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PRELIMINARY REPORT ON THE OSTEOLOGY AND RELATIONSHIPS OF A NEW ABERRANT CRYPTOCLEIDOID PLESIOSAUR FROM THE SUNDANCE FORMATION, WYOMING

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ABSTRACT

The cryptocleidoid plesiosaur *Tatenectes laramiensis*, new genus, is described from the Redwater Shale Member of the Sundance Formation, Natrona County, Wyoming. The holotype of this species was a partial skeleton that has since been lost. A neotype is designated that preserves the same elements present in the holotype. A second specimen is referred to the taxon, and this specimen includes cranial material. The preserved cranial elements are the left squamosal, a partial right frontal, several isolated teeth, the parasphenoid, and large portions of the left and right pterygoids. The skull shares many traits with that of *Kimmerosaurus*, a cryptocleidoid plesiosaur from the Kimmeridge Clay of England. However, the palate is derived, and resembles those of the poorly-understood cimoliasaurid plesiosaurs of the Cretaceous of the southern hemisphere. This similarity is established via comparison with the skull of an undescribed taxon from late Jurassic of Cuba. The cryptocleidoid plesiosaurs underwent an extensive radiation in the Late Jurassic, and more research attention is needed, beginning with additional preparation and collection of *Tatenectes*.

INTRODUCTION

Upper Jurassic plesiosaur material has been known from the (Oxfordian) Redwater Shale member of the Sundance Formation of Wyoming since the end of the 19th century, being first mentioned by Marsh in 1891, and later elaborated by Marsh (1893, 1895) and by Knight (1898, 1900). Mehl (1912) advanced the hypotheses that two small plesiosaur taxa occurred in the Redwater Shale, and that both showed affinities to the cryptocleidoids (*sensu* O'Keefe 2001) of the (Callovian) Oxford Clay of England. The Sundance Formation plesiosaurs received no further attention until the 1990s, when field crews of the Tate Museum in Casper, Wyoming began collecting new plesiosaur material from Natrona county. The taxonomic history of Sundance plesiosaurs, and the status of *Pantosaurus striatus*, are reviewed in the preceeding paper by O'Keefe and Wahl (2003). *Pantosaurus* seems to have had the longer neck of the two taxa present in the Redwater Shale. This taxon possesses at least 35 cervical vertebrae that are long antero-posteriorly, and that are very similar to those of the long-necked taxon *Muraenosaurus*. No cranial material is currently known from *Pantosaurus*, although Knight's specimen of '*Plesiosaurus shirleyensis*' (now lost) did preserve teeth and a fragment of mandible possibly from this taxon (Knight 1900).

This paper offers a preliminary description of a second cryptocleidoid taxon from the Redwater Shale. The case will be made that this taxon is the same as the taxon '*Tricleidus*?' *laramiensis* erected by Mehl (1912), itself a revision of the taxon '*Cimoliosaurus*' *laramiensis* Knight 1900. However, the taxonomy of this species is quite complex, and the difficulties are compounded by the fact that Knight's holotype cannot be located today. The tack taken here is to erect a neotype of this species based on Knight's original (valid) description, assign a new genus name as the species is currently without a valid one, and then refer other material to the taxon. The taxonomic issues involved are discussed at length below.

Cryptocleidoid Phylogeny and Relevance—As will be shown below, the cranial anatomy of this second Redwater Shale taxon is quite derived and very important, because it sheds light on the anatomy and relationships of the group of animals defined as the Cimoliasauridae by O'Keefe (2001). This group of bizarre animals is best known from the Cretaceous taxa

Kaiwhekea and *Aristonectes*, but also includes the Jurassic taxon *Kimmerosaurus* (O'Keefe 2001). A cladistic analysis performed below shows that the second Redwater Shale taxon is yet another member of this group. Sorting out the relationships of the Cimoliasauridae has assumed new importance with the recent publication of a paper contending that *Aristonectes* (and material referred to it) is an elasmosaur (Gasparini et al. 2003). It is our view that this assignment is incorrect; this view is supported by much character evidence in the cladistic analysis, and will be discussed below. Some necessary background on plesiosaur phylogeny is therefore introduced here.

The phylogeny of the Plesiosauria, and of clade Cryptocleidoidea in particular, has undergone extensive taxonomic revision of late. Carpenter's (1997) assertion that the Pliosauridae as traditionally defined was polyphyletic motivated a cladistic analysis by O'Keefe (2001; see also O'Keefe in press a), who found that the Pliosauridae contained members of three clades: the primarily Jurassic rhomaleosaurs and true pliosaurs, and the Cretaceous polycotylids. O'Keefe found strong support for a clade containing the Polycotylidae and the traditionally defined Cryptoclididae (including the Jurassic taxa *Cryptoclidus*, *Tricleidus*, and *Kimmerosaurus*, as well as other, more derived Cretaceous forms). O'Keefe also found that *Muraenosaurs*, often considered an elasmosaur, was also a member of this clade. O'Keefe (2001) therefore redefined Williston's (1925) Cryptocleidoidea to include *Muraenosaurus* and the Polycotylidae as well as other 'cryptoclidid' taxa. Given these relationships, the Upper Jurassic cryptocleidoid taxa assume greater importance, because they are near the base of a radiation giving rise to both plesiosauromorph and pliosauromorph taxa (O'Keefe, 2002). The bizarre and poorly-understood members of the Cimoliasauridae constitute a third lineage diverging during this radiation. Cryptocleidoid material from Wyoming has the potential to shed light on the morphology and relationships of the clade at an early period in its history. This material is also biogeographically important, because Upper Jurassic cryptocleidoids are known almost entirely from England at present.

SYSTEMATIC PALEONTOLOGY

Suborder Plesiosauria de Blainville, 1835
Genus *Tatenectes* new genus

Type Species--*Tatenectes laramiensis*, by monotypy.

Diagnosis--as for species.

Etymology--Tate, in honor of Marion and Inez Tate, founders of the Tate Museum in Casper, Wyoming in 1980. -Nectes, Greek, meaning diver.

Tatenectes laramiensis Knight 1900, new combination
(Figures 1,2,3,4,5).

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: UW 24215

Occurrence--Redwater Shale member of the Sundance Formation, Late Jurassic (Oxfordian); Natrona and Carbon Counties, Wyoming.

Diagnosis--A small plesiosaur with an unknown number of cervical vertebrae, but probably less than 31. Cervical vertebrae are much shorter than wide, are not waisted, and do not have elongate articulations for cervical ribs. The foramina subcentralia are widely spaced, and the rims of articular faces are poorly ossified. The humerus possesses radial and ulnar articulations that are subequal in length, articulations for two supernumerary ossifications in the epipodial row, and a long, slender shaft. The scapula possesses a medial process extending toward the midline but not contacting its neighbor, and certainly lacking a long midline suture. Suture between scapula and coracoid in center of glenoid. Teeth narrow and recurved with long roots, and striated all around. Anterior interpterygoid vacuity present; the pterygoids behind this vacuity are developed into a deep block of bone giving a distinct shelf to the basicranium. Pterygoid processes extend caudally in a U-shape to effect articulation with the basioccipital tubers.

DESCRIPTION

Tatenectes laramiensis is represented by the following material: the neotype UW 15943 and UW 24801, an articulated skeleton consisting of pectoral girdle, distal humerus, and partial axial skeleton comprising ribs and dorsal and two posterior cervical vertebrae; and UW 24215, a fragmentary skull and articulated vertebral column. UW 15943 and UW 24801 were collected from a Redwater Shale outcrop near Roughlock Hill in Natrona County, Wyoming (UW locality V-95010). UW 24215 was found in a Redwater Shale outcrop (UW locality V-92066) near the town of Arminto in Natrona County. The neotype specimen (UW 15943 & UW 24801) was designated as such because it contains the same elements figured and described by Knight (1900) in the lost holotype skeleton (see Discussion). The features of the neotype skeleton will be described first, followed by a discussion of the cranial and cervical anatomy of the referred specimen (UW 24215).

The neotype specimen of *Tatenectes laramiensis* (UW 15943 & UW 24801) is illustrated here in Figure 1. The humerus was given its own number because it was found as float just beneath the quarry that yielded the concretion containing the axial skeleton and most of the pectoral girdle. We believe it is likely that the humerus fragment weathered out of the concretion because the concretion contains a thoracic axial column and associated pectoral girdle, and pieces of the coracoid (later reassembled) were found with the humerus fragment beneath the quarry. The style of preservation is identical.

The pectoral girdle of UW 15943 consists of the articulated left scapula and coracoid (Figure 1). The scapula is mostly complete, missing only a portion of the dorsal process just antero-dorsal to the glenoid. The coracoid is complete anteriorly, but fragments posteriorly where the element was weathering out of the limestone concretion. The glenoid fossa is well-developed but rather large, its anterior edge is broken away, and the scapula-coracoid suture is near its center as in most plesiosaurs (but unlike *Tricleidus* or *Cryptoclidus*, Brown 1981). The coracoid also broadly resembles those in other crytpocleidoids, although its edges are fragmented and detailed comparison impossible. There does not seem to have been a pectoral bar formed by anterior extensions of the coracoids as in other cryptocleidoid taxa (Brown 1981 p. 331). The presence of this feature varies ontogenetically (Brown 1981), but the advanced state of ossification of the humerus would seem to indicate that this specimen was an adult. The neural arches of the dorsal and cervical vertebrae are also fused to the centra, another indicator of adult status (Brown 1981).

The dorsal process of the scapula is unusual; the portion that is preserved seems to suggest that the process projected anteriorly rather than postero-dorsally as in most plesiosaurs. Given the lack of preservation and the possibility of post-depositional deformation, however, caution should be exercised in taking this morphology at face value. In contrast, the medial process of the scapula is well preserved and very unusual. The process is well-developed but does not extend to the midline, and is therefore intermediate between early taxa (e.g. *Plesiosaurus*) that lack a suture of the scapulae on the midline, and later taxa (e.g. *Cryptoclidus*, *Tricleidus*, all elasmosaurs) where the scapulae meet in a long midline suture (O'Keefe 2001 and references therein). The medial process of the *Tatenectes* scapula is unlike that in any plesiosaur yet known. The condition displayed by *Tatenectes* may be a consequence of ontogeny; Andrews (1910) demonstrated that the medial process is the last part of the scapula to ossify in *Cryptoclidus*. Again, however, the humerus is well-ossified and the neural arches are fused, indicating that the animal was not a juvenile. We therefore accept the configuration of the medial process of the scapula as an adult feature.

The axial skeleton of *Tatenectes* is comprised almost entirely of dorsal vertebrae. The vertebrae are clearly plesiosaurian in having deep, oval-shaped rib articulations on the transverse processes, neural arches more narrow than the centra, and possessing high, blade-like neural spines (O'Keefe 2001 and references therein); however, they lack differentiating characters from within the Plesiosauria. Fortunately there are two posterior cervical vertebrae preserved with the specimen (Figure 1b). The cervicals are not prepared and are exposed on the surface of a weathered block from the concretion, but several characters are apparent. First is the presence of two widely-spaced foramina subcentralia on each centra, proving these vertebrae are plesiosaur cervicals (O'Keefe 2001). These foramina are more widely spaced than they are in *Pantosaurus*. Additionally, the centra are compressed antero-posteriorly, and while measurement was not possible, the vertebrae are clearly more compressed than those of *Pantosaurus*. The cervical rib heads are rounded, not oblong, and are not carried on a pedestal as they are in *Pantosaurus*. Lastly, the rim of the articular facet of each centrum is not well ossified, and the rim is poorly defined, similar to *Tricleidus*, *Cryptoclidus*, and *Kimmerosaurus*, but unlike *Muraenosaurus* or *Pantosaurus*. The present material also lacks the fine striations of the ventral surfaces of the bottoms of the centra observed in the later two taxa. It is impossible to know how long the neck was in this taxon without more material; however, the amount of antero-posterior compression probably indicates that the number of cervicals was probably less than 31, as these two measurements are often correlated (O'Keefe 2002).

The distal humerus fragment from the neotype of *Tatenectes* is illustrated in Figure 1c. The identification of this bone as a humerus seems secure given the fact that it carries articulations for two supernumerary ossifications in the epipodial row; no known plesiosaur femur carries two supernumerary articulations, and when this feature occurs it is always on the humerus. The humerus of *Tatenectes* differs significantly from *Pantosaurus* in that the radial articulation is relatively shorter; this articulation is about as long as that for the ulna, and is more similar to other Oxford Clay cryptocleidoids (Andrews 1910) than to *Pantosaurus* (O'Keefe and Wahl 2003). The radius itself is correspondingly small, and while it is larger than the ulna it again resembles Oxford Clay cryptocleidoids in

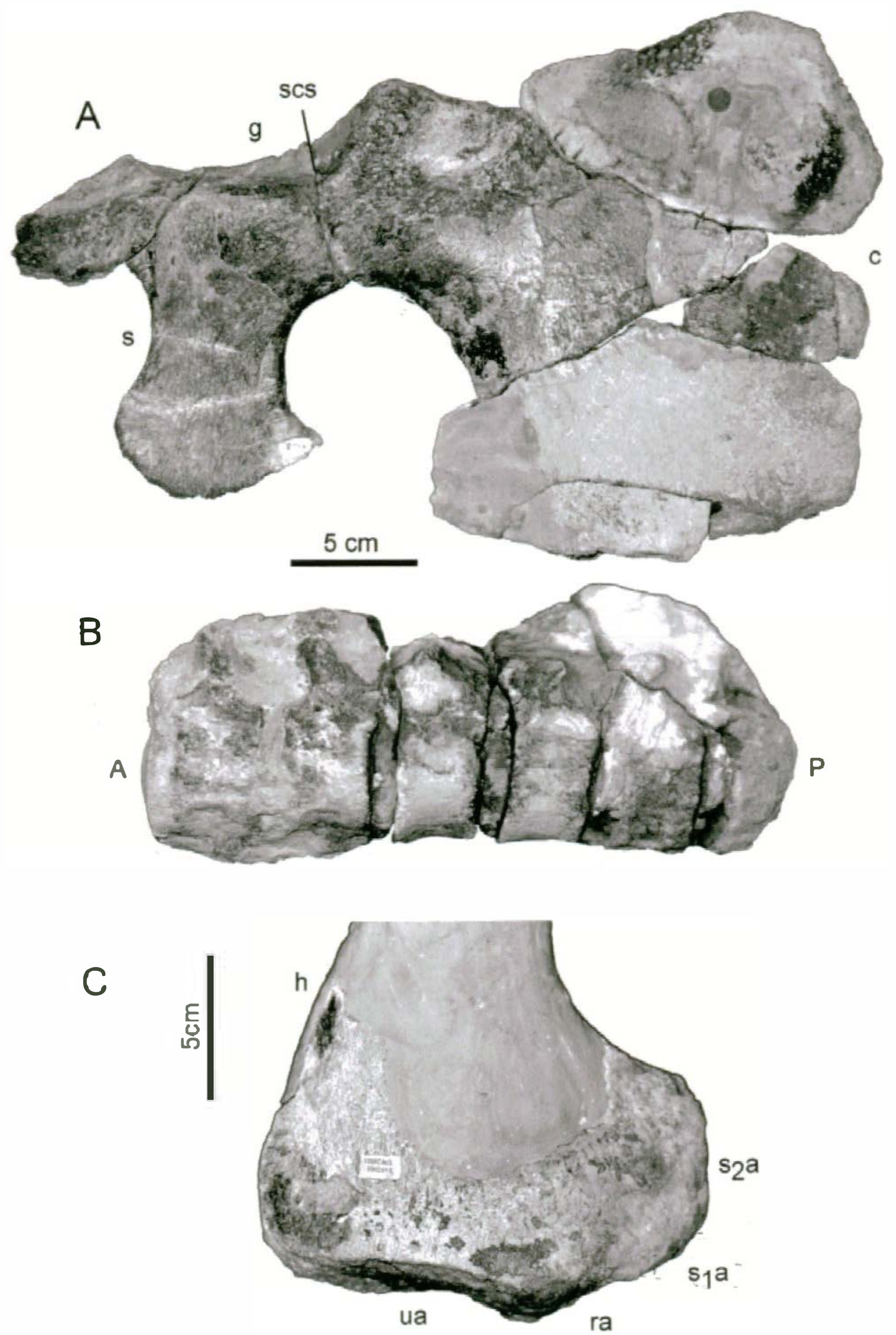

FIGURE 1. Elements of the neotype of *Tatenectes laramiensis* new genus, UW 15943 & UW 24801. A: pectoral girdle. B: cervical and pectoral vertebrae, anterior to the left. C: distal end of humerus. Abbreviations are: c, coracoid; g, glenoid; h, humerus; ra, radius articulation; s, scapula; scs, scapula/coracoid suture; s_1a, supernumerary ossification one articulation; s_2a, supernumerary ossification two articulation; ua, ulna articulation.

relative size. The radius carries a depression in its anterior face, at least in the Knight specimen (illustrated in Mehl 1912); this feature is present in *Muraenosaurus* and *Cryptoclidus* but absent in *Pantosaurus* and *Tricleidus*. The humerus also possesses two articulations for supernumerary ossifications rather than one, resembling *Tricleidus* or *Colymbosaurus* rather than *Muraenosaurus*, *Cryptoclidus*, or *Pantosaurus*. The forelimb of *Tatenectes* is very similar to that of *Tricleidus* in most respects, as acknowledged my Mehl; it is perhaps most similar to *Colymbosaurus* given that that humeral shaft is long and slender relative to *Tricleidus*. It certainly varies in many important respects from the forelimb of *Pantosaurus*.

Cranial Anatomy--Discussion of the cranial anatomy of *Tatenectes laramiensis* is derived from the referred specimen (UW 24215), a partially articulated skeleton comprising a partial skull, an articulated series of cervical vertebrae, and possibly some dorsal vertebrae, although the exact contents of the unprepared portions of the jacket are unknown. Unlike most articulated skeletons from the Redwater Shale, this skeleton is not in a limestone concretion, instead being preserved in the unlaminated gray-green glauconitic shale common to this member of the Sundance Formation. The nature of the matrix makes preparation easy, but has adversely affected preservation; gypsum infiltration is a problem in many of the bones, and many are fractured and incomplete. The referral of this specimen to *Tatenectes* is made on the basis of the cervical vertebrae. These share the proportions and other identifying characters present in the neotype specimen.

The cranial material of UW 24215 comprises several isolated teeth, an essentially complete left squamosal, large portions of the left and right pterygoids, the parasphenoid, and a fragment of the left frontal. The squamosal is illustrated here in Figure 2. This bone is a rather delicate, triradiate element bearing extensive similarities to those of other cryptocleidoid taxa such as *Tricleidus*, *Cryptoclidus*, or *Kimmerosaurus* (Brown 1981; Brown et al 1986). The dorsal process of the squamosal arches over the back of the skull to contact its neighbor on the dorsal midline to form the 'squamosal arch', the apomorphic form of the occiput characteristic of all plesiosaurs (and *Pistosaurus*, O'Keefe 2001 char. 27). This dorsal process is quite gracile, however, and ends in a small bulb for articulation with the opposite squamosal, most similar to the dorsal process of *Tricleidus* (Brown 1981) or the known portions of *Kimmerosaurus* (Brown et al. 1986). The anterior process is again similar to these two taxa, being a gracile process forming the ventral margin of the deep temporal fenestra, and articulating with the jugal anteriorly. The exact nature of this articulation is not discernible due to breakage. The ventral process is long and thin, and carries a long, shallow depression or socket for articulation with the quadrate. The ventral process would have covered the quadrate almost entirely in lateral view, a diagnostic character possessed by all cryptocleidoids including the polycotylids (O'Keefe 2001).

The pterygoids and basicranium are the most diagnostic—and most unusual—elements of *Tatenectes*, and are illustrated in Figure 2. The preserved portions of the left and right pterygoids display the posterior margin of the anterior interpterygoid vacuity medially, but are fragmented anteriorly and laterally, resulting in a lack if information on articulation with maxilla or ectopterygoid. The pterygoids meet in a median suture behind the anterior pterygoid vacuity, and the area of union is expanded dorso-ventrally into a deep block of bone on the midline. This block fills the area of the posterior interpterygoid vacuities present in most other plesiosaurs. We believe this area is composed entirely of pterygoid, although there is no sign of a midline suture. This block of bone continues caudally and then narrows dorso-ventrally while expanding laterally into two processes. Of the two processes the right is the better preserved, and this carries a shallow cup on its dorsal surface. This feature was probably an articulation for the basioccipital tuber. The two lateral processes form a U-shaped excavation in the posterior aspect of the pterygoids. A low boss protrudes from the base of this excavation on the midline; we believe this process articulated with a shallow pit on the anterior face of the basioccipital. This pit is present on the two isolated Redwater Shale basioccipitals (see below), as well as in the basioccipital of *Aristonectes* (Chatterjee and Small 1989).

If this supposition is correct, at least part of the midline block of bone must be composed of basisphenoid, albeit completely enveloped by the pterygoids anteriorly and ventrally. A small shelf of bone is (poorly) preserved on the dorsal surface of the pterygoid block, and this may represent the dorsum sellae and sella turcica. The presence of these features would identify this region as the basisphenoid, and furthermore would place these structures in the correct position relative to the supposed location of the basioccipital (O'Keefe in press b). If the supposed locations of the endochondral braincase elements is correct (i.e. basioccipital and basisphenoid), the palate of *Tatenectes* is extremely derived in that the pterygoids produce a deep ventral process on the midline just beneath the forebrain. This process gives a distinct topography to the palate, one that is very unusual in cryptocleidoids, a group in which the palate is generally planar (O'Keefe in press a).

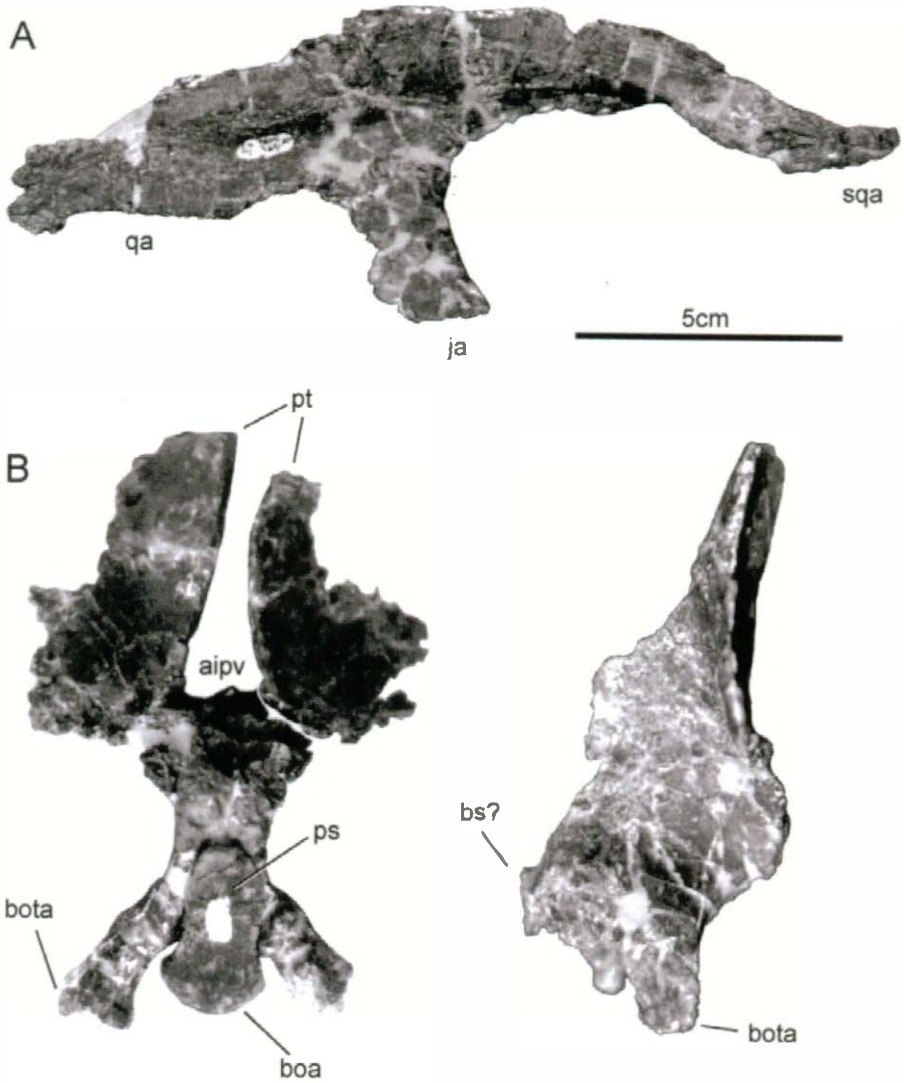

FIGURE 2. Cranial elements of UW 24215. Specimen A is the left squamosal in antero-medial view. Specimen B comprises left and right pterygoid fragments in ventral (left) and lateral (right) views. The ventral view also includes the parasphenoid. Abbreviations are qa, quadrate articulation; ja, jugal articulation; sqa, squamosal articulation; pt, pterygoid; aipv, anterior interpterygoid vacuity; bota, basioccipital tuber articulation; boa, basioccipital articulation; ps, parasphenoid; bs, basisphenoid.

In the ventral view in Figure 2, another element here interpreted as the parasphenoid is included. This element is a small splint of bone that is slightly curved, possessing no clear articulation on its anterior end, but possessing a wide boss with two clear articulations on its posterior end. These articulations presumably contacted the antero-ventral edge of the basioccipital in a condition strongly reminiscent of *Tricleidus* (Andrews 1910). The location of the parasphenoid in Figure 2 is probably too posterior; in life this element probably reached about two-thirds of the way to the anterior interpterygoid vacuity. However, without material found in articulation it is impossible to determine the exact location of the parasphenoid, and the bizarre morphology in this region is difficult to interpret relative to other plesiosaurs. There is some precedent for the parasphenoid occurring ventral to the pterygoids in plesiosaurs, as this condition occurs in *Dolichorhynchops*; however, the morphology of the present taxon differs radically from any polycotylid.

Figure 3 illustrates two other cranial elements. The first is a fragment of the right frontal. This element is broken on all edges except the midline suture. However, the preserved portion does carry a shallow depression on the lateral side, rimmed by a thickened ridge running down the midline, and by a low ridge trending antero-laterally from the midline. These particulars are very similar to the ventral surface of the frontal of *Kimmerosaurus* illustrated by Brown (1981 p. 307), and allow identification of the bone, although neither anterior or posterior sutures are preserved. A small area of finished bone edge is preserved on the lateral edge of the fragment, demonstrating that the frontal was quite narrow in this region, and that the prefrontal and postfrontal did not meet over the orbit. Again these features are very similar to *Kimmerosaurus*. The last element is a single tooth preserving most of the crown and a long, although not complete, root. The crown carries fine striations all around as does *Kaiwhekea* (Cruickshank and Fordyce 2002), although in *Tatenectes* these are more developed on the lingual surface. The tooth crown curves lingually and is slender relative to its length, resembling those of *Kimmerosaurus* (although this taxon lacks tooth striations). The tooth is more robust than those preserved with *Aristonectes* (Chatterjee and Small 1989).

The last cranial element of interest is the basioccipital, two examples of which are known from the Redwater Shale, and neither of which were associated with UW 24215. The first is a weathered specimen in the float collection and was not found associated with other material. The second basioccipital is larger and the preservation is better, and was found with UW 15938. This specimen is an associated, but not articulated, group of cervical and dorsal vertebral centra collected as float over an area of about 25 square meters. The vertebral centra are probably from the same individual and are referable to *Pantosaurus* (O'Keefe and Wahl 2003). The basioccipital seems too small to belong with the cervical centra, but too few of these are preserved to document this quantitatively. Both basioccipitals lack a groove anterior to the occipital condyle and possess exoccipital articulations that intrude into the dorsal surface of the condyle. The dorsal surface of the body of the basioccipital carries a Y-shaped groove of finished bone between the exoccipital articulations. These conditions closely resemble that of *Kimmerosaurs* and differ from that of *Muraenosaurus*. The basioccipital tubers are confluent with the basisphenoid articulation, however, a feature shared by *Tricleidus*, *Aristonectes*, and the polycotylids, but lacking in *Kimmerosaurus*. Given the marked similarity between these isolated basioccipitals and that of *Kimmerosaurus*, it seems probable that they belong to *Tatenectes* rather than *Pantosaurus*; however, until articulated material is found this referral is provisional. The basioccipital is scored as belonging to *Tatenectes* in the cladistic analysis below; exclusion of this material does not effect the resulting topology.

Axial Skeleton—Preparation of UW 24215 has so far yielded 14 cervical vertebrae, two of which are the articulated atlas/axis complex. Two of these cervicals are illustrated in Figure 4, along with two isolated centra from the float collection. The isolated centra represent the two morphotypes of small plesiosaur cervicals occurring in the Redwater shale. The first, longer centrum is assignable to *Pantosaurus* (O'Keefe and Wahl 2003) by virtue of its possession of the following characters: length of centrum subequal to width; body of centrum constricted; cervical rib articulation carried on a pedestal; cervical rib articulation elongate; fine striations present on the ventral surface of the centrum near the articular faces; and rim of articular faces well ossified. The second centrum is assignable to *Tatenectes* given the following characters: length of centrum much shorter than width; centrum not constricted; cervical rib articulation not carried on pedestal; cervical rib articulation round; no striations on ventral surface, and poorly ossified articular rims. The UW 24215 cervicals are clearly assignable to the second of these morphotypes as they possess all of the diagnostic characters listed.

The foramina subcentralia are prominent but not otherwise remarkable, and the centra lack both a ventral and lateral keel. The cervical ribs are large, single-headed, and lack anterior processes. Several of the cervicals preserve neural arches, and these are fused to the centra, although the suture between arch and centrum is clearly apparent. The neural spines are not compressed, are angled backward, and are rather

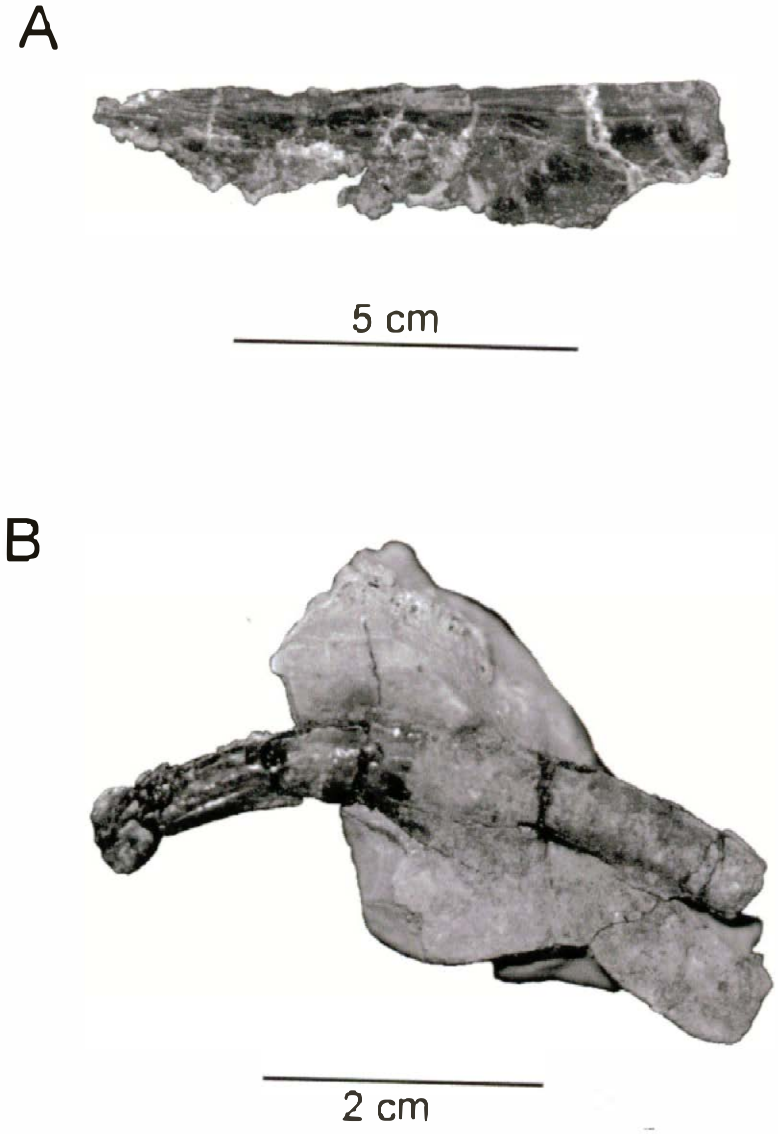

FIGURE 3. Cranial elements of UW 24215. Specimen A is a fragment of the left frontal in ventral view. Specimen B is an isolated tooth partially freed from matrix.

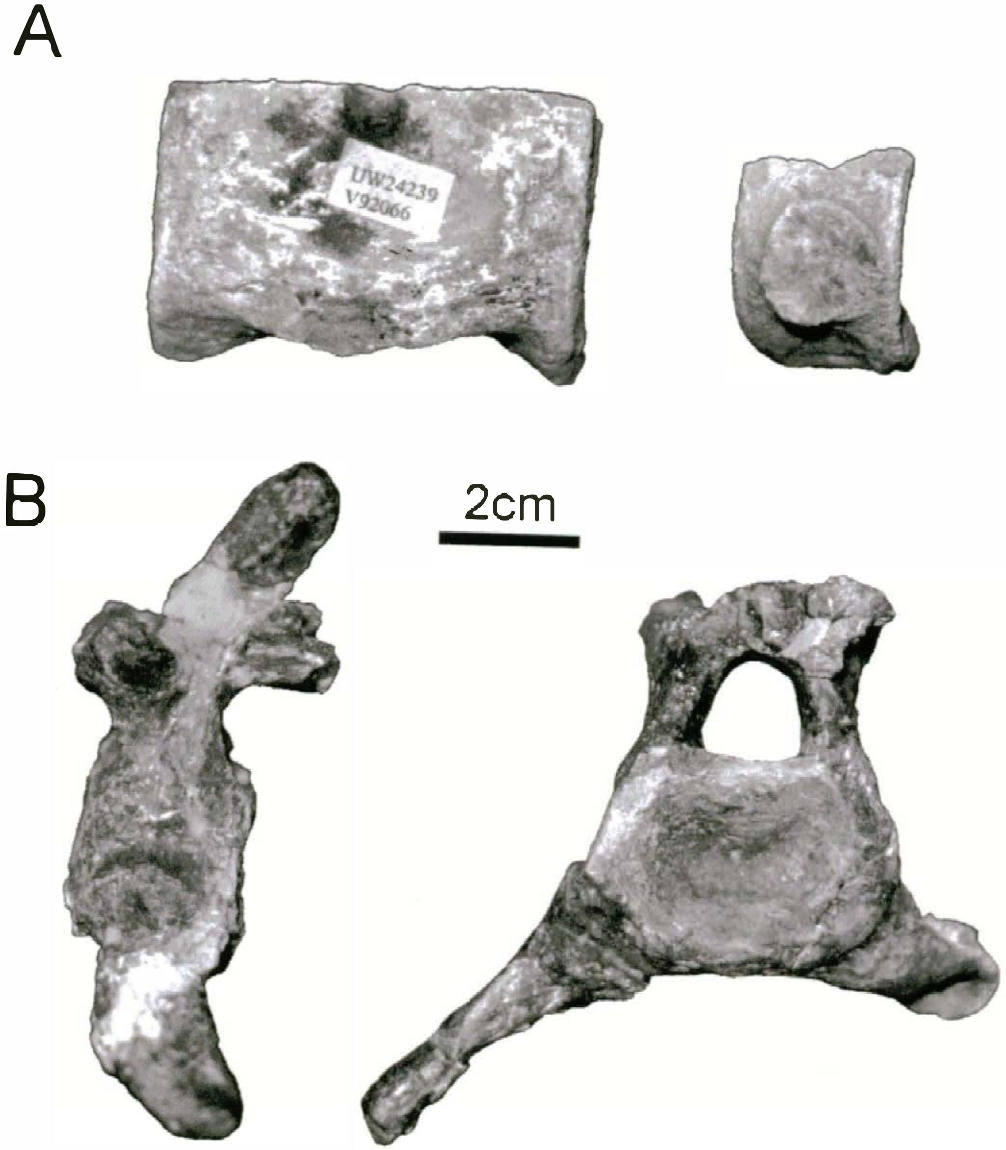

FIGURE 4. Cervical vertebrae of *Tatenectes*, with representative vertebral centra of Redwater Shale plesiosaurs for comparison. Top left is an isolated float specimen, UW 24239, referable to *Pantosaurus striatus*. Top right is an isolated float specimen, UW unnumbered, referable to *Tatenectes laramiensis*. Bottom two vertebrae are cervicals from UW 24215 *Tatenectes laramiensis* referred specimen, left is in left lateral view, right is in posterior view.

short. In general terms the cervicals of *Tatenectes* are closely comparable to those of *Kimmerosaurus* (Brown et al. 1986), the only difference being that the neural spines of the later taxon are not angled backwards.

The atlas neural arch contacts the atlas intercentrum laterally, excluding the atlas centrum from the rim of the occipital articulation. This is the condition in most plesiosaurs (and in amniotes generally, Romer 1956) but not *Muraenosaurus* or *Cryptoclidus* (Andrews 1910). The atlas carries a well-developed atlas rib, accompanied by a very large rib on the axis. Ventrally, the axis intercentrum carries a prominent ridge on the midline; this feature was termed the 'hypapophysial ridge' by Andrews (1910 p. 168), and occurs in *Muraenosaurus*, *Cryptoclidus*, *Tricleidus*, and *Polycotylus*, but is poorly developed in *Dolichorhynchops*, *Trinacromerum* (pers. obs.), and *Aristonectes* (Chatterjee and Small 1989). This feature is absent in elasmosaurs (Welles 1943, plate 22), pliosaurs (Andrews 1913) and in more primitive plesiosaurs (Andrews 1909). The contact between the atlas and axis intercentra on the ventral midline--illustrated by Williston (1903) and included as a cladistic character by O'Keefe (2001) linking the polycotylids and cimoliasaurid cryptocleidoids-- does seem to be present in *Tatenectes*, although the state of preservation prevents absolute certainty.

CLADISTIC ANALYSIS

In order to develop a hypothesis of relationship for *Tatenectes*, a preliminary cladistic analysis was performed on this taxon, here taken to consist of the neotype material (UW 15943 and UW 24801, UW 24215), and the isolated basioccipitals found as float. Inclusion or removal in the basioccipital characters did not affect the resulting tree topology. The data matrix is an extensively revised and updated version of that found in O'Keefe 2001, and is identical to the one in O'Keefe in press a. The matrix contains 13 taxa scored for 95 morphological characters (for characters see Appendix 1; data matrix is Appendix 2). All analyses were performed using PAUP* 4.0 (Swofford 2001). Sixty-two of the characters are parsimony-informative; autapomorphies were retained in the matrix to aid in the diagnosis of individual genera. The outgroup (*Plesiosaurus* and *Brancasaurus*) was defined prior to parsimony analysis and constrained to be paraphyletic to reflect the topology in O'Keefe 2001, although the same clade topology is obtained with this constraint not in force. Parsimony analysis was performed using the branch-and-bound algorithm and yielded four most-parsimonious trees (MPTs) having a tree length of 160, a consistency index (CI) excluding uninformative characters of .675, and a rescaled consistency index (RCI) of .532. A strict consensus tree of the four MPTs is presented in Figure 7. Bootstrap percentages based on 1000 replicates, as well as decay indices, are presented next to the relevant node on the cladogram.

DISCUSSION

Taxonomy of *Tatenectes*--The taxonomic issues surrounding *Tatenectes laramiensis* are complex. The taxon was originally erected by W.C. Knight (1900) as '*Cimoliosaurus*' *laramiensis*, based on a specimen consisting of a partial axial skeleton and a nearly complete front limb. Mehl (1912) reexamined Knight's material, and some new material of his own, and concluded that two plesiosaur taxa were present in the Redwater Shale. Mehl therefore took '*Cimoliosaurus*' *laramiensis* as a valid taxon, but felt that the genus *Cimoliosaurus* was a *nomen dubium*. He then assigned the name '*Tricleidus*?' *laramiensis* to the taxon to reflect similarities between its humerus and that of the Oxford Clay taxon *Tricleidus*. However it is unclear from Mehl's work that this second taxon is in fact congeneric with *Tricleidus*. This confusion stems at least partially from Mehl's almost exclusive reliance on humerus morphology, which is diagnostic in the case of *Pantosaurus* but probably not for the second taxon (also see discussion in O'Keefe and Wahl 2003).

The humerus of *Tatenectes* is in fact quite similar to that of *Tricleidus*: the radial and ulnar articular facets are subequal in length; the distal end of the humerus possesses clear articulations for two supernumerary ossifications in the propodial row, the second of which makes a roughly 90 degree angle with the epipodial articulations; and the anterior edge of the humerus carries a continuation of the radial articulation (similar to *Tricleidus* and *Muraenosaurus* but differing from *Pantosaurus*; Figure 5). The only particular in which the Wyoming humerus differs is the shaft, which is significantly longer and more gracile than in *Tricleidus* (see Mehl's illustration of Knight's original specimen, reproduced here as Figure 5. This limb is certainly a forelimb, because the tuberosity is offset to the posterior aspect of the shaft, as is the case in many cryptocleidoid humeri but no known femur [Andrews 1910, O'Keefe and Wahl 2003], and possesses articulations for two supernumerary ossifications, a feature also found only in humeri). Therefore, if we accept Mehl's characterization of his taxon '*Tricleidus*'? *laramiensis* on the basis of characters of the humerus alone, it can be demonstrated that it differs from *Pantosaurus*. However, it cannot be conclusively demonstrated that it differs from the Oxford Clay *Tricleidus*. To complicate matters further, the original holotype of '*Cimoliosaurus*' *laramiensis* Knight 1900 has been lost. Knight figured the humerus of his holotype, but not the axial column.

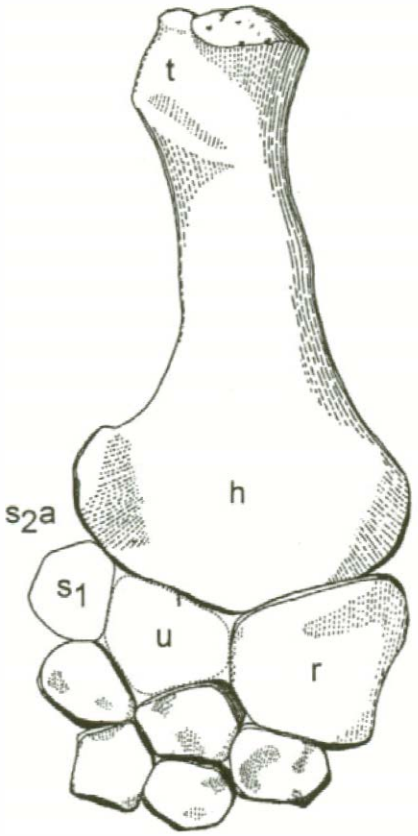

FIGURE 5. Mehl's 1912 illustration of the humerus of the holotype of '*Cimoliosaurus*' *laramiensis* Knight 1900; labels have been added. Abbreviations are: h, humerus; r, radius; s_1, supernumerary ossification one; s_2a, supernumerary ossification two articulation; u, ulna.

Fortunately, it is possible to characterize Knight's holotype further from his original description, because he included measurements of two cervical vertebrae. It is clear from these measurements that the vertebrae are compressed antero-posteriorly-- that they are much wider than they are long-- and so represent the second of the two cervical vertebra morphotypes identifiable in the Redwater Shale (see Figure 4). We therefore can establish an association between the humerus figured by Knight and the compressed cervical morphotype. This association is identical to that observed in one of the new specimens collected by the Tate Museum (UW 15943 & UW 24801). The humerus fragment of this specimen agrees in all particulars with that of Knight's holotype specimen, and the cervical vertebrae are of the compressed morphotype. Given this agreement, we decided to designate (UW 15943 & UW 24801) as the neotype of '*Cimoliosaurus*' *laramiensis*, because it overlaps well with the lost holotype, and shares all of its characters that are now possible to determine. Lastly, it is clear from the pectoral girdle of the neotype that '*Cimoliosaurus*' *laramiensis* is not congeneric with *Tricleidus*. We therefore erected a new genus for the taxon, creating *Tatenectes laramiensis* Knight 1900 (new combination).

Cladistic Analysis and *Aristonectes*--The cranial and cervical material of *Tatenectes* described here, although fragmentary, is sufficient to demonstrate that this taxon is very similar to *Kimmerosaurus* in many respects. The cervical vertebrae are almost identical, as are the squamosal, the frontal, and the general dimensions of the teeth. The cladistic analysis reflects this general impression, with *Tatenectes* falling out as the sister taxon of *Kimmerosaurus* in all MPTs. Both are members of the family Cimoliasauridae as defined by O'Keefe 2001; this taxon of poorly known animals also includes *Aristonectes* from Antarctica and South America. The present analysis finds the recently-described New Zealand taxon *Kaiwhekea* (Cruickshank and Fordyce, 2002) to be the sister group of this family, forming a monophyletic clade with good decay index and bootstrap support. The family Cimoliasauridae should probably be broadened to include *Kaiwhekea*; however, continued instability is seemingly guaranteed in this clade given the lack of knowledge concerning many of its members. Also, the genus *Cimoliasaurus* is a taxonomic morass that must be revised, and the validity (or lack thereof) of the genus name may affect the family name. We therefore refrain from revising the family until the taxonomy at the genus level stabilizes.

The issues surrounding the Cimoliasauridae have been further complicated recently by the publication by Gasparini et al. on *Aristonectes* (2003). These authors have two central contentions, the first being that the genus '*Morturneria*' (Chatterjee and Small 1989) is a junior synonym of *Aristonectes* Cabrera 1941. We have viewed the '*Morturneria*' material, but not that of *Aristonectes*, and so cannot hold an informed opinion about this issue; we have therefore accepted the suggested synonymy in this publication. However, the second contention of Gasparini et al.-- that *Aristonectes* is an elasmosaur, and that there are no cryptocleidoid plesiosaurs in the Late Cretaceous -- is more problematical. The cladogram offered here (Figure 7) clearly places *Aristonectes* within the Cryptocleidoidea and does not cluster it with the primitive elasmosaur *Brancasaurus*, and this is a well-supported finding (bootstrap support .95, decay index six). Furthermore, a cladistic analysis of the entire clade produces the same result. This second analysis was based on a matrix of 35 taxa and 170 characters, and is an updated version of the matrix in O'Keefe (2001). Constraining *Aristonectes* to membership in a clade with the other elasmosaurs resulted in a tree *nine* steps longer than the

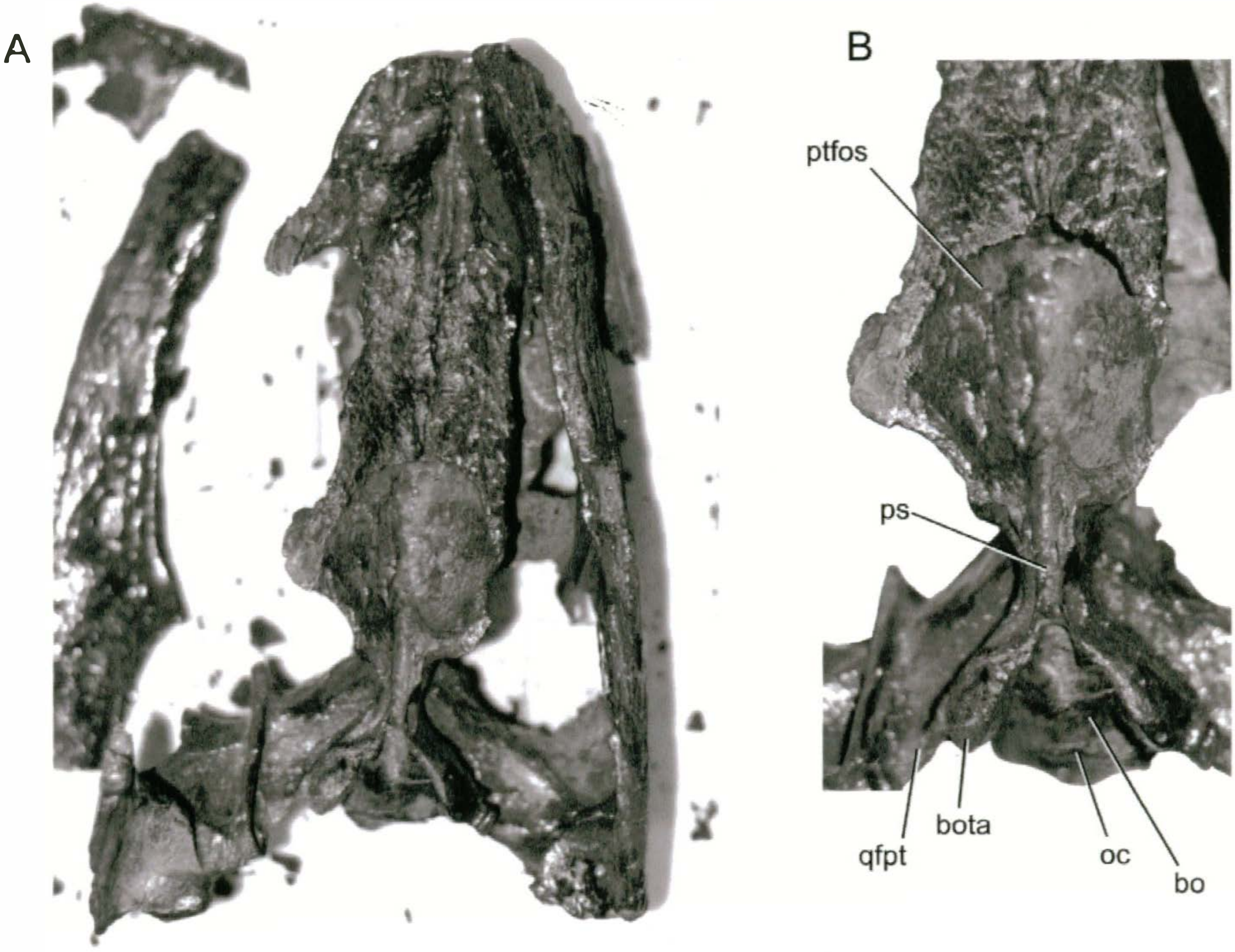

FIGURE 6. Palatal views of USNM 419640, the enigmatic Cuban skull. Abbreviations are: ptfos, pterygoid fossa; ps, parasphenoid; qfpt, quadrate flange of the pterygoid; bota, basioccipital tuber articulation; oc, occipital condyle; bo, basioccipita

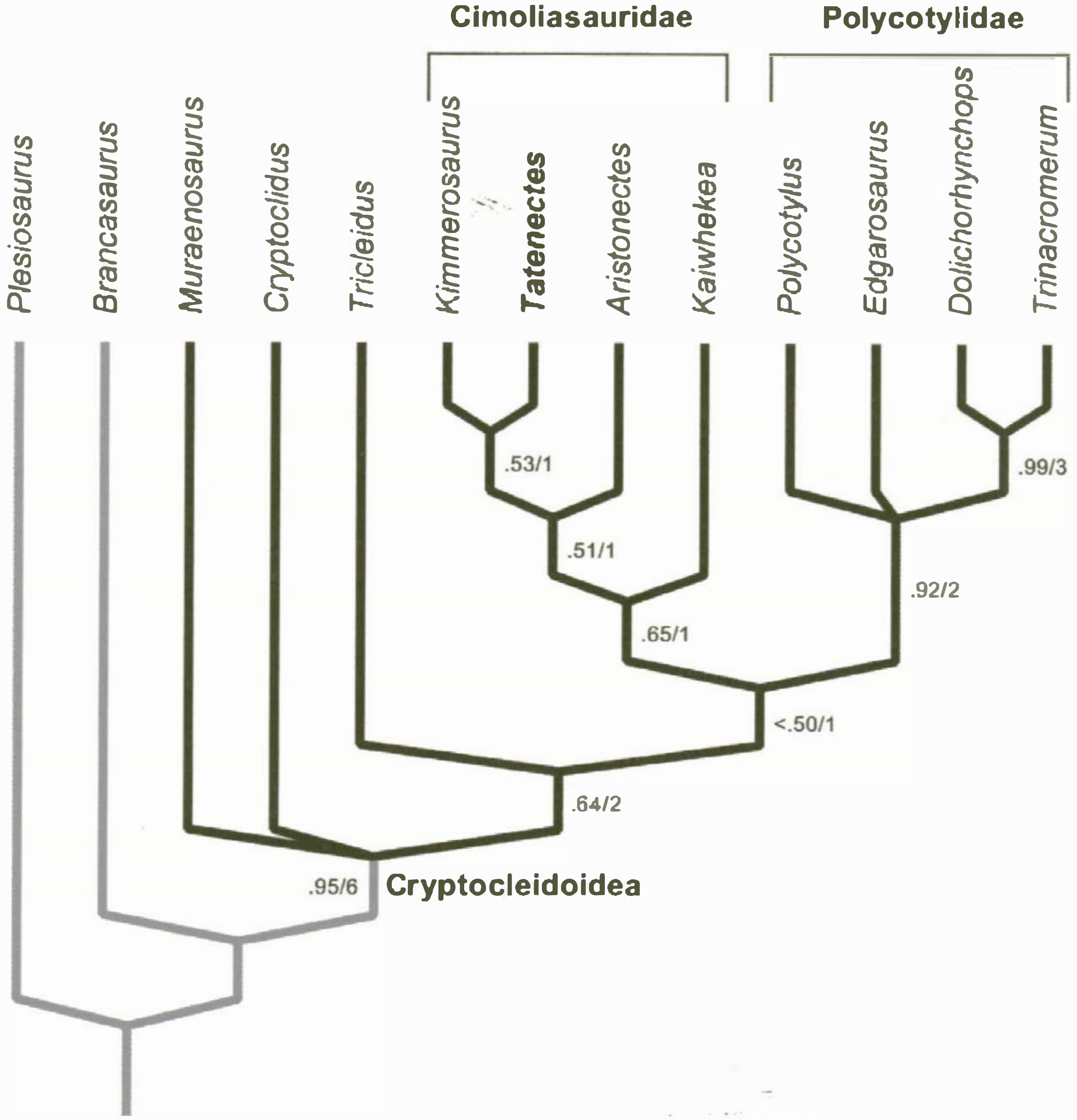

FIGURE 7. Cladogram of the Cryptocleidoidea. Numbers beneath each node are bootstrap values/decay indices. For discussion of the analysis see text.

most parsimonious tree. The cladistic matrix in Gasparini et al. contains ten taxa scored for twenty characters, and those authors do not consider most of the anatomical evidence presented both here and in O'Keefe 2001. Because the Gasparini et al. data set is so restricted, and because the analysis of a more inclusive data set yields a strongly contrary result, we do not accept their conclusion that *Aristonectes* is an elasmosaur. Clearly, the phylogeny of the Cimoliasauridae is a problem demanding immediate research attention.

***Tatenectes* and Future Study**—The most distinctive trait displayed by *Tatenectes* is the deep structure developed by the pterygoids on the posterior palate midline, and the concomitant lack of posterior interpterygoid vacuities. The possession of posterior interpterygoid vacuities is a hallmark of almost all plesiosaurs (O'Keefe in press b, O'Keefe 2001); another is the possession of a planar or nearly planar palate and basicranium. The suite of characters displayed by *Tatenectes* is in fact shared by only one complete skull, a presently undescribed specimen in the Smithsonian Institution (USNM 419640) from the Late Jurassic of Cuba, here illustrated in Figure 6. This skull is apparently from the Jagua Formation (Oxfordian), although it was not listed with the other plesiosaur skulls in the catalogue of Cuban reptile material published by Iturralde-Vinent and Norell (1996). Additional information on the stratigraphy and provenance of Cuban marine reptiles can be found in this reference; the exact provenance of USNM 419640 is currently unknown. The relation of this skull to that described by Gasparini et al. 2002 has yet to be determined.

Unfortunately the Cuban skull is in very poor condition; the skull was apparently collected in a limestone concretion and then acid-prepared, and damage to the bone surface is severe. At present the skull is held together by a thick coat of varnish, with fragments defoliating on all sides, including large portions of the left skull roof and left mandible. No original bone surface or suture is visible on the skull roof or on the mandible fragments. The overall shape of the skull indicates that it belongs to a cryptocleidoid plesiosaur similar to *Tricleidus*. Although this specimen is undoubtedly a new taxon we have chosen not to name it at present, as the state of preservation makes adequate description difficult.

The palate has suffered less from acid damage than has the skull roof, and the one suture visible on the skull— the midline suture on the palate-- is preserved here. The palate is remarkable in that it possesses the union of the pterygoids on the posterior midline, the deep dorso-ventral development of the pterygoids in this region, and the loss of the posterior interpterygoid vacuities, all described above for *Tatenectes*. The Cuban skull also possesses the distinct processes for articulation with the basioccipital tubers present in *Tatenectes*. However, the Cuban skull also lacks an anterior interpterygoid vacuity (present in *Tatenectes*), and in this region the pterygoids develop a deep fossa on the midline. This fossa is identical to one preserved on a large palatal fragment with the '*Morturneria*' type material (not figured by Chatterjee and Small 1989; pers. obs.). While no teeth are preserved with the Cuban skull, the alveoli indicate they were very slender, again as in *Aristonectes*. The Cuban skull, therefore, may be a Late Jurassic representative of the aberrant cryptocleidoid radiation thought to be restricted to the Late Cretaceous of the southern hemisphere by Cruickshank and Fordyce (2002).

The anatomy of the palate of *Tatenectes* is bizarre, although not as bizarre as that displayed by the Cretaceous cimoliasaurids, with whom it shares many traits. *Tatenectes* retains an anterior interpterygoid vacuity as in *Kimmerosaurus* and other cryptocleidoids. The skull of *Tatenectes* is also similar to that of *Kimmerosaurus* in other respects, such as the squamosal, the frontal, and the dentition, and in *Kimmerosaurus* there is at least some development of medial processes of the pterygoids (Brown 1981 p. 308). *Tatenectes* can therefore be thought of as intermediate between *Kimmerosaurus* on one hand and the derived cimoliasaurids-- *Aristonectes*, *Kaiwhekea*, and the Cuban taxon-- on the other. As such it is of critical importance, because it has the potential to untangle the anatomy and relationships of this strange group of animals. There is no cladistic support for this hypothesis as present apart from the sister relationship between *Kimmerosaurus* and *Tatenectes*; the taxa *Kaiwhekea* and *Aristonectes* actually fall more basal than the former taxa in the cladogram in Figure 7. We believe this result is due to the large amount of missing data for *Kaiwhekea* and *Aristonectes*; much of the detailed anatomy of these taxa is simply not available.

It is becoming clear that a large radiation of cryptocleidoid plesiosaurs occurred in the Late Jurassic, giving rise to long-necked forms (*Muraenosaurus* and *Pantosaurus*), short -necked forms (the Polycotylidae), and the aberrant Cimoliasauridae. More research is badly needed on this interesting time in plesiosaur evolution, beginning with the fauna of the Redwater Shale and *Tatenectes* in particular. This taxon may prove to be the sister taxon of the Cretaceous cimoliasaurids, but to demonstrate this more and better cranial material of *Tatenectes* must be found. Lastly, research attention on the cimoliasaurids is long overdue.

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Appendix 1. Cladistic characters used in phylogenetic analysis. For more complete character descriptions of characters 1-88 see O'Keefe 2001.

	Character	States/Coding
1	Relative skull length	primitive/ 'nothosaurian' (0), large (1), small (2)
2	Relative neck length	primitive (0), long (1), short (2)
3	Relative length of ischium/pubis	subequal (0), ischium longer (1), pubis longer (2)
4	Relative length of humerus/femur	subequal (0), humerus longer (1), femur longer (2)
5	Preorbital and postorbital skull length	subequal (0), longer preorbital (1), shorter (2)
6	Fin aspect ratio	high (0), low (1)
7	Elongate rostrum	absent (0), premaxilla only (1), very long with maxilla included (2), elongate and hoop-like/ unconstricted (3)
8	Dorso-medial process of premaxilla	contacts frontal (0), contacts parietal at pineal foramen(2), contacts anterior extension of the parietal (1)
9	Premaxilla/ external naris contact	present (0), absent (1)
10	Frontals paired/fused in adult	paired (0), fused (1)
11	Frontal with or without distinct postero-lateral process	without processes (0) with processes (1)
12	Frontal enters margin of temporal fenestra	does not (0) does narrowly (1)
13	Frontal contacts external naris	does contact (0), does not contact (1)
14	Pineal foramen bordered anteriorly by frontals on dorsal skull surface	not bordered by frontal (0), bordered by frontal (1)
15	Frontal process projects into orbit	absent (0), present (1)
16	Parietal skull table	relatively broad (0), constricted (1), sagittal crest (2)
17	Squamosal produces long, thin process covering quadrate laterally	no medial process (0), medial process and socket-like squamosal (1)
18	Squamosal/ postorbital contact	contact (0), no contact (1)
19	Jugal extends anteriorly along ventral orbital margin	anterior margin (0), middle of orbit (1), restricted to posterior margin (2)
20	Jugal forms narrow bar between orbit and temporal emargination	does not (0), does (1)
21	Maxilla/ squamosal contact	no contact (0), contact (1), expanded posterior flange (2)
22	Exoccipital participates in formation of occipital condyle	do not participate (0), do participate (1)
23	Occipital condyle morphology	hemispherical with groove (0), short with no groove (1)
24	Paraoccipital process morphology	gracile (0), robust (1)
25	Paraoccipital process articulation	squamosal exclusively (0), quadrate exclusively (1), both quadrate and squamosal (2)
26	Ventral extent of paraoccipital process	does not extend ventral to occipital condyle (0), extends past condyle (1)
27	Nature of paraoccipital process/ quadrate pterygoid flange contact	no contact (0), contact at lateral articulation only (1), long contact along bodies of processes (2)
28	Quadrate produces distinct process for articulation with pterygoid flange	process absent (0), process present (1)
29	Dorsal wing of epipterygoid	broad/ columnar (0), reduced (1)
30	Epipterygoid dorsal process contacts parietal	contact (0), no contact (1)
31	Quadrate embayed/ dished-shaped anteriorly	massive quadrate (0), dished anteriorly (1)
32	Supraoccipital depth/sigmoid suture	Shallow (0), deep antero-posteriorly/ sigmoid suture with exoccipital and prootic (1)

33	Squared lappet of pterygoid underlies quadrate pterygoid flange	no squared lappet (0), squared lappet (1)
34	Anterior interpterygoid vacuity	absent (0), slit-like (1), broad with round ends (2)
35	Pterygoids meet posterior to posterior interpterygoid vacuity	pterygoids do not meet (0), pterygoids meet (1), meet but are covered by posterior parasphenoid process (2)
36	Pterygoids meet between anterior and posterior interpterygoid vacuities	do not meet between vacuities (0), do meet between vacuities (1)
37	Columnar ectopterygoid contacts postorbital bar	no contact (0), contact (1)
38	Dished pterygoids	absent (0), present (1)
39	Posterior pterygoid/parasphenoid contact	Absent (0), present (1)
40	Parasphenoid morphology	long, tapering anteriorly (0), short and blunt(1)
41	Parasphenoid exposure anterior to posterior interpterygoid vacuities	anterior parasphenoid not exposed on palate surface (0), exposed via extension of posterior interpterygoid vacuities (1), exposed with lateral pterygoid sutures (2)
42	Parasphenoid/ basioccipital contact on midline.	absent (0), present (1)
43	Basioccipital tubers reduced	not reduced (0), reduced/ tuber facets confluent with basisphenoid articulation (1)
44	Palatine/ internal naris	palatine enters internal naris border (0), excluded by vomer/maxilla contact (1)
45	Premaxilla/ anterior border of internal naris	premaxilla enters anterior border (0), is excluded by vomer/ maxilla contact (1)
46	Sub-orbital fenestration	absent (0), present (1)
47	Vomers extend far posterior to internal nares on midline	do not (0), extend posterior and meet pterygoids in wide interdigitating suture (1)
48	Mandibular symphysis	short (0), somewhat enforced (1), scooplike (2), long (3)
49	Splenial participates in symphysis	does not participate (0), does participate (1), angulars extend past symphysis (2)
50	Coronoid	present (0), absent (1)
51	Coronoid exposed on lateral jaw surface	no exposure (0), exposure (1)
52	Prearticular shelf/ groove	absent (0), present (1)
53	Jaw articulation in relation to tooth row	above or at collinear with tooth row (0), lower than tooth row (1)
54	One or two caniniform teeth on maxilla	present (1), absent (0)
55	tooth form	gracile, small root, narrow, no wear (0) robust, large root, wear (1), very small/needle-like (2)
56	number of premaxillary teeth	5 (0), 6(1), 7(2), greater than 7(3)
57	Maxillary teeth	less than twenty (0), more twenty to thirty (1), many more than thirty (2)
58	Articulation of axis rib	broad articulation with atlas centrum and/or other elements (0), head confined to axis centrum (1)
59	Atlas/axis morphology	no lateral exposure of atlas centrum on cup face (0), lateral exposure (1), no lateral exposure, but atlas and axis intercentra exclude atlas centrum ventrally (2)
60	Number of cervical vertebrae	primitive (0), increased (1), reduced (2), greater than 50
61	Proportions of cervical centra	length equal to height (0), length greater than height (1), length less than height (2)
62	Distinct change in zygopophyseal angle along cervical column	no change in angle (0), change (1)
63	Ventral keel on cervical vertebrae	absent (0), present (1)
64	Binocular shaped anterior cervical centra	absent (0), present (1)
65	Width of cervical zygopophyses	wider than centrum (0), subequal with centrum (1), more narrow than centrum (2)

66	Posterior articulation for succeeding neural spine, cervical vertebrae	absent (0), present (1)
67	Cervical rib articulation greatly elongate/ cervical ribs expanded and blade-like	circular or subcircular (0), elongate (1)
68	Anterior process of cervical ribs	present (0), absent (1)
69	Anterior neural flange on cervical neural spines	absent (0), present (1)
70	Neural spines, cervical vertebrae	angled backward (0), not angled (1)
71	Lateral compression of neural spines, dorsal and cervical vertebrae	not compressed (0), compressed and blade-like (1)
72	Interclavicle posterior process	present (0), absent (1)
73	Presence of clavicles and interclavicle	present (0), interclavicle absent (1), both absent (2)
74	Clavicle median symphysis	symphysis (0), separated by interclavicle (1), meet only behind notch (2)
75	Scapulae meet in anterior median symphysis	separated by clavicles/interclavicle (0), meet medially but leave notch for dermal elements (1), meet in long symphysis with no notch (2)
76	Anterior intrascapular fenestra	absent (0), present (1)
77	Longitudinal pectoral bar	absent (0), formed by clavicle and coracoid (1), formed by scapula and coracoid (2)
78	Median coracoid perforations	absent (0), present (1)
79	Posterior coracoid extension with deep median embayment	absent (0), present (1)
80	Pubis ventral (medial) margin	convex (1), concave (0)
81	Median pelvic bar	absent (0), present (1)
82	Angled humerus	absent (1), present (0)
83	Distal end of humerus has two distinct planes in adult	absent (0), present (1)
84	Distinct facet on distal humerus for supernumery ossification	absent (0), present (1)
85	Distinctly lunate ulna	absent (0), present (1)
86	Epipodial morphology	longer than broad (0), equal or broader than long (1)
87	Supernumery ossifications, forelimb	none (0), epipodial row/pisiform (1), propodial (2), both (3)
88	Interlocking distal phalanges anterior to fifth phalangeal row	absent (0), present (1)
89	Marked groove around margin of dorsal and cervical vertebral articular surfaces	absent (0), present (1)
90	Process of postorbital extends posteriorly along lateral margin of temporal fenestra	present (1), absent (0)
91	Deep notch in posterior margin of clivus	present (1), absent (0)
92	Length of retroarticular process	short (0), long (1)
93	Width of central pterygoid plate	central plate absent (0), narrow (1), broad (2)
94	Height of sagittal crest	low (0), high (1)
95	Sigmoid humeral shaft	absent (0), present (1)

Appendix 2. Cladistic character data used in phylogenetic analysis.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
Plesiosaurus	0	0	2	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	1
Muraenosaurus	2	1	0	2	0	1	0	0	0	0	0	0	0	1	0	2	1	0	2
Cryptoclidus	2	0	0	2	0	1	0	0	0	0	0	0	1	1	0	2	1	0	2
Tricleidus	2	0	?	0	2	1	0	0	0	0	?	0	?	0	0	2	1	?	2
Kimmerosaurus	?	?	?	?	2	?	3	0	?	0	0	0	?	1	0	2	1	?	?
Aristonectes	?	?	?	?	2	1	3	?	?	?	?	?	?	?	?	?	?	1	?
Edgarosaurus	0	2	?	?	0	1	1	0	1	0	0	0	1	0	0	2	1	0	2
Polycotylus	?	2	1	0	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?
Dolichorhynchops	1	2	1	0	1	1	2	1	0	x	0	0	?	0	1	2	1	0	2
Trinacromerum	1	2	1	1	1	1	2	1	0	x	0	0	?	?	1	2	1	0	2
Brancasaurus	2	1	2	0	0	0	0	0	0	1	0	1	?	1	0	2	1	0	2
Tatenectes	?	?	?	?	?	?	?	0	?	0	?	?	?	?	0	?	1	?	?
Kaiwhekea	2	0	?	?	2	1	0	1	0	x	0	?	1	0	0	2	1	?	?

	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38
Plesiosaurus	0	1	?	0	0	?	?	?	1	1	1	1	0	0	1	0	0	0	0
Muraenosaurus	?	?	0	1	0	?	0	?	?	?	?	1	1	0	2	0	0	1	0
Cryptoclidus	1	0	1	1	0	1	0	0	0	?	?	1	1	0	2	0	0	1	0
Tricleidus	1	0	0	0	0	1	1	0	0	?	?	1	?	0	2	0	0	1	0
Kimmerosaurus	1	?	1	1	0	0	0	0	0	?	?	1	1	0	2	0	0	?	0
Aristonectes	?	?	0	0	1	0	?	1	?	?	?	1	1	?	?	?	0	?	0
Edgarosaurus	0	2	0	0	1	?	?	?	0	?	?	?	1	0	2	1	0	1	1
Polycotylus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Dolichorhynchops	0	2	0	0	0	1	1	1	0	0	0	1	1	0	2	2	0	1	1
Trinacromerum	0	2	?	0	0	1	1	?	?	0	0	1	?	1	2	2	0	?	1
Brancasaurus	0	1	0	0	0	?	0	?	?	?	?	0	1	?	0	?	?	?	0
Tatenectes	1	?	1	1	?	?	?	?	?	0	?	?	?	?	2	?	1	?	0
Kaiwhekea	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?

	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57
Plesiosaurus	0	0	1	0	0	0	0	0	0	0	?	?	0	0	0	0	0	0	?
Muraenosaurus	0	1	1	0	0	1	0	0	1	0	0	0	1	1	0	0	0	0	0
Cryptoclidus	0	1	2	0	0	0	?	0	0	0	0	0	1	1	0	0	0	1	0
Tricleidus	1	1	2	1	1	?	0	?	0	0	0	0	?	1	1	0	0	0	?
Kimmerosaurus	1	?	2	1	0&1	?	?	?	?	0	0	1	1	1	1	0	2	3	2
Aristonectes	?	1	2	1	1	0	1	?	?	?	?	?	?	0	1	0	2	2	2
Edgarosaurus	1	1	2	?	?	?	?	0	?	2	1	0	1	1	1	1	1	1	0
Polycotylus	?	?	?	1	?	?	?	?	?	?	?	0	1	1	1	?	1	?	?
Dolichorhynchops	1	1	2	1	1	0	1	1	0	3	2	0	1	1	1	0	0	0	0
Trinacromerum	1	1	2	1	1	?	?	1	?	3	2	?	1	1	1	0	0	0	1
Brancasaurus	0	0	?	0	0	0	1	?	1	?	?	?	?	?	?	0	0	0	?
Tatenectes	1	1	x	1	1	?	?	?	?	?	?	?	?	?	?	?	2	?	?
Kaiwhekea	?	?	?	?	?	?	?	?	?	0	0	?	?	?	0	?	2	2	2

	58	**59**	**60**	**61**	**62**	**63**	**64**	**65**	**66**	**67**	**68**	**69**	**70**	**71**	**72**	**73**	**74**	**75**	**76**
Plesiosaurus	?	0	1	0	?	0	0	2	1	0	0	0	1	1	?	1	0	0	0
Muraenosaurus	0	1	1	1	0	0	?	2	1	1	1	1	1	1	?	0	1	1	1
Cryptoclidus	0	1	0	0	1	0	0	2	0	1	1	1	1	1	?	0	0	1	1
Tricleidus	?	1	0	0	1	0	0	2	1	0	1	1	1	0	0	0	2	1	0
Kimmerosaurus	?	?	?	2	?	0	0	2	?	1	1	?	1	0	?	?	?	?	?
Aristonectes	0	2	?	2	?	?	1	2	?	0	?	?	?	?	?	?	?	?	?
Edgarosaurus	1	2	2	2	?	1	0	?	?	0	?	?	?	?	?	?	?	?	?
Polycotylus	1	2	2	2	0	?	0	1	1	0	?	1	1	0	x	0	2	0	1
Dolichorhynchops	1	2	2	2	1	?	0	2	1	0	?	1	1	0	x	0	2	0	1
Trinacromerum	1	2	2	2	1	?	0	2	1	0	?	1	1	0	x	0	2	0	1
Brancasaurus	1	0	1	1	?	?	0	2	1	0	?	0	0	1	1	0	0	1	?
Tatenectes	?	2	?	2	?	0	1	2	0	0	1	1	0	0	?	?	?	1	?
Kaiwhekea	?	?	1	2	?	1	1	2	?	0	1	?	1	1	?	?	?	?	?

	77	**78**	**79**	**80**	**81**	**82**	**83**	**84**	**85**	**86**	**87**	**88**	**89**	**90**	**91**	**92**	**93**	**94**	**95**
Plesiosaurus	1	0	0	1	1	0	0	0	1	0	1	0	0	1	1	1	0	0	0
Muraenosaurus	2	0	0	1	0	1	1	1	0	1	1	0	1	?	0	0	1	0	0
Cryptoclidus	2	0	0	1	0	1	1	0	0	1	1	0	1	0	0	0	1	0	0
Tricleidus	2	0	0	1	0	1	1	1	0	1	2	?	1	0	0	0	1	0	0
Kimmerosaurus	?	?	?	?	?	?	?	?	?	?	?	?	1	0	?	0	1	0	?
Aristonectes	?	?	?	?	?	1	?	?	?	1	?	?	1	?	?	?	x	?	?
Edgarosaurus	?	?	?	?	?	1	1	1	0	1	?	1	?	0	?	0	2	0	?
Polycotylus	1	1	?	1	0	1	1	1	0	1	3	?	1	?	?	0	1	0	1
Dolichorhynchops	1	1	0	1	0	1	1	0	0	1	3	1	1	0	0	1	2	1	1
Trinacromerum	1	1	0	1	0	1	1	0	0	1	3	1	1	0	0	1	2	0	1
Brancasaurus	2	0	1	0	1	1	?	?	0	1	?	?	0	0	?	1	0	0	0
Tatenectes	0	0	0	?	?	1	1	1	?	1	2&3	?	1	?	?	?	x	?	0
Kaiwhekea	?	?	?	?	?	?	?	?	?	1	?	?	1	?	?	0	?	1	?