconitic shale punctuated by irregular sandstone beds and oyster shoals, and is dated reliably to the Early Oxfordian (Pipiringos, 1957). The specimens reported on here were found in sediments from the top of the formation, the 'Redwater Shale' member of Imlay (1947). The 'Redwater Shale' is highly fossiliferous, containing abundant invertebrates and occasional vertebrate fossils. Vertebrate fossils occurring in these strata are usually isolated elements, although articulated ichthyosaur remains are locally common, often in limestone concretions. Plesiosaur fossils are always relatively rare, and articulated plesiosaur material is very rare. A stratigraphic section has not been taken in the vicinity where this specimen was found due to the poor quality of the outcrop in the principle field area; sections derived from other areas are not applicable due to the extreme lateral and sequential heterogeneity at the top of the Upper Sundance member.

TAXONOMIC BACKGROUND

The plesiosaur taxon reported on here, now known as Tatenectes laramiensis, was first described by Knight (1900). Knight's original name of the species was 'Cimoliosaurus' laramiensis, and this name was revised to 'Tricleidus?' laramiensis by Mehl (1912). Knight's holotype has since been lost, so a neotype was designated by O'Keefe and Wahl (2003b). The species also lacked a valid genus name, as the material is clearly not referable to Tricleidus; hence the genus Tatenectes was erected, the correct appellation now being Tatenectes laramiensis Knight 1900 (O'Keefe and Wahl, 2003b). The single neotype specimen, numbered UW 15943 and UW 24801 (see O'Keefe and Wahl, 2003b for discussion), contains many of the same elements of the holotype, based on Knight's (1900) description of that specimen. Both the holotype and the neotype contain axial skeleton and forelimb elements. The neotype also contains ribs and pectoral girdle elements, and another specimen, UW 24215, described and referred to the taxon by O'Keefe and Wahl (2003b), adds cranial material to the record of Tatenectes laramiensis.

MATERIALS

Much of the material presented here, including axial elements and the pectoral girdle, is part of UW 24215, but was not prepared in time for the previous publication. The new material of Tatenectes laramiensis described here includes a tooth, a right squamosal, posterior cervical vertebrae, a pectoral girdle, and a phalanx from specimen UW 24215. Also herein described are an anterior cervical vertebra collected as float with several others, and an isolated right humerus.

SYSTEMATIC PALEONTOLOGY

SAUROPTERYGIA Owen, 1860
PLESIOSAURIA de Blainville, 1835
PLESIOSAUROIDEA Welles, 1943
Family ELASMOSAURIDAE Cope, 1869

Cimoliasauridae DeLair 1959 (original description)
Cimoliasauridae DeLair: Persson 1962 (emended diagnosis)
Cimoliasauridae DeLair: Persson 1963 (emended diagnosis)

CRYPTOCLEIDOIDEA O'KEEFE, 2001
Family ARISTONECTIDAE new family

Cimoliasauridae DeLair: O'Keefe 2001 (emended diagnosis)

Diagnosis—Cryptocleidoid plesiosaurs possessing the following unique combination of characters: rostrum relatively long but unconstricted and wide anteriorly, with a narrow symphysis (i.e., one symphysial tooth); paraoccipital process articulates with squamosal only; teeth small (crown length < 1 cm) and relatively narrow; number of premaxillary teeth seven or greater, number of maxillary teeth much greater than thirty; palate with a ventrally expanded boss projecting out of the plane of the palate between the posterior and anterior interpterygoid vacuity (if present); number of cervical vertebrae greater than 32; cervical vertebrae much wider than long; cervical vertebrae with poorly defined rims of articular surfaces (due to lack of ossification); marked dorso-ventral constriction of cervical centra on the ventral midline ('binocular-shaped centra') in derived members of clade; cervical neural arch and canal very small relative to centrum diameter.

Tatenectes O'Keefe and Wahl, 2003
Type Species: Tatenectes laramiensis, by monotypy.

Diagnosis: as for species.

Tatenectes laramiensis (Knight, 1900)

Holotype—W. C. Knight, uncatalogued. Disarticulated axial skeleton and nearly complete forelimb. This specimen is lost, but was figured and described by Knight (1900) in adequate detail to validate the name.

Neotype—UW 15943 & UW 24801, a partial skeleton comprising axial skeleton, ribs, pectoral girdle, and forelimb elements.

Referred Material—UW24215, USNM 536970, USNM 536976

Stratigraphic Occurrence—Upper Member of the Sundance Formation ("Redwater Shale" informal member), Upper Jurassic (Oxfordian); Natrona and Carbon Counties, Wyoming.

Diagnosis—A small (total body length of about 2 meters) plesiosaur with an unknown number of cervical vertebrae. Cervical vertebrae much shorter than wide, not constricted at midcentrum, and with well-defined rib articulations that are not elongate; foramina subcentralia widely spaced; the rims of articular faces of cervical vertebrae are poorly defined due to lack of ossification; humerus with long, slender shaft and radial and ulnar articulations that are subequal in length; articulations for two supernumerary ossifications in the epipodial row; scapulae medial processes meet in a median symphysis anterior to the pectoral fenestrae, but symphysis is relatively short, and the medial process of the scapula is short antero-posteriorly; short anterior extensions of the scapulae are separated on the midline by a deep notch, which is covered dorsally by a reduced, plate-like clavicle; teeth small, narrow and recurved with relatively long roots, and lightly lineated all around; anterior interpterygoid vacuity present; pterygoids behind anterior pterygoid vacuity are developed into a deep block of bone projecting ventrally out of the plane of the palate; parasphenoid not visible in palatal view.

Discussion of Family Taxonomy—Before presenting a formal revised diagnosis of Tatenectes laramiensis, the taxonomic status of the family Cimoliasauridae must be resolved. This family name was first erected by DeLair 1959, and was emended by Persson (1962, 1963). The status of this family has always been questionable, because the genus Cimoliasaurus is a classic 'garbage can' taxon erected in the 19th century on equivocal material, and later received many non-diagnostic referrals. This unsatisfactory state of affairs was accepted explicitly by DeLair (1959) when he coined the family name; Persson (1963) thereafter offered a formal but vague systematic diagnosis. Most recently, O'Keefe (2001) redefined the family to encompass the Upper Cretaceous austral cryptocleidoids (i.e., Aristonectes, "Morturneria," and Kaiwhekea) and their Jurassic relatives, the later comprising only the Kimmeridge Clay taxon Kimmerosaurus at that time. In retrospect this referral was of dubious validity and unwise, serving only to add to the confusion surrounding the family name. Myriad fossils have been referred to the genus Cimoliasaurus; for complete lists see Welles, (1962), Brown, (1981), and Kear, (2002).
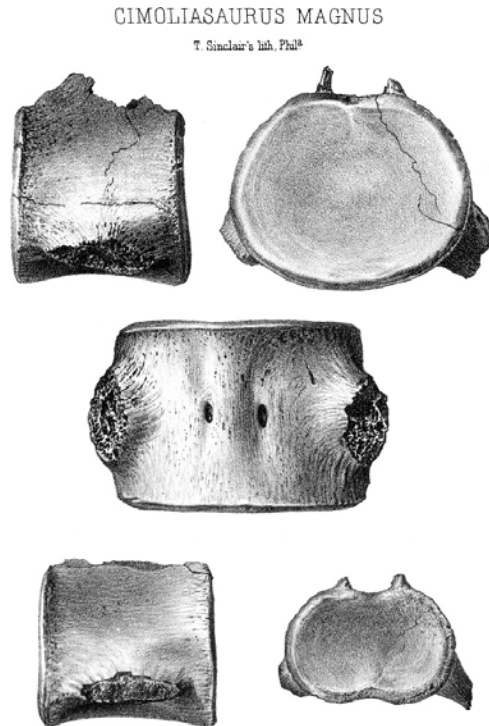

CIMOLIASAURUS MAGNUS

T. Sinclair's lith, Phil.ᵃ

FIGURE 1. Reproduction of the original plate depicting the holotype of Cimoliasaurus magnus Leidy 1851. The cervical vertebral centra illustrated here demonstrate several characters diagnostic for elasmosaurids, including well-defined articular margins; single-headed, long, and dorso-ventrally compressed cervical rib articulations; and binocular-shaped articular faces in more anterior vertebrae.

Welles (1952) considered the genotype of Cimoliosaurus diagnostic, a conclusion accepted by Persson (1963). The genotypic species is Cimoliasaurus magnus Leidy, 1851, from the Late Cretaceous green sands of New Jersey. The holotype consists of an articulated string of 13 vertebral centra (one pectoral, 12 posterior cervical). In his original publication, Leidy (1851) figured one centrum, and then figured others in a later paper (1865; two of these centra are reproduced here as Fig. 1). Various authors referred other material to the taxon (notably Cope; the many instances are reviewed in Welles, 1952); Persson (1959) also erected a new species of the genus to contain other, very similar vertebrae from Sweden.

We have reviewed the description of Cimoliasaurus magnus, and it is clearly referable to Elasmosauridae. While the cervical centra are relatively shorter than is typical of elasmosaurids from the Late Cretaceous of the North American Western Interior Seaway (WIS), their dimensions are typical of the more conservative elasmosaurs found in California and New Zealand (Aphrosaurus and Mauisaurus respectively; O'Keefe and Hiller, 2006). The cervicals also possess well-defined, ossified articular margins, elongate cervical rib articulations, and binocularshaped articular faces on the more anterior vertebrae, all of which are characteristic of Elasmosauridae (Fig. 1; O'Keefe, 2004). The Cimoliasaurus material referred by Persson (1959) shares all of these features, while the 'short and stout' propodials mentioned in Persson's diagnosis (1963) are also a characteristic elasmo-saurian feature. Therefore available evidence suggests that the genus Cimoliasaurus is an elasmosaur, and the first recognized as such from the Cretaceous North Atlantic.

Cimoliasaurus is certainly not a cryptocleidoid, and the use of the genus as a basis for a family of cryptocleidoids is therefore not acceptable under the current International Code of Zoological Nomenclature rules (International Commission of Zoological Nomenclature, 1999; Articles 61-65). However, some authors posit that the austral Cretaceous cryptocleidoids are actually derived elasmosaurids, not cryptocleidoids (Gasparini et al., 2003). Even in this case, however, the correct family assign-ment for these animals would be Elasmosauridae, not Cimoliasauridae; additionally, large scale cladistic analyses have not supported this view (O'Keefe, 2004). For these reasons we therefore erect a new family name for the austral Cretaceous cryptocleidoids, based on the earliest-discovered, undoubted member of the group, which is Aristonectes parvidens Cabrera, 1941. The resulting family name is Aristonectidae. Concerning the family Cimoliasauridae, it is a junior synonym of Elasmo-sauridae.

Description

Summary of Previously Known Material—We first summarize what is currently known about Tatenectes before describing the new material presented in this paper. Previously described skull roof material from UW 24215 includes the left squamosal, the fragmentary left frontal, and a poorly preserved tooth. Palate and braincase elements include the basioccipital and much of the left and right pterygoids (O'Keefe and Wahl, 2003b). Features of the squamosal, especially the dorsal and anterior processes, are quite similar to those of other cryptocleidoids including Tricleidus, Cryptoclidus, and Kimmerosaurus (Brown, 1981); the squamosal is short anterio-posteriorly and high dorsoventrally, with a very long descending postero-lateral process covering the quadrate laterally. The dorsal process of the squamosal is anteriorly directed. The left frontal is highly fragmented, with the only preserved edges being those of the midline suture and part of the lateral edge, but the combination of depressions and ridges following the midline and running antero-laterally from the midline on the lateral face of the frontal closely resembles that of Kimmerosaurus. The teeth of Tatenectes are relatively small and narrow, like the teeth of Kimmerosaurus, but the teeth of Tatenectes also have lineations on the crown, and are similar to the teeth of Kaiwhekea (Cruickshank and Fordyce, 2002).

A unique feature of Tatenectes is the structure of the pterygoids, which suture together posterior to the anterior ptery-goid vacuity. The bone is greatly thickened here and the usual posterior interpterygoid vacuities do not exist. Posteriorly, the bone spreads into two dorso-ventrally compressed, laterally separate articulations, most likely for the basioccipital tuber (O'Keefe and Wahl, 2003b). The ventral palate surface is much less planar than in most cryptocleidoids (O'Keefe and Wahl, 2003b), and resembles only the fragmentary skull of the Maastrichtian genus Aristonectes ("Morturneria") from Antarctica (Chatterjee and Small, 1989; pers. obs.), and a complete but very poorly preserved skull from the Late Jurassic of Cuba (figured in O'Keefe and Wahl, 2003b). While the fragmentary nature of this material is frustrating, enough of the pterygoid morphology is preserved to demonstrate that the Cuban taxon is probably an archaic aristonectid. Opallionectes may also be an aristonectid based on cervical vertebral characters, although the fragmentary nature of this specimen makes comparison difficult.

Significant postcranial material of Tatenectes also exists, which is fortunate given that the postcranium is essentially unknown for the more derived aristonectid plesiosaurs. The purpose of this paper is to describe this new material, along with additional cranial material.

New Material—The squamosal (Fig. 2) described here is the right-hand counterpart to the left squamosal described by O'Keefe and Wahl (2003b; both bones are from the same skull). The right squamosal preserves the long, ventrally extended lateral process and socket for the quadrate articulation. This process is also seen in Tricleidus, Kimmerosaurus (Brown, 1981), and Cryptoclidus (Brown, 1981; Brown and Cruickshank, 1994). The anterior process of the squamosal is very deep dorsoventrally, although its anterior extent, where it contacts the jugal, is not known due to breakage. At its dorsal margin, which forms the ventral margin of the temporal fenestra, the bone forms a pronounced ridge, while the bone is much thinner ventrally. The anterior process of the squamosal is therefore much deeper dorso-ventrally than is typical for cryptocleidoid plesiosaurs (Brown, 1981), and more similar to that of Kaiwhekia (Cruickshank and Fordyce, 2002). The dorsal process by which the right squamosal would have contacted its neighbor is not preserved. The left squamosal does preserve the dorsal process; these processes arched over the posterior portion of the skull to meet on the midline as is typical for plesiosaurs. The anteroposterior length of the sagittal crest is short, a condition typical of cryptocleidoids.
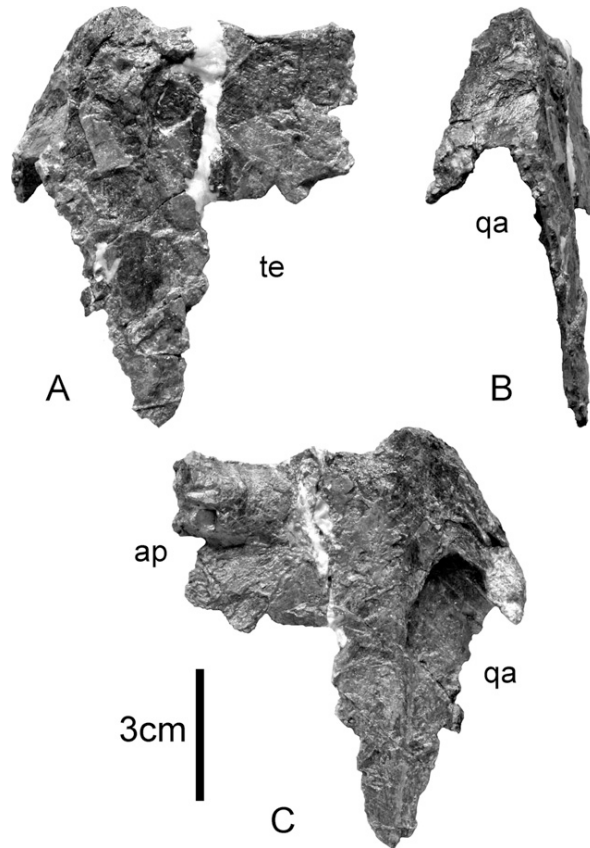
FIGURE 2. Right squamosal of Tatenectes laramiensis, UW24215. The squamosal is essentially complete except for the dorsal process and the end of the anterior process. Views are: A, right lateral; B, posterior; C, right medial. Abbreviations: ap, anterior process; te, temporal emargination, qa, quadrate articulation.

While the root of the new tooth described here is not preserved, the crown is fairly complete and its preservation is better than in the one previously known tooth (Fig. 3). The crown is small and needle-like in morphology, more gracile than most other plesiosaurs. Enough of the curving lingual surface remains to show fine lineations. These are similar to those seen on the teeth of Kaiwhekea (Cruickshank and Fordyce, 2002), and the overall morphology (shape, curvature, and length) resembles the teeth of Kimmerosaurus (Brown, 1981) and Opallionectes (Kear, 2006). The tooth shape is also similar to that of Aristonectes, although the teeth of Tatenectes are longer than in that taxon (Chatterjee and Small, 1989).

The anterior cervical vertebra from specimen USNM 536970 (Fig. 4) clearly shows the widely-spaced (relative to other cryptocleidoids like Cryptoclidus) foramina subcentralia. A crack slightly obscures this feature on the more posterior cervical from UW 24215 (Fig. 5). The cervical vertebral centra are markedly compressed antero-posteriorly, the length being much shorter than the height. The cervical vertebrae of Tatenectes are significantly more compressed antero-posteriorly than is typical of Cryptoclidus and Muraenosaurus (Brown, 1981). The anterior cervicals resemble the cervicals of Kaiwhekea and Aristonectes, in that both are highly compressed antero-posteriorly and that the rib articulations are set very near the ventral surface (Chatterjee and Small, 1989). However, Tatenectes and Aristonectes cervicals look very different in anterior view, even though both are also dorso-ventrally compressed, because the vertebrae of Aristonectes have a distinct 'binocular' shaped outline (Chatterjee and Small, 1989). The rims of the articular facets of the centra are poorly ossified. As in the previously described vertebra of UW 24215, the centra lack ventral keels.

The referred specimen UW 24215 preserves evidence of many ribs and gastralia. Thepoorly preserved, and were very difficult to extricate from the surrounding concretion. In this material the ribs are gracile and posses single, dorso-ventrally expanded heads. Several fragments Interpreted as gastralia are of relatively large diameter and appear to be pachyostotic. However, no complete elements are known, and this interpretation is equivocal. Pachyostosis is uncommon in plesiosaurs (Cruickshank et al., 1996 and references therein), having been observed previously in only a few pliosaurs. Pachyostosis is most developed in the pliosaur Pachycostasaurus dawni Cruickshank et al., 1996, from the Oxford Clay, where the gastralia, ribs, and dorsal vertebrae are all expanded and heavily ossified (Cruickshank et al., 1996). If our interpretation is correct, Tatenectes would be less pachyostotic, with the condition limited to the gastralia only.
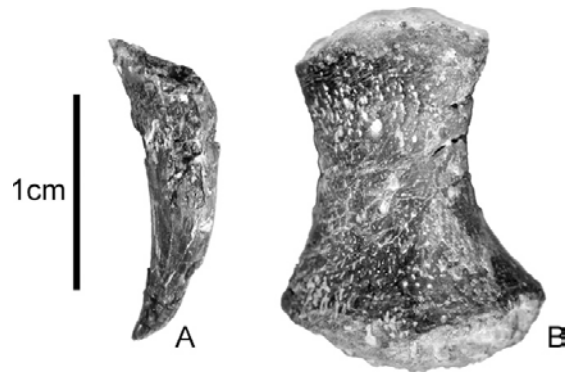
FIGURE 3. Tooth crown (A) and phalanx (B) of Tatenectes laramiensis, UW 24215.

FIGURE 4. Well-preserved adult cervical centrum of Tatenectes laramiensis, USNM 536970. Note poorly defined margins of articular faces, extreme anterior-posterior compression, and small size. Views are: top left, posterior; top right, right lateral; bottom left, ventral; bottom right, dorsal.
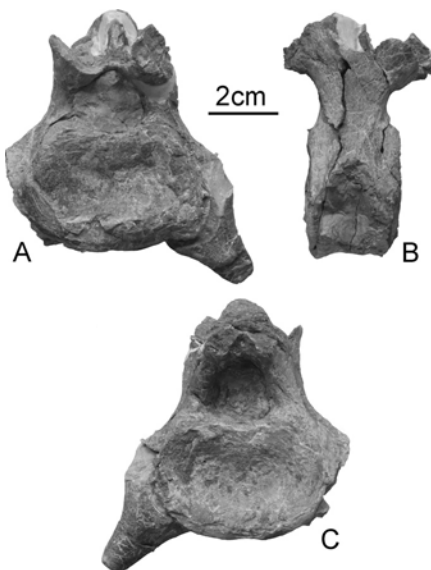

FIGURE 5. Posterior cervical vertebra of Tatenectes laramiensis, UW 24215. Views are: A, anterior; B, left lateral; C, posterior.
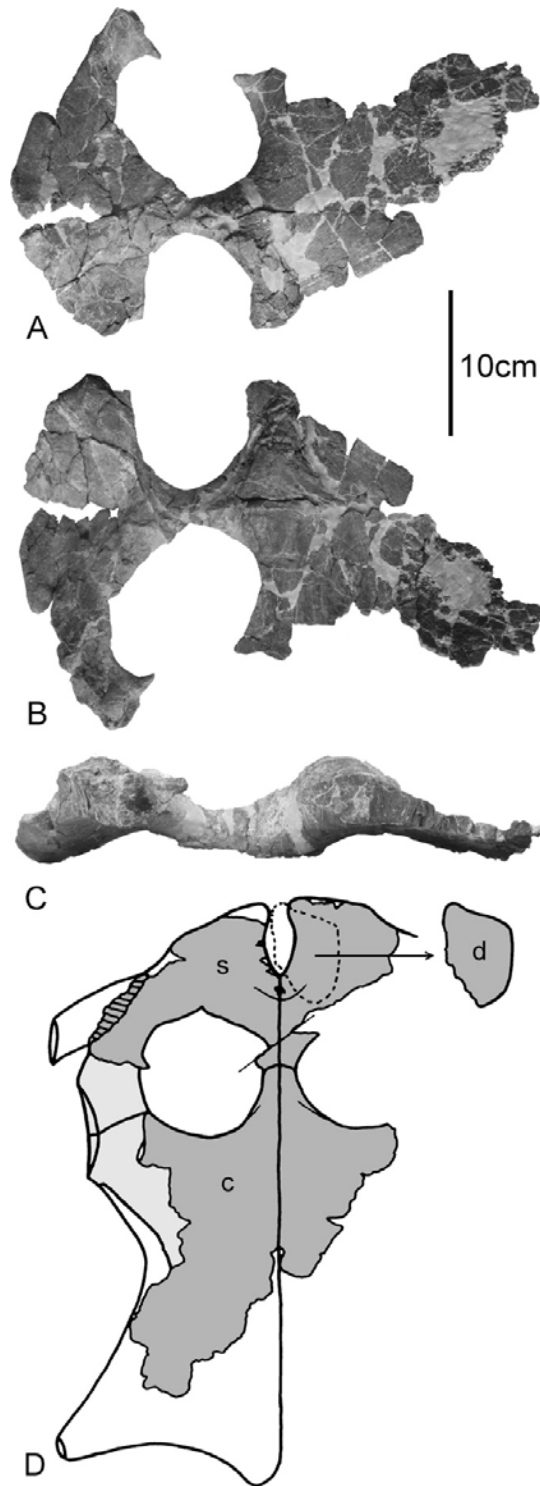
FIGURE 6. Pectoral girdle of Tatenectes laramiensis. The three top views are the partial girdle of UW 24215 as preserved; A, ventral surface, B, dorsal surface, C, left lateral view. The composite (dorsal) reconstruction in D is based primarily on this specimen (dark gray), with input from the juvenile pectrum from UW 15943 (light gray). The black line in D illustrates the plane of rotation for the anterior girdle relative to the posterior fragment. The dermal location of the preserved dermal element is shown as a dotted line; the element has been moved laterally for clarity. Abbreviations: c, coracoid; d, dermal element (either clavicle or interclavicle); s, scapula.

A much more complete pectoral girdle is now available for Tatenectes (UW 24215; Fig. 6), and is quite different from that described by O'Keefe and Wahl (2003a; UW 15943 & 24801). Some of these differences are ontogenetic, as the new specimen is an adult, while others result from reinterpretation. The juvenile pectoral girdle is difficult to interpret (noted in O'Keefe and Wahl, 2003a), and the new adult material provides context for interpretation and a more confident reconstruction (Fig. 6). In the new specimen, a fracture in the anterior end of the pectoral bar misaligns the preserved parts of the scapulae. The reconstruction was created by combining the material from UW 24215 and neotype specimen UW15943.

One notable feature of the pectoral girdle of Tatenectes is that the medial processes (anterior to the pectoral fenestrae) are short antero-posteriorly. The scapulae do not meet at the midline anteriorly, and encompass a notch that was covered by dermal elements (clavicle and interclavicle) in life. The pectoral fenestrae are very large and round in outline. The posterior end of the coracoid is still unknown in Tatenectes. However, the posterior-most portion of the pectoral girdle of UW 24215 is greatly reduced in thickness, indicating that a complete coracoid could not be much longer than what is preserved in this specimen. When the neotype was described by O'Keefe and Wahl (2003a), it was noted that the scapulae did not meet at the midline. When the pectoral girdle of UW 15943 is compared to the pectoral girdles of Cryptoclidus, it is quite likely that the neotype represents a juvenile specimen in which the scapulae had not completely ossified (Andrews, 1910); a misinterpretation of the midline suture also contributed to the erroneous interpretation. With more ossification, the scapulae would have met on the midline, matching what is seen in the pectoral girdle of UW 24215. The girdle of Tatenectes is even shorter anterior to the pectoral fenestra than that of Tricleidus. The transverse scapula-coracoid midline suture is located more anteriorly than in Muraenosaurus, more closely resembling Tricleidus (Brown, 1981). The anterior notch between the scapulae of Tatenectes, however, more closely resembles that of Muraenosaurus than that of Tricleidus, which is less constricted (Brown, 1981). A single plate-like, rectangular dermal element, probably clavicle but possibly interclavicle, is preserved in articulation on the dorsal side of the right scapula. In Cryptoclidus the clavicles are plate-like and surround an extremely reduced interclavicle, while in Muraenosaurus the interclavicle is large and plate-like while the clavicles are reduced (Brown 1981).

The proximal and distal ends of the right humerus (Fig. 7A, B) of USNM 536976 were found, but the exact length and proportions of the humerus are unknown because the midshaft is missing. The shaft is interpreted as relatively long and gracile. The proximal end of the humerus bears a tuberosity on the dorsal side, and the articular face is very rugose. The posterior margin of the distal end is marked by a pronounced flange. The distal margin has four articular facets for the radius, ulna, and two supernumerary elements (pre- to postaxial). The gracile morphology of the humeral shaft more closely resembles polycotylids than other cryptocleidoids (O'Keefe and Wahl, 2003b) and is most similar to that of Colymbosaurus (Brown, 1981). Both taxa have a distinct posterior flange on the humerus with articulations for two supernumerary ossifications.

Phylogenetic Analysis—A cladistic analysis of eleven cryptocleidoid taxa was performed in order to place Tatenectes in a phylogenetic context. Three taxa from other subclades within Plesiosauria were designated as the outgroup (Thalassiodracon, Plesiosaurus, and Brancasaurus; Fig. 8). We did not include more elasmosaurids in the analysis because the goal was in group relationships of the Cryptocleidoidea; a full analysis of the position of the aristonectids relative to other major plesiosaur clades is an important problem, but will require a revised and expanded analysis of the clade Plesiosauria, which is beyond the scope of this study. The character matrix is a revised version of that given in O'Keefe and Wahl, 2003a (Appendix 1). The matrix comprises 90 characters, four of which were ordered multistate. The data matrix was analyzed using the parsimony criterion in PAUP* (Swofford, 2001); most parsimonious trees (MPTs) were identified using the branch-and-bound algorithm. The analysis returned two MPTs, each with a tree length of 169, and 80 of the characters were parsimony-informative. The ten parsimony-uninformative characters were left in the character matrix due to their species-level diagnostic value; their effect on the analysis can be seen in the difference between the consistency index and rescaled consistency index. The consistency index (CI) was 0.692, the rescaled consistency index (RCI) was 0.506, and the retention index (RI) was 0.73. The only topological difference between the two most parsimonious trees is the location of Cryptoclidus. One tree grouped Cryptoclidus with Muraenosaurus, while the other placed Cryptoclidus as an outgroup of a monophyletic clade containing Tricleidus, the Aristonectidae, and the Polycotylidae. The strict consensus tree of these two most parsimonious trees places both Muraenosaurus and Cryptoclidus as outgroup taxa to that clade (Fig. 8). Tricleidus is always placed as an outgroup to the Aristonectidae and Polycotylidae, and does not group with Muraenosaurus and Cryptoclidus. Tatenectes is always the sister taxon of Kimmerosaurus, and this clade in turn is the sister group to the more derived aristonectid taxa. Bootstrap analyses were performed to test tree stability (1000 replicates), and decay indices were generated by manually saving trees of successive greater length saving surviving nodes. Some of the bootstrap values are strong, including those at the node uniting the Cryptocleidoidea, the node grouping the Tricleidea, and the node uniting the Polycotylidae. Relationships within the Aristonectidae are not as strongly supported.

CONCLUSION

This study addresses several current problems in cryptocleidoid morphology and taxonomy. The first problem is the family-level taxon 'Cimoliasauridae' DeLair, 1959, whose status has been problematic since its inception due to a lack of clarity concerning the familial type genus. As discussed above, Cimoliasaurus Leidy, 1851 is diagnostic to family, and is an elasmosaurid. Its vertebrae resemble the more conservative, relatively short-necked elasmosaurids found in California (Aphrosaurus,

Morenosaurus) and Australia (Mauisaurus) more than those of taxa from the Western Interior Seaway, but all share a diagnostic suite of family-level characters. The family name 'Cimoliasauridae' is therefore invalid, because the familial type genus is referable to a previously extant family. A new family, the Aristonectidae, is erected to accommodate the derived cryptocleidoids of the austral Cretaceous and their Jurassic relatives. If the Kimmeridge Clay taxon Colymbosaurus does prove to be a senior synonym of Kimmerosaurus, then it will be the historically oldest taxon in the clade Aristonectidae; however, according to the ICZN a familial type genus is not restricted to the first occurring genus name, so the Aristonectidea will stand in any case.
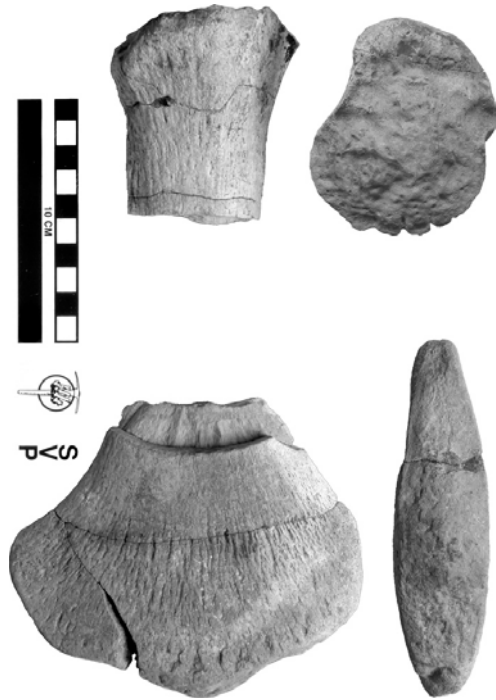

FIGURE 7. Isolated right humerus of Tatenectes laramiensis, USNM 536976. The element is from an adult and is well preserved, but is missing much of the diaphysis. Left, dorsal surface; top right, proximal articular surface; bottom right, distal articular surface.
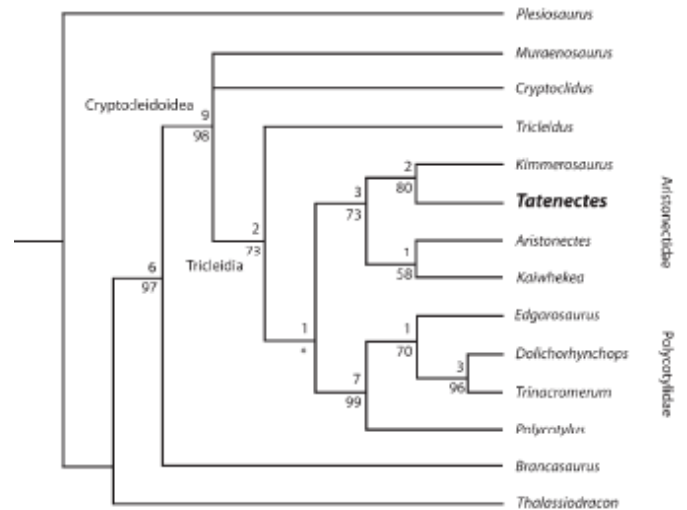

FIGURE 8. Hypothesis of relationships among the members of the Cryptocleidoidea. Integers at each node are decay indices (above branch); bootstrap values are below each branch. An asterisk represents values below 50%.

The new material of Tatenectes laramiensis reported here is significant in several ways. The well-preserved tooth crown clearly illustrates the taxon's gracile dental morphology, while the right squamosal fragment illustrates that the cheek region was deeper dorso-ventrally than previously believed, with a relatively deep anterior squamosal process. These three features resemble the condition found in later aristonectid plesiosaurs (e.g., Kaiwhekea), and further strengthen the link between Tatenectes and those taxa. Along with Kimmerosaurus, Tatenectes is a stratigraphically early and morphologically primitive sister taxon to the aristonectids of the austral Cretaceous, and bridges the gap between these taxa and more plesiomorphic Jurassic cryptocleidoids.

The new, adult pectoral girdle described here allows a more confident reconstruction of this region in Tatenectes. The tentative interpretation of the previously-known juvenile pectoral girdle (UW 15943) is incorrect due to an error in the interpretation of the midline suture. The composite reconstruction from the two known girdles lacks only the posterior terminus of the coracoid, and reveals morphology broadly similar to that of Oxford Clay cryptocleidoids, resembling Muraenosaurus beloclis (Brown, 1981) most closely. The scapula carries an anterior process bordering an open notch on the midline, as is typical of Muraenosaurus; however the anterior process is quite short, and the remainder of the scapula shorter antero-posteriorly relative to that genus. The scapulae do meet on the midline anterior to the pectoral fenestrae (contra O'Keefe and Wahl, 2003b).

A phylogenetic analysis of the Cryptocleidoidea reveals several interesting findings. The first is the unstable position of Cryptoclidus, perhaps the best known of all cryptocleidiods, if not all plesiosaurs. An examination of the character data reveal that this phylo-genetic ambiguity may be real; Cryptoclidus is actually rather derived relative to other cryptocleidoids, possessing only a vestigial fenestra between the anterior processes of the scapulae, and a reduced interclavicle relative to the relatively robust clavicles. Both characters are autapomorphic, as is the greatly expanded distal humerus. Among other cryptocleidoid taxa, Tricleidus possesses a much more primitive clavicle and interclavicle than others members of the clade; however, its palatal morphology is relatively derived, being more similar to the condition found in the Polycotylidae. Muraenosaurus leedsi and the

closely related taxa M. beloclis and Pantosaurus deserve further study, as their morphology may be more representative of the clade as a whole than that of Cryptoclidus.

ACKNOWLEDGMENTS

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APPENDIX 1. Character list and state codings for characters used in the phylogenetic analysis.

	Character	Coding
1	Relative skull length	(0) primitive/'nothosaurian', (1) long, (2) short
2	Relative neck length	(0) primitive, (1) long, (2) short
3	Relative ischium to pubis length	(0) subequal, (1) ischium longer, (2) pubis longer
4	Relative humerus to femur length	(0) subequal, (1) humerus longer, (2) femur longer
5	Preorbital and postorbital skull length	(0) subequal, (1) longer preorbital, (2) shorter
6	Fin aspect ratio	(0) high, (1) low
7	Elongate rostrum	(0) absent, (1) premaxilla only, (2) very long with maxilla included, (3) elongate and hoop-like/ unconstricted
8	Dorso-medial process of premaxilla	(0) contacts frontal, (1) contacts anterior extension of the parietal
9	No premaxilla/ external naris contact	(0) present, (1) absent
10	Frontals paired or fused in adult	(0) paired, (1) fused
11	Frontal enters margin of temporal fenestra	(0) does not, (1) does narrowly
12	Frontal contacts external naris	(0) does contact, (1) does not contact
13	Pineal foramen anterior border	(0) not bordered by frontal, (1) bordered by frontal
14	Parietal skull table	(0) relatively broad, (1) constricted, (2) sagittal crest
15	Squamosal lateral process	(0) no medial process, (1) medial process and socket-like squamosal
16	Anterior extent of the jugal	(0) middle of orbit, (1) restricted to posterior margin
17	Jugal cheek bar	(0) does not, (1) does
18	Maxilla/squamosal contact	(0) no contact, (1) contact, (2) expanded posterior flange
19	Exoccipital/occipital condyle	(0) does not participate, (1) does participate
20	Occipital condyle morphology	(0) hemispherical with groove, (1) short with no groove
21	Paraoccipital process articulation	(0) squamosal exclusively, (1) quadrate exclusively
22	Paraoccipital process ventral extent	(0) does not extend ventral to occipital condyle, (1) extends past condyle
23	Supraoccipital depth	(0) shallow, (1) deep antero-posteriorly/ sigmoid suture with exoccipital and prootic
24	Squared pterygoid lappet	(0) no squared lappet, (1) squared lappet
25	Morphology of anterior interpterygoid vacuity	(0) slit-like, (1) absent, (2) broad with round ends
26	Pterygoids meet posteriorly to the posterior interpterygoid vacuity	(0) pterygoids do not meet, (1) pterygoids meet
27	Pterygoids meet between the interpterygoid vacuities	(0) do not meet between vacuities, (2) do meet between vacuities
28	Ectopterygoid/postorbital bar contact	(0) no contact, (1) contact
29	Dished pterygoids	(0) absent, (1) present
30	Posterior pterygoid/parasphenoid contact	(0) absent, (1) present
31	Parasphenoid morphology	(0) long, tapering anteriorly, (1) short and blunt
32	Parasphenoid exposure anterior to the posterior interpterygoid vacuities	(0) exposed via extension of interpterygoid vacuities, (1) exposed with lateral pterygoid sutures
33	Parasphenoid/basioccipital contact	(0) absent, (1) present
34	Basioccipital tubers reduced	(0) not reduced, (1) reduced/ tuber facets confluent with basioccipital articulation
35	Palatine/internal naris	(0) palatine enters internal naris border, (1) excluded by vomer/maxilla contact
36	Premaxilla/anterior border of interior naris	(0) premaxilla enters anterior border, (1) excluded by vomer/maxilla contact
37	Sub-orbital fenestration	(0) absent, (1) present
38	Vomers extend far posterior to the internal nares on the midline	(0) do not, (1) extend posterior and meet pterygoids in wide, interdigitating suture
39	Mandibular symphysis	(0) short, (1) scoop-like, (2) long
40	Splenial in symphysis	(0) does not participate, (1) does participate, (2) participates significantly
41	Coronoid	(0) present, (1) absent
42	Coronoid exposure on lateral mandible	(0) no exposure, (1) exposure
43	Prearticular shelf/groove	(0) absent, (1) present
44	Jaw articulation relative to tooth row	(0) above or collinear with tooth row, (1) lower than tooth row
45	One or two caniniform maxillary teeth	(0) absent, (1) present
46	Tooth form	(0) gracile, small root, narrow, no wear, (1) robust, large root, wear, (2) small/needle-like
47	Number of premaxillary teeth	(0) 5 or fewer, (1) 6, (2) 7, (3) more than 7
48	Maxillary teeth	(0) fewer than 25, (1) more than 25
49	Axis rib articulation	(0) broad articulation with atlas centrum and/or other elements, (1) head confined to axis centrum
50	Atlas/axis morphology	(0) no lateral exposure of atlas centrum on cup face, (1) lateral exposure, (2) no lateral exposure, but atlas and axis intercentra exclude atlas centrum ventrally
51	Number of cervical vertebrae	(0) primitive, (1) increased, (2) reduced, (3) greater than 50
52	Cervical centrum proportions	(0) length equal to height, (1) length greater than height, (2) length less than height
53	Zygopophyseal angle change	(0) no change in angle, (1) change
54	Cervical ventral keel	(0) absent, (1) present
55	Binocular-shaped cervical centra	(0) absent, (1) present
56	Cervical zygopophyses width	(0) subequal with centrum, (1) narrower than centrum
57	Posterior articulation for succeeding neural spine, cervical vertebrae	(0) absent, (1) present
58	Cervical rib articulation greatly elongate/ cervical ribs expanded and blade-like	(0) circular or sub circular, (1) elongate and blade like, (2) elongate and rectangular
59	Anterior process of the cervical ribs	(0) present, (1) absent
60	Anterior neural flange on vertical neural spine	(0) absent, (1) present
61	Neural spines, cervical vertebrae	(0) angled backward, (1) not angled
62	Lateral compression of neural spines, dorsal and cervical vertebrae	(0) not compressed, (1) compressed and blade-like
63	Interclavicle posterior process	(0) absent, (1) present
64	Interclavicular form	(0) large with no scapula contact, (1) plate-like and dorsal to scapula, (2) reduced, (3) trapezoidal and perforate

	Character	Coding
65	Clavicle form	(0) long and bar-like, (1) reduced to a thin sheet on interclavicle, (2) triangular with posterior embayment and midline contact
66	Scapulae meet in anterior median symphysis	(0) separated by clavicals/interdavical, (1) meet on midline
67	Anterior scapula process	(0) absent, (1) present
68	Longitudinal pectoral bar	(0) absent, (1) formed by clavide and coracoid, (2) formed by scapula and coracoid
69	Median coracoid perforations	(0) absent, (1) present
70	Posterior coracoid extension with deep median embayment	(0) absent, (1) present
71	Pubis ventral (medial) margin	(0) convex, (1) concave
72	Median pelvic bar	(0) present, (1) absent
73	Angled humerus	(0) present, (1) absent
74	Distal end of humerus has two	(0) absent, (1) present
75	Distinct facet on distal end for supernumerary ossification	(0) absent, (1) present
76	Distinctly lunate ulna	(0) present, (1) absent
77	Epipodial morphology	(0) longer than broad, (1) equal or broader than broad
78	Supernumerary ossifications, forelimb	(0) none, (1) epipodial row/pisiform, (2) propodial, (3) both
79	Humerus posterior flange	(0) absent, (1) present
80	Marked grove around margin of cervical vertebral articular faces	(0) absent, (1) present
81	Process of postorbital extends posteriorly along lateral margin of temporal fenestra	(0) present, (1) absent
82	Deep notch in posterior margin of clivus	(0) present, (1) absent
83	Length of retroarticular process	(0) short, (1) long
84	Width of central pterygoid plate	(0) central plate absent, (1) narrow, (2) broad
85	Height of sagittal crest	(0) low, (1) high
86	Sigmoid humeral shaft	(0) absent, (1) present
87	Pectoral foramen shape	(0) small and diagonal, (1) large and round
88	Anterior process coracoid	(0) none or very short, (1) half of pectoral fenestra or longer
89	Medial scapula process	(0) does not contact coracoid, (1) does contact coracoid
90	radius shape	(0) hourglass shaped, (1) convex anterior margin, (2) concave anterior margin

APPENDIX 2. Phylogenetic data matrix for the analysis in this paper.

Plesiosaurus	2020000000 0001000000 ?000000000 000000000? ?000000??0 10?001000 1100000100 0000000100 1110000110
Muraenosaurus	2101010000 001211??01 101020000100 11001001100 011000001 1100?11111 1111111200 0111111310 ?001001112
Cryptoclidus	0001010000 0112111011 101020001000 11000?0000 0110001001 0010010011 1112211200 0111011111 0001001112
Tricleidus	00?0210000 0?02111000 1110200101 1111?0?000 0?11000??1 0010011011 101101200 0111111311 0001001111
Kimmerosaurus	0???2?30?0 0?12111011 0010200?01 ?110&1????00 111102310? ?22?001?21? 10??????? ??????????1 0?010??????
Aristonectes	0???213??? ?????????00 0?1??0?0? 111101??0? ??01022102 ?22?11?2?? ?????????? ??1??1??0 ???x??????
Edgarosaurus	12??111010 0102110200 ??102101 11 11??0?11 0111111012 22?10?20?? ?????????? ??11?11??? 0?020??1
Polycotylus	1212?1???? ????????0? ??1??0?0? ??11??1??? 0111?1?12 220?0010?1 1003200?1? 0111111311 ??01011111
Dolichorhynchops	121211211x 0102110200 1110210111 111011022 0111000012 221001 10?1 1003200110 01 11011311 0012111101
Trinacromerum	121211211x 01?2110220 1111210?11 1111??1222 ?111000012 221?01 10?1 1003200110 0111111311 0012011111?
Brancasaurus	2120000001 1012010100 ?01?1?x?00 0?0001?1?? ????000?10 11?01107?0 0110010201 101??11?00 0?1000?110
Tatenectes	0???????0?0 ????1??11 ???2?1?01 1x1?????? ???72???? ?220010211 00?1111200 ??111?311 ??2x?01112
Kaiwhekea	00??21010x ?1021?1?? ??????????? ??????00 ??0022?1?? 12?111?21? 11??????? ??????1?0 ??0?1?????
Thalassiodracon	0000000000 0000000000 0000001000 ?000?0010 ?0000000?? 00?0000000 00?0000000 0000000000 1110??0000