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CURRENT TAXONOMIC STATUS OF THE PLESIOSAUR *PANTOSAURUS STRIATUS* FROM THE UPPER JURASSIC SUNDANCE FORMATION, WYOMING

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ABSTRACT

Plesiosaur material has been known from the Redwater Shale member of the Sundance Formation (Jurassic: Oxfordian) of Wyoming for over 100 years, but has received little research attention. Here we report on the taxonomic status of a long-necked cryptocleidoid plesiosaur from the Redwater Shale, the correct identity of which is *Pantosaurus striatus* Marsh 1893. The taxon *Muraenosaurus reedii* Mehl 1912 is shown to be a junior synonym of *Pantosaurus striatus*. *Pantosaurus* is described on the basis of the holotype and referred specimens, and found to be a cryptocleidoid plesiosaur possessing between 35 and 40 cervical vertebrae. These vertebrae are very similar in proportion and anatomical detail to those of *Muraenosaurus leedsii* from the Oxford Clay of England. However, the forelimb of *Pantosaurus* is diagnostic and differs from that of *Muraenosaurus* in several particulars, the most important being the relatively large size of the radius and its corresponding humeral articulation. Although no cranial material is available at this time, we believe that *Pantosaurus striatus* is a valid taxon.

INTRODUCTION

This paper concerns the current taxonomic status of a long-necked cryptocleidoid plesiosaur from the Upper Jurassic Sundance formation of Wyoming. Jurassic plesiosaur material from Wyoming has been known since the 19th century, but has received comparatively little research attention. Recent field work by teams from the Tate Museum in Casper, Wyoming has succeeded in gathering significant new plesiosaur material from this formation that sheds light on the taxonomy and relationships of Sundance plesiosaurs. Analysis of this material supports Mehl's (1912) conclusion that there are two small cryptocleidoid taxa in the Sundance Formation: *Pantosaurus striatus* Marsh 1893, and a new taxon that is described in a following paper. (O'Keefe and Wahl 2003). This report will review the taxonomic history of the plesiosaur *Pantosaurus striatus*, establish that *Muraenosaurus reedii* is a junior synonym of *Pantosaurus striatus*, discuss new material referable to this taxon, and offer observations on its possible relationships.

Stratigraphic Context--The Sundance Formation is a heterogeneous group of Upper Jurassic marine sediments found widely in Wyoming, Montana, and South Dakota. The Sundance Formation is underlain by the Lower Jurassic Nugget Sandstone Formation, and overlain by the Morrison Formation (Pipiringos 1957). The most fossiliferous of the seven members of the Sundance is the Redwater Shale member identified by Pipiringos, who describes it as: "Redwater shale member: 94' Greenish-black calcareous shale and siltstone; contains thin sandy limestone interbeds and smooth dense septarian limestone concretions; is conspicuously glauconitic, oolitic and fossiliferous throughout; contains *Cardioceras* sp. at the base. *Pachyteuthis "densus"* is common, especially in the lower half. Makes ledgy slope." (Pipiringos 1957 p. 11). The Redwater shale member is believed to be Oxfordian in age, and is therefore slightly younger than the mostly Callovian Oxford Clay. The Redwater Shale member yields disarticulated elements and articulated skeletons (in concretions) of marine reptiles, and was originally termed the '*Baptanodon* beds' by Marsh (1891, 1893).

Taxonomic History--Plesiosaur material (Reptilia: Sauropterygia) from the Redwater Shale Member of the Sundance Formation was first noted by O. C. Marsh in 1891. Marsh first mentioned a plesiosaur specimen during his discussion of the ichthyosaur *Baptanodon* (Marsh 1891), where he devoted a single sentence to a small plesiosaur from the '*Baptanodon* beds' and bestowed the name "*Parasaurus*" on the specimen. Marsh later realized this name was preoccupied, however, and suggested the name *Pantosaurus* for the specimen in 1983 (Marsh 1893). In 1895 Marsh described and figured his Wyoming plesiosaur for the first time: "In 1885, a new outcrop of the *Baptanodon* beds was found in the

Freeze Out mountains in Wyoming, and here several skeletons of *Baptanodon* were obtained, all in concretions of limestone, as in the original locality. One concretion from this new locality enclosed the skeleton of a small Plesiosaur of much interest, being the first Jurassic form observed from this country. This specimen was named by the writer *Parasaurus striatus*, the specific term denoting a characteristic feature of the vertebrae, which are all strongly grooved, as indicated in the one shown in Figure 4, below. This generic name also proved preoccupied, and was replaced by *Pantosaurus*, the name of the species now being *Pantosaurus striatus*.

The skull in this genus was provided with teeth. The neck was long and slender. The vertebrae preserved, resemble most nearly in form and size those of *Plesiosaurus plicatus* Phillips." (Marsh 1895).

Marsh's holotype of *Pantosaurus striatus* still exists and resides in the collections of the Peabody Museum at Yale (specimen YPM 543); however, no trace of teeth or other cranial material is currently with the specimen.

The next worker to deal with Sundance plesiosaurs was W. C. Knight, who described the large pliosaur *Megalneusaurus rex* from the Sundance Formation in 1898. This taxon remains the only large Jurassic pliosaur known from North America, and has received almost no research attention since its original description despite its potential relevance to the anatomy and biogeography of the well-known large pliosaurs from the Jurassic Oxford Clay of England (Andrews 1913). The holotype material of *Megalneusaurus rex* still resides at the University of Wyoming (UW 4602). In a later publication, Knight (1900) also briefly described two other taxa from the same formation, naming one '*Plesiosaurus shirleyensis*' and the other '*Cimoliosaurus*' *laramiensis*.

The matter rested here until 1912, when M. G. Mehl attempted to rationalize the Wyoming material with regard to the then-recent publication of Andrew's seminal first volume on Oxford Clay plesiosaurs (Andrews 1910). Mehl (1912) determined that the taxon '*Plesiosaurus shirleyensis*' Knight was founded on fragmentary and non-diagnostic material, and was therefore not useful-- a *nomen dubium* in modern parlance. However, Knight's original description (1900) mentions fragments of a lower jaw, as well as teeth that were "large, numerous, incurved, elliptical in cross-section, [and with] interior surface of teeth covered with numerous very fine striae." Mehl apparently did not have access to this cranial material at the time of his redescription and does not mention it. Knight also states that 'many' cervical vertebrae were found with the specimen (Knight 1900 p. 115), and that the neck was 'long' (ibid p. 116). Given that none of this material is locatable today, and that Knight did not figure any of it, we are forced to accept Mehl's conclusion that *Plesiosaurus shirleyensis* is a *nomen dubium*. Also, if we hypothesize that this specimen represents the longer-necked of the two Sundance cryptocleidoids, '*Plesiosaurus shirleyensis*' would be a junior synonym of Marsh's *Pantosaurus striatus* in any case.

Mehl (1912) had access to additional plesiosaur material from the Freeze Outs (UW 5544, locality UW V-18001), and this material still resides in the collections of the University of Wyoming. Mehl concurred with Knight in believing that there were probably two valid taxa of small plesiosaurs present in the Sundance Formation (for information on the second taxon see O'Keefe and Wahl 2003). Mehl based this conclusion primarily on humerus morphology (Figures 1,2); one of Mehl's new specimens was a partial forelimb possessing humerus, epi- and metapodials, and some phalanges, while Mehl accepted the forelimb of Knight's holotype material of '*Cimoliosaurus*' *laramiensis* as diagnostic. Both forelimbs were derived and showed undoubted affinities to Oxford Clay taxa such as *Muraenosaurus*, *Cryptoclidus*, and *Tricleidus*. Mehl's specimen still exists in the collections of the University of Wyoming, and was examined in the course of this study (UW 5544). This specimen was given the name *Muraenosaurus reedii* by Mehl, the use of the genus name *Muraenosaurus* indicating similarities between this humerus and that of *Muraenosaurus leedsii*. Mehl also provided a line drawing of a partial propodial from the Yale *Pantosaurus* holotype taken from a photograph, and maintained that the humeri were not similar. However, the similarities between this humerus and that of *Muraenosaurus* are questionable, and comparison with the *Pantosaurus* material was enlightening.

In summary, the taxa erected on potentially diagnostic material and in need of clarification here are: *Pantosaurus striatus* Marsh 1893, holotype YPM 543; *Muraenosaurus reedii* Mehl 1912, holotype UW 5544; and *Tricleidus*? *Laramiensis* Knight (Mehl 1912), holotype lost, but figured in Knight (1900) and Mehl (1912). *Pantosaurus striatus*, and its probable junior synonym *Muraenosaurus reedii,* are handled below, while *Tricleidus*? *Laramiensis* is discussed in the following paper (O'Keefe and Wahl 2003).

MATERIALS

All currently known plesiosaur material from the Redwater Shale was surveyed in the course of this study. The relevant material for the present paper are the *Pantosaurus striatus* holotype at Yale (YPM 543, concreted articulated skeleton); an associated vertebral

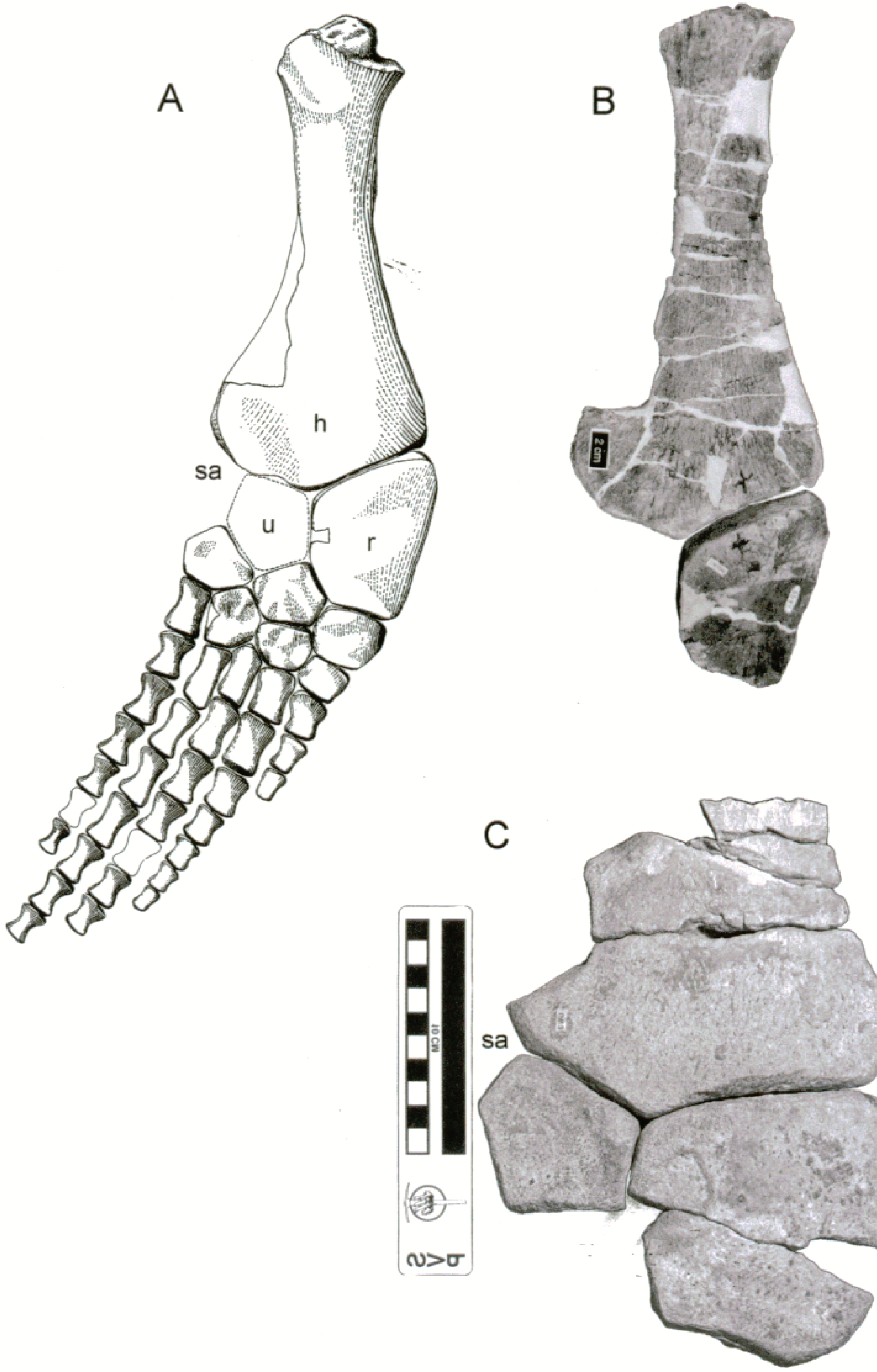

FIGURE 1. Forelimbs of *Pantosaurus striatus* Marsh from the Redwater Shale Member of the Sundance Formation. A: UW 5544 as drawn in Mehl 1912; B: UW 5544, right forelimb in dorsal view; C: UW 3, left forelimb in dorsal view (reversed). Abbreviations are: h, humerus; r, radius; sa, supernumerary ossification articulation; u, ulna.

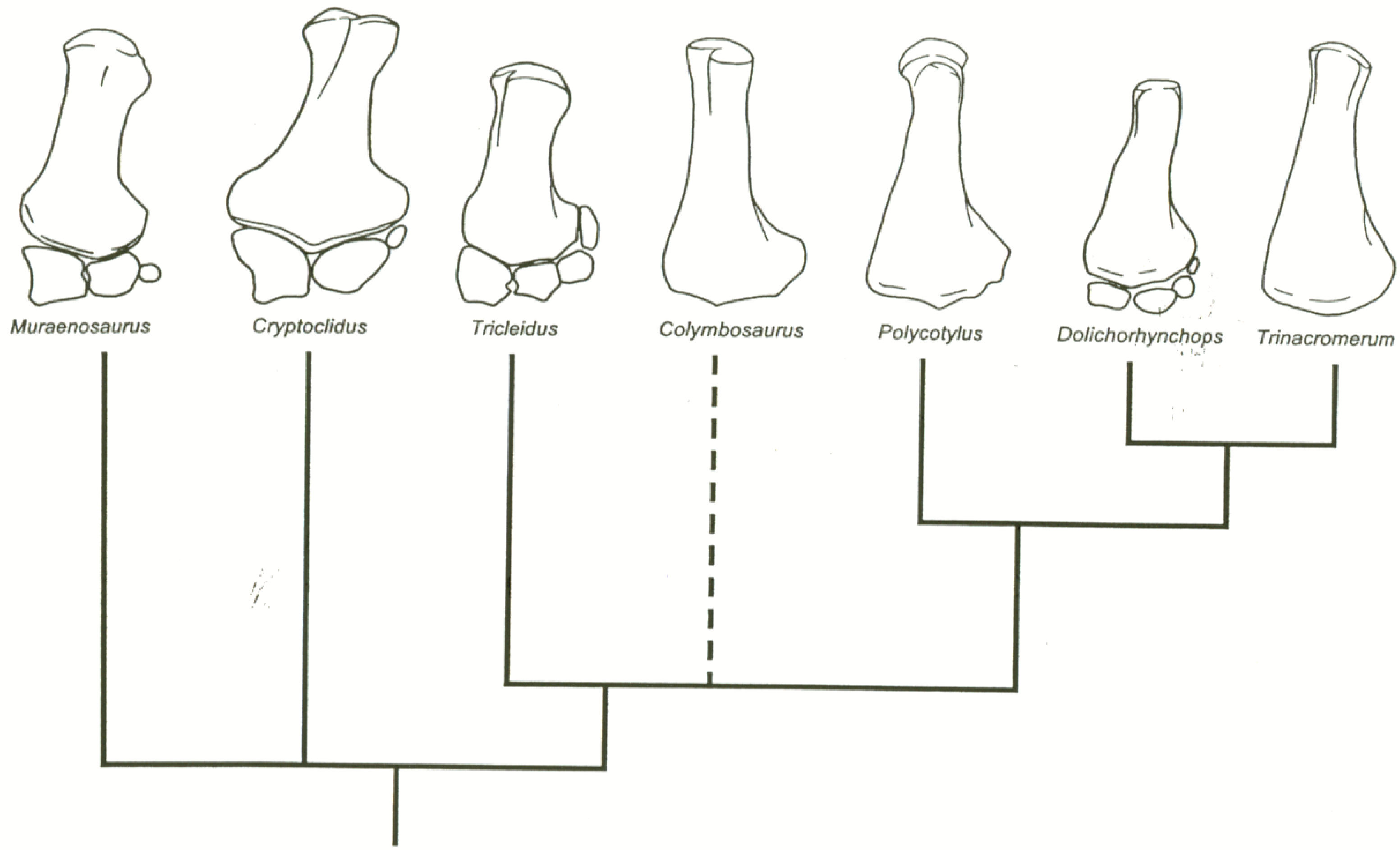

FIGURE 2. Schematic drawings of humeri from relevant cryptocleidoid taxa. Phylogeny modified from O'Keefe 2001, O'Keefe in press. *Colymbosaurus* has not been included in any cladistic analysis to date. First three taxa after Andrews 1910; *Colymbosaurus* after Brown 1981; *Polycotylus* after Williston 1906, *Dolichorhynchops* after Williston 1903; *Trinacromerum* after Williston 1908.

column and basioccipital (UW 15938, collected as float); and a large collection of isolated float gathered from various Redwater Shale localities. All of this material save the Marsh specimen was collected by the staff and volunteers of the Tate Museum, Casper, Wyoming, over the last decade, and we gratefully acknowledge their efforts. The exact location where Marsh's specimen was found is not known, the only recorded information being 'near the Freezeout Mountains' in Carbon County, Wyoming. Mehl (1912) states that his and Knight's specimens also come from this general area. Pipiringos (1957) documents a section of the Sundance Formation in the northern Freezeout Hills, and the historical plesiosaur specimens probably originate from outcrops of the Redwater Shale member in this area.

The UW 15938 specimen was found at a locality off 33 Mile Road near Roughlock Hill in Natrona county, Wyoming, where a large outcrop of Redwater Shale has also yielded several ichthyosaur specimens (Massare and Sperber 1999). Most of the float specimens also originate from this area, including UW 3.

DESCRIPTION

Muraenosaurus reedii Mehl

Mehl's (1912) figure of the *Muraenosaurus reedii* forelimb is reproduced here in Figure 1, along with a recent photograph of the *M. reedii* humerus and radius in articulation (UW 5544). Also illustrated is a well-preserved distal humerus, radius, and ulna (UW 3) from the float collection that is probably referable to the same taxon. Both humeri share several unusual characteristics that are potentially diagnostic. The radial articular facet on the humerus is much longer than the ulnar articulation. In cryptocleidoids the radial articulation is often the longer of the two facets; however this condition is much more pronounced in the Wyoming humeri than in any Oxford Clay taxon (Andrews 1910; Brown 1981 p. 333). The radius is also much larger than then ulna, being about twice the length and breadth of the later element. The humeral shaft is relatively long and rather gracile, more similar to *Colymbosaurus* (Brown 1981) or *Polycotylus* (Williston 1906) than to Oxford Clay taxa such as *Tricleidus*, *Muraenosaurus*, or *Cryptoclidus* (Andrews 1910; Figure 2). The humerus also bears a clear articulation for one supernumerary ossification in the epipodial row, a feature shared by many cryptocleidoids (the condition described by O'Keefe 2001 is an oversimplification. More cryptocleidoid taxa than listed in that paper have this feature [Brown 1981], and it is the possession of *four* facets on the humerus that *Tricleidus* shares with *Colymbosaurus* and *Polycotylus;* see schematics, Figure 2).

This forelimb of *Muraenosaurus reedii* differs from that of *Muraenosaurus leedsii* (Andrews 1910, p. 112; Figure 2) in several respects. The humeral shaft is relatively longer and more slender in the Wyoming taxon, and the radial articulation does not extend onto the anterior edge of the humerus as it does in *M. leedsii*. The radius in *M. leedsii* is also similar in size to the ulna, unlike the derived, large radius in the Wyoming taxon. The Wyoming taxon also lacks the depression in the anterior face of the radius that is present in *M. leedsii*. In summary, Mehl's taxon *Muraenosaurus reedii* is probably not congeneric with *Muraenosaurus* from the Oxford Clay, and displays several characters that are potentially diagnostic.

Pantosaurus striatus Marsh

The type material of *Pantosaurus* (YPM 543) is a partial skeleton preserved in a hard limestone concretion, portions of which have been prepared out to yield a distal humerus, four articulated carpals, a fragment of coracoid (Figure 3), and several isolated cervical vertebrae (Figure 4). The preservation of all elements is excellent and the bone is not deformed. Many ribs and rib fragments occur on and in the concretion; the ribs are not articulated with the dorsal vertebrae and are quite disorganized. The axial skeleton comprises an articulated string of cervical and dorsal vertebrae, broken into several sections. The anterior end of the cervical series is numbered '1' in orange paint, although it is not an atlas or axis. The column is numbered sequentially through the pectoral series and into the dorsal series, and the last numbered vertebra seems to be number '42'. The transition from cervical to pectoral vertebrae occurs around vertebrae '32'-'34', although the exact transition from cervical to pectoral is not prepared. There are therefore about 32 or 33 preserved cervical vertebrae with the specimen. Most are still in the limestone concretion and the state of preparation varies, although one centrum freed from matrix is depicted in Figure 4.

The vertebrae at the anterior end of the cervical column possess very low neural spines that are blade-like, much as in *Cryptoclidus* (Brown 1981) or *Muraenosaurus* (Andrews 1910). However, the neural spines in *Pantosaurus* are angled backward more than those of the former taxa. The cervical centra are remarkable in several respects. The centra are rather long antero-posteriorly, although they are a bit shorter than they are wide; in general proportion the centra are quite similar to *Muraenosaurus*, and longer than in *Kimmerosaurus*, *Tricleidus*, or *Cryptoclidus* (for analysis and data see Figure 5 and discussion below).

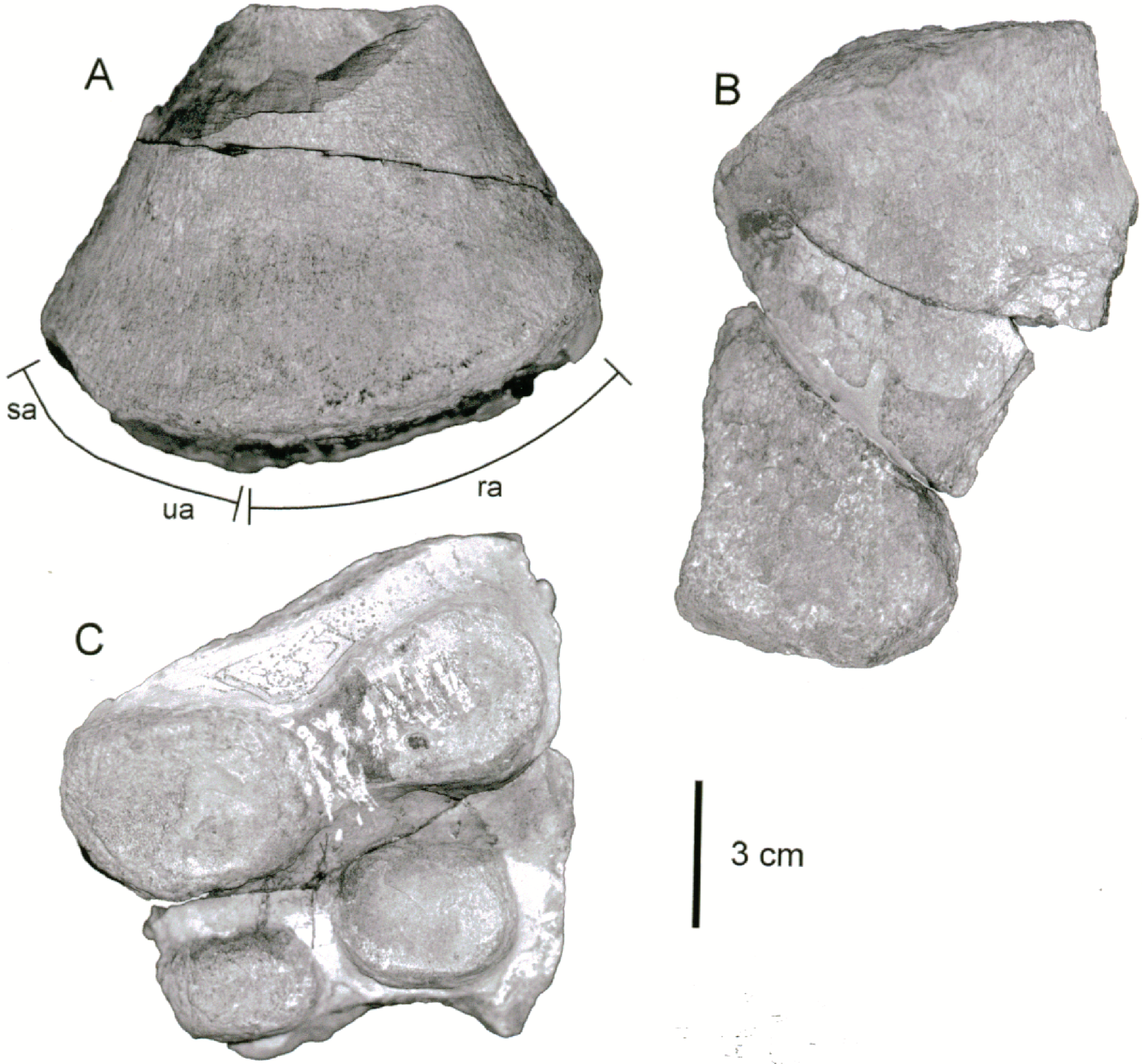

FIGURE 3. Elements of the holotype of *Pantosaurus striatus* Marsh, YPM 543. A, distal end of right humerus. B, fragment of coracoid, probably right. C, articulated group of right carpals. Abbreviations are: ra, radial articulation; ua, ulnar articulation; sa, supernumerary ossification articulation.

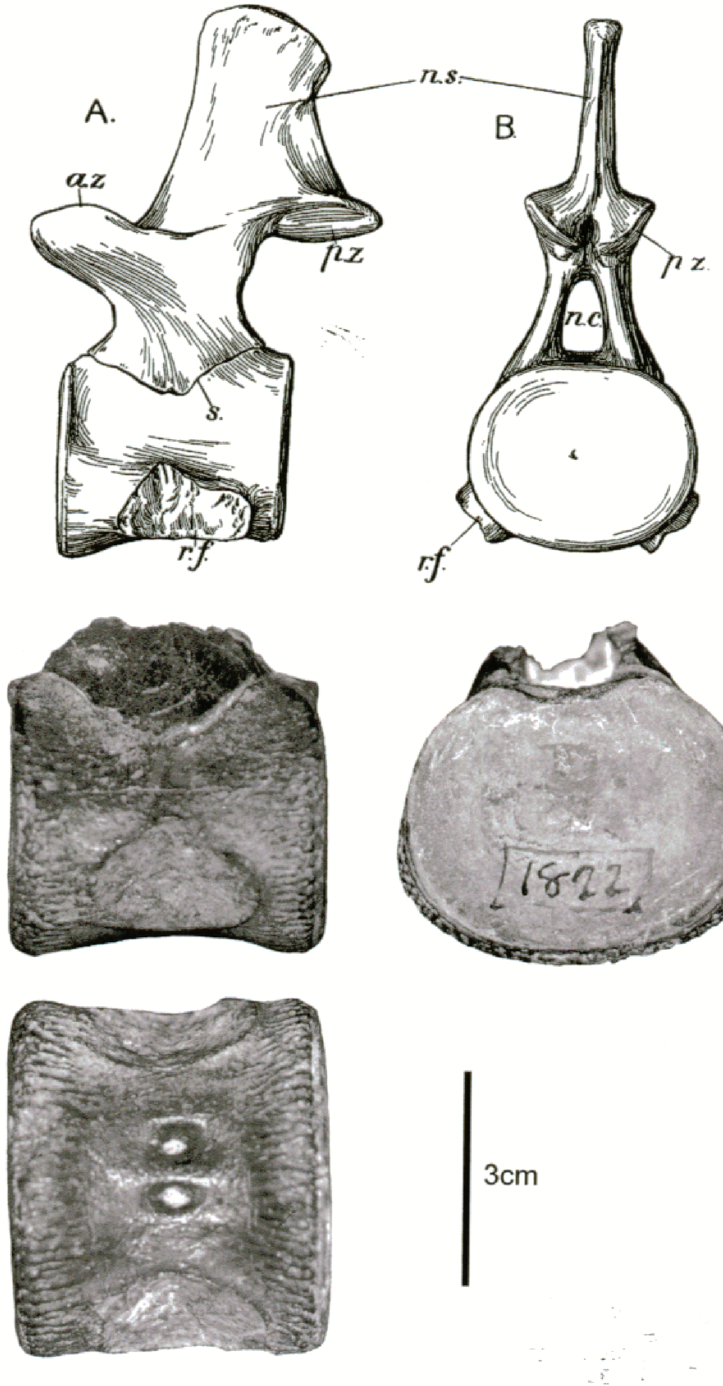

FIGURE 4. Representative cervical vertebra of *Pantosaurus striatus* Marsh, YPM 543. Top two drawings are *Muraenosaurus leedsii*, reproduced from Andrews 1910.

The centra are also 'waisted', meaning that the middle of the centrum has a smaller diameter than either articular face. The foramina subcentralia occur on the ventral surface of the centrum as they do in all plesiosaurs, and are closely spaced and set at the bottom of small, shallow depressions. The cervical rib head articulation is single and carried on a low pedestal or boss, is elongate antero-posteriorly, and possesses an excursion on its dorsal margin for a process of the cervical rib. The articulation for the neural arch is closer to the anterior articular face than to the posterior. The margins of the articular faces are well-ossified and defined, unlike the condition in *Tricleidus* or *Kimmerosaurus*. In all of these features, *Pantosaurus* is closely comparable to *Muraenosaurus* (compare Figure 4). This similarity extends to the fine striae ornamenting the ventral part of the centrum near both articular faces that so impressed Marsh; the only other taxon possessing this feature is *Muraenosaurus* (Andrews 1910). The vertebral centra of *Pantosaurus* are in fact almost identical to those of *Muraenosaurus*, the only difference being that those of *Pantosaurus* are a bit shorter on average in the antero-posterior direction.

Analysis of *Pantosaurus* neck length--Unfortunately the neck of *Pantosaurus* (UW 543) is not complete; about 33 cervicals are preserved, but the atlas and axis are not, and there is no direct indication of the number of missing cervicals. This number is important because it is highly labile in plesiosaurs and varies among all genera (data in O'Keefe 2002), and so is useful in diagnosing taxa. The posterior portion of the neck is available, however, and some of the vertebrae are exposed well enough for measurement. Measurements were made with dial calipers on the best-preserved of these vertebrae to allow comparison with other cryptocleidoids.

Plots of the antero-posterior lengths of cervical vertebrae are presented in Figure 5. Measurements from five cryptocleidoid taxa are depicted: *Dolichorhynchops*, *Tricleidus*, *Cryptoclidus*, *Muraenosaurus*, and *Pantosaurus*. The data for *Dolichorhynchops* (n=2), *Cryptoclidus* (n=2), and the *Pantosaurus* holotype are taken from the specimens, while data for *Tricleidus* (n=1) and *Muraenosaurus* (n=3) are taken from Andrews (1910). In order to make specimens of different body sizes comparable, the lengths of each vertebra within each column was standardized by dividing each measurement by the length of the fifth cervical vertebra in each column. This transformation effectively sets the length of each fifth cervical equal to one and is a first-order size approximation. Taxa for which multiple specimens were available are pooled into single analyses. The length of the fifth cervical vertebra in *Tricleidus* is not available from Andrews (1910); however, the lengths of the third and seventh vertebrae are identical, and the other measures for this taxon were size-standardized to this length. Because *Pantosaurus* lacks atlas and axis the numbers assigned to the cervical vertebrae are arbitrary. For the purpose of this analysis the vertebra labeled '1' was arbitrarily assigned to position 5 on the column.

Second-order polynomial regressions were fitted to the plots for each taxon; the regression equations are reported in Figure 5 (size-standardized lengths were multiplied by 10 before calculation of the regression equations to improve accuracy of the X^2 coefficient). In *Dolichorhynchops*, the taxon with the least number of cervical vertebrae (c=19), the regression is essentially linear, the coefficient of the X^2 term being .002. As one proceeds caudally down the column the vertebrae get larger, and the length of successive central increases monotonically. However, as the number of cervical vertebrae increases in the series of taxa *Tricleidus* (c=25) --*Cryptoclidus* (c=31) -- *Muraenosaurus* (c=42), the value of the X^2 coefficient decreases (i.e. -.004, -.007. -.009). This decrease indicates that the length of each centrum no longer increases monotonically as cervicals are added to the series. In *Cryptoclidus* the length of the centra stops increasing about c24, but does not decrease, while in *Muraenosaurus* the most posterior centra are actually shorter than those preceding.

The pattern displayed by *Pantosaurus* is interesting. The coefficient of the X^2 term in this regression is -.012, less than any other taxon measured. However, the centra definitely do not decrease in length at the rear of the column, as is the case in *Muraenosaurus*. There are several difficulties here: the actual number of each cervical is not known, there are few measurements to constrain the regression, and the specimen is a juvenile. Given that the lengths of the cervicals do not decrease at the end of the column, we tentatively concluded that the neck in *Pantosaurus* did not include as many vertebrae as *Muraenosaurus*. The constant length of cervicals at the rear of the column most resembles *Cryptoclidus*; however, at least 33 cervicals are preserved with the specimen, and two more were certainly present (i.e. axis and atlas). This constraint puts the minimum number of cervical vertebrae in *Pantosaurus* at 35. Given the lack of centrum length decrease the actually number is probably closer to 35 than to the 42 of *Muraenosaurus*, and 35 or 36 is probably the most likely estimate of the number of cervical vertebrae. More accurate measurements of the *Pantosaurus* axial skeleton may improve this estimate, but this will involved further preparation.

Elements of the appendicular skeleton of *Pantosaurus* are illustrated in Figure 3, including the distal end of a humerus. Examination of the

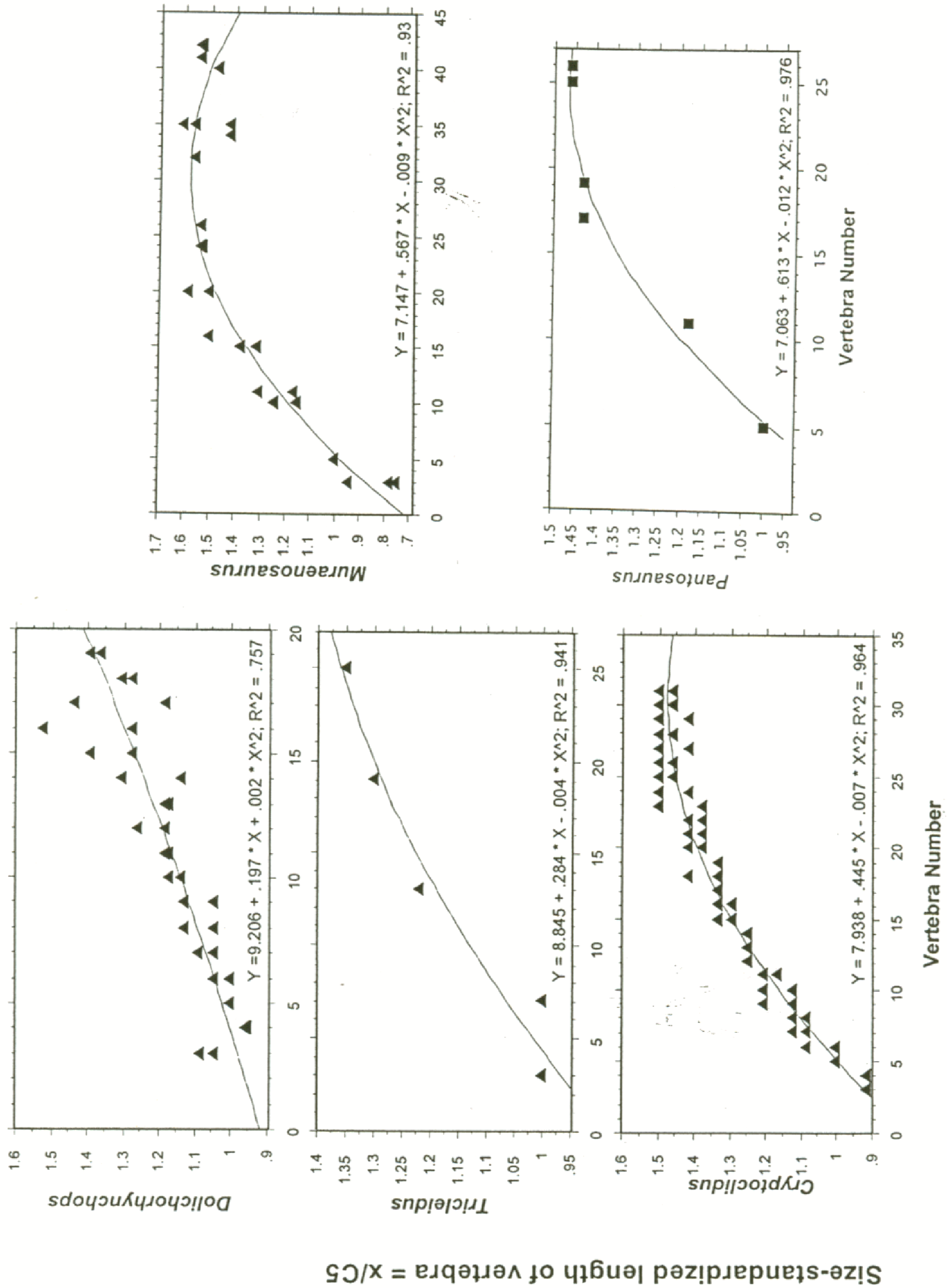

FIGURE 5. Graphs of size-standardized lengths of successive cervical vertebrae, split by taxon. For further discussion see text.

Pantosaurus material reveals that this specimen is probably a juvenile. The articular facets on the distal end of the humerus are poorly defined and ossified, the carpals are rounded and poorly ossified, and the neural arches of the cervical vertebrae are not tightly sutured to the vertebral bodies. All of these features are thought to indicate juvenile status in plesiosaurs (Caldwell 1997; Brown 1981). However, once allowance is made for the ontogenetic lack of ossification, the *Pantosaurus* humerus possesses all of the characters of Mehl's taxon *M. reedii*: the shaft appears to have been slender, there is one articulation for a supernumerary ossification in the epipodial row, and most importantly, the radial articulation is very large relative to the ulnar articulation (Figure 3). The poorly-ossified humerus of *Pantosaurus* is also smaller than either of the *M. reedii* humeri in Figure 1, which is consistent with *Pantosaurus* being a juvenile. The coracoid fragment is identifiable as such given the shape of its cross section and posterior extension, but displays little diagnostic morphology. The carpals are poorly ossified and are not diagnostic of themselves.

DISCUSSION

Mehl (1912) contented that there were two small plesiosaur taxa in the Redwater Shale based on differences he observed in the humeri and epipodials at his disposal. This is somewhat unfortunate as plesiosaur humeri display delayed ossification (Brown 1981) and are marginally diagnostic at best. However, O'Keefe (2001, in press) identified at least four humerus characters that he felt were useful, three of which are found in cryptocleidoids. The humerus in cryptocleidoids varies more, and is more diagnostic, in this group than in most other plesiosaurs (Figure 2), although caution must still be used because the number of diagnostic characters is small and ontogenetic variation is a confounding factor. Given Mehl's designation of the taxon *Muraenosaurus reedii* on the basis of a forelimb (holotype UW 5544), however, we cannot avoid the task of evaluating whether this taxon is valid based on the type material, and furthermore we must determine if the diagnostic characters (if any) can be identified in other Redwater Shale specimens. Another issue is the identification of all three propodials in this paper as forelimbs rather than hindlimbs; this assignment seems safe given that in cryptocleidoids (i.e. *Cryptoclidus*, Andrews 1910) there is a distinct angle between the midline of the humerus and the midline of the distal forelimb. This angle is much less pronounced in the hindlimb. The three limbs shown in Figures 2 and 3 display the pronounced angle observed in other cryptocleidoid forelimbs.

We believe that Mehl's taxon *Muraenosaurus reedii* is valid, and can be demonstrated to be *Pantosaurus striatus* Marsh. Mehl himself (1912) considered and rejected this possibility; however he had only a photograph of the *Pantosaurus* humerus to work from, and may have mistaken two of the four carpals for epipodials. He also did not consider the juvenile status of *Pantosaurus*. Given that the humerus *Muraenosaurus reedii* is distinctive-- especially in the relative size of the radius articulation and the presence of one articulation for a supernumerary ossification-- and that the humerus of *Pantosaurus* seems to display these distinctive characters, we hypothesize that Mehl's taxon *Muraenosaurus reedii* is synonymous with *Pantosaurus striatus* Marsh. Marsh's name has priority as it was the first published; *Muraenosaurus reedii* is therefore a junior synonym of *Pantosaurus striatus* Marsh.

This study supports the conclusion of Mehl (1912) that there is a long-necked cryptocleidoid in the Sundance Formation, and that this taxon is similar to the Oxford Clay taxon *Muraenosaurus*. We further conclude that the correct name of this taxon is *Pantosaurus striatus* Marsh 1893. The holotype of *Pantosaurus* consists of most of a neck, a distal humerus, and other fragmentary girdle bones. This taxon possesses cervical vertebrae very similar to those of *Muraenosaurus leedsii*; however, the humerus and radius are derived and diagnostic. The number of cervical vertebrae in the neck is not known with certainty, but was at least 35, and probably less than 40 based on analyses above. No skull material is currently known for this taxon, the only possibility being an isolated basioccipital collected as float (UW 15938); however it is not clear that this element belongs with the rest of the material as the specimen was not articulated when found.

SYSTEMATIC PALEONTOLOGY

Suborder Plesiosauria de Blainville, 1835
Genus *Pantosaurus* 1893

Type Species--*Pantosaurus striatus*, by monotypy.

Diagnosis--As for species.

Pantosaurus striatus Marsh 1891
(Figures 2, 3, 4)

Synonymy--*Muraenosaurus reedii* Mehl 1912

Holotype--YPM 543, a partial skeleton comprising axial skeleton, ribs, pectoral girdle and limb fragments.

Referred Material--UW 5544 (holotype of '*Muraenosaurus reedii*'), UW 15938, UW 3

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

Diagnosis--A small cryptocleidoid plesiosaur possessing 35-40 cervical vertebrae. The cervical vertebrae are almost as long as they are wide, are waisted, and carry an elongate cervical rib articulation on a pedestal. Foramina subcentralia are small and placed closely together, articular faces of centra have well-ossified rims, and the ventral surface of each centrum carries fine striations near each articular face. Anterior neural spines are low, blade-like, and angled backward. Humerus with long, narrow shaft, radial articulation much longer than ulnar articulation; possessing an articulation for one supernumerary ossification in the epipodial row. Radius much longer and broader than ulna.

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