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# A NEW PARTIAL SKELETON OF A CRYPTOCLEIDOID PLESIOSAUR FROM THE UPPER JURASSIC SUNDANCE FORMATION OF WYOMING

BENJAMIN C. WILHELM and F. ROBIN O'KEEFE

**ABSTRACT**—Cryptocleidoid plesiosaurs from the Upper Jurassic are well known from the Oxford Clay (Callovian) of the United Kingdom. The plesiosaurs of the nearly coeval Sundance Formation (Oxfordian) of North America are poorly known, but are thought to include two cryptocleidoid taxa: *Pantosaurus striatus* and *Tatenectes laramiensis*. Here we present two specimens recently recovered from the Bighorn Basin of Wyoming. The first specimen comprises three articulated adult cervical vertebrae and fragments of a fourth. This specimen preserves a posteriorly directed cervical neural spine, a character diagnostic of *Pantosaurus striatus*. It also resembles *Pantosaurus* in the morphology of its cervical rib articulations. The second specimen is a partial articulated skeleton comprising a complete pelvic girdle, dorsal, sacral, and caudal vertebrae, and numerous ribs and gastralia. This specimen displays a number of unique characters, including posteriorly directed dorsal, sacral, and caudal neural spines, highly autapomorphic illia, and a pathologically asymmetric pelvic girdle. Despite the lack of overlapping material, it is tentatively referred to *Pantosaurus* on the basis of posteriorly directed neural spines. These specimens represent the first significant adult material provisionally referable to *Pantosaurus striatus*, as well as the first posterior axial column and pelvic girdle.

## INTRODUCTION

Cryptocleidoid plesiosaurs of the Upper Jurassic occur commonly in the Oxford Clay (Callovian) of the United Kingdom. Cryptocleidoid taxa from this formation, including *Muraenosaurus* and *Cryptoclidus*, are well known from both cranial and postcranial material and have been described extensively by Andrews (1910). Coeval taxa from outside the Western Tethys Sea are known only from the Jagua Formation of Cuba (Iturralde-Vinent and Norell, 1996; Gasparini et al., 2002) and the Sundance Formation of the western United States; all are comparatively poorly known at present. The Jugua Formation has at least one cryptocleidoid, *Vinialesaurus caroli* De La Torre et al., 1949, known from cranial material only, and of uncertain taxonomic affinities. The Sundance taxa are thought to include two cryptocleidoid plesiosaurs (O'Keefe and Wahl, 2003b), *Tatenectes laramiensis* Knight, 1900, and *Pantosaurus striatus* Marsh, 1891, known mostly from postcranial and disarticulated cranial material.

The new material described herein is provisionally referred to the genus *Pantosaurus* on the basis of the posteriorly directed neural spines seen in both specimens; however, this referral is equivocal for the partial skeleton (see Discussion). The first material of *Pantosaurus*, the anterior axial column and forelimb of a juvenile, was described by Marsh (1891) and named "*Parasaurus*"

*striatus*. This name was preoccupied (Marsh, 1893), necessitating the change to *Pantosaurus*. Marsh formally described and figured the holotype in 1895. Mehl (1912) figured a forelimb from the Sundance Formation, which he referred to “*Muraenosaurus reedii*,” a taxon determined to be a junior synonym of *Pantosaurus striatus* by O’Keefe and Wahl (2003a). Mehl also mentioned holotype material from the posterior axial column, including dorsal and caudal vertebrae, but this material now appears to be lost (O’Keefe, pers. observ., 2003)

O’Keefe and Wahl (2003a) thoroughly reviewed all available *Pantosaurus* material. After more than a decade, *Pantosaurus striatus* is still known from only a handful of specimens, the most complete of which is the holotype, a concretioned, articulated juvenile skeleton (Marsh, 1891). This skeleton displays many similarities to *Muraenosaurus leedsi* of the Oxford Clay, including similar dimensions of the cervical vertebrae, a dorsal excursion on the rib facet for a tubercle of the cervical rib, and striations of the anteroventral and posteroventral edges of the anterior cervical centra. O’Keefe and Wahl (2003a) determined that the holotype was diagnostic based on humeral morphology; the radial articulation is much larger than the ulnar articulation. Additionally, they noted the relatively long cervical vertebral centra and posteriorly directed neural spines present in the holotype. However, because the holotype is a juvenile, comparison to adult material is necessary to see if these characters are true autapomorphies or are attributable to the incomplete ossification of the holotype.

Here we describe two specimens recovered from the Bighorn Basin of Wyoming. The first specimen comprises four articulated cervical vertebrae, whereas the second is a partial skeleton comprising dorsal, sacral, and caudal vertebrae, a nearly complete pelvic girdle, and numerous ribs and gastralia. These specimens represent the first significant adult material provisionally referable to *Pantosaurus striatus*, as well as the first posterior axial column and pelvic girdle.

**Institutional Abbreviations**—USNM, Smithsonian Institution, Washington, D.C.; UW, University of Wyoming, Museum of Geology, Laramie, Wyoming; YPM, Yale Peabody Museum, New Haven, Connecticut.

## GEOLOGICAL SETTING

The Sundance Seaway was a shallow epicontinental seaway that covered much of Wyoming and parts of Montana, South Dakota, and Colorado in the late Jurassic (Kvale et al., 2001). Marine sediments deposited by this seaway in southeastern



FIGURE 1. Map of north-central Wyoming showing Sundance Formation outcrops and localities. Open stars indicate localities of USNM 536963 (1) and USNM 536965 (2). Closed stars indicate localities of University of Wyoming specimens.

Wyoming were named the “Shirley Stage” by Knight (1900), and later the Sundance Formation by Reeside (1919). In the Laramie Basin, Imlay (1947) divided the Sundance Formation into seven members. In the Bighorn Basin, where the specimens described here were recovered, Kvale et al. (2001) divided the Sundance into Lower and Upper Members. This more general division is the one in current use given the lateral heterogeneity of the Sundance Formation and the fact that Imlay’s (1947) detailed stratigraphy is highly localized.

Both specimens reported here were found near the top of the Upper Member of the Sundance Formation, in the equivalent of the ‘Redwater Shale Member’ of Imlay (1947). This set of beds represents the last transgressive-regressive cycle of the Sundance Seaway (Brenner and Peterson, 1994). Molluscan biostratigraphy

places this member in the Oxfordian (Kvale et al., 2001). It is highly fossiliferous, with numerous invertebrate remains and occasional, usually isolated, vertebrate remains. Articulated ichthyosaur remains are locally common, whereas articulated plesiosaur remains are relatively rare (O’Keefe and Street, 2009). Both specimens described here were found in articulation and were discovered in outcrops near the towns of Greybull and Shell, Wyoming (Fig. 1).

## MATERIALS

USNM 536963 comprises three articulated posterior cervical vertebrae and fragments of a fourth; this last is probably the first pectoral. USNM 536965 is a partial articulated skeleton comprising dorsal, sacral, and caudal vertebrae, a nearly complete pelvic girdle, and numerous ribs and gastralia. Embryonic ichthyosaurian gut contents found with this specimen were previously described by O’Keefe et al. (2009). The complete fusion of the neural spines to all centra, and the heavily ossified pelvic girdle, suggest that both new specimens presented here are adult (Brown, 1981).

Both specimens are crushed to some degree, but are not deformed like much of the Oxford Clay plesiosaur material. Vertebral centra are generally well preserved; neural arches and spines are present but crushed laterally in many cases, whereas

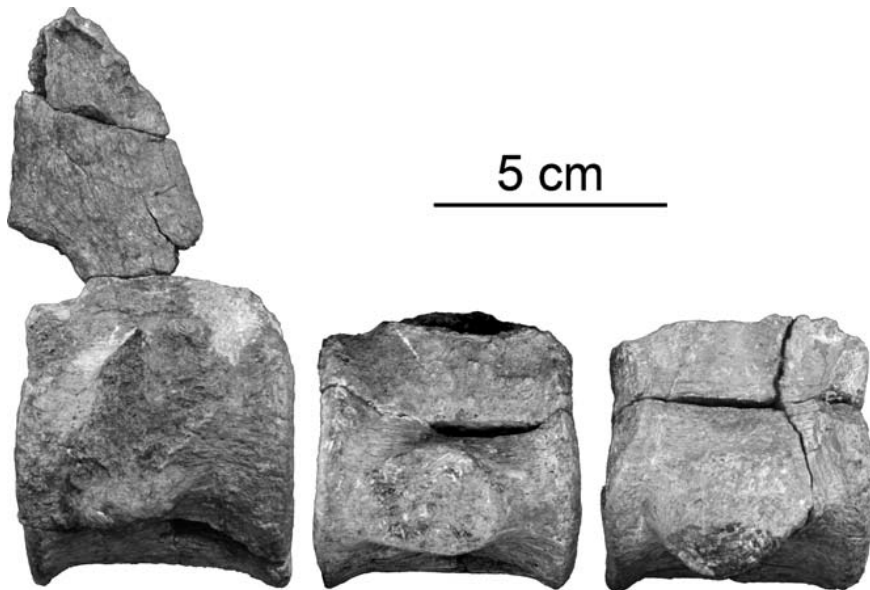


FIGURE 2. USNM 536963, in right lateral view, showing posteriorly directed neural spine.

sacral ribs and transverse processes are largely undeformed. The right pubis is shattered but complete and has been reassembled, whereas the left pubis is fragmentary. Both ischia are well preserved, as are both ilia.

## SYSTEMATIC PALEONTOLOGY

SAUROPTERYGIA Owen, 1860  
PLESIOSAURIA de Blainville, 1835  
PLESIOSAUROIDEA Welles, 1943  
CRYPTOCLEIDOIDEA O'Keefe, 2001  
*PANTOSAURUS STRIATUS* Marsh, 1891  
(Figs. 2–8)

*Parasaurus striatus* Marsh, 1891:338 (original description).

*Pantosaurus striatus* (Marsh, 1891): Marsh, 1893:158 (name changed due to preoccupation).

*Muraenosaurus reedii* Mehl, 1912:344, figs. 1, 3 (synonym).

**Holotype**—YPM 543. Concreted, partial articulated skeleton, partially prepared to yield a distal humerus, four articulated carpals, a fragment of the coracoid, and several isolated cervical vertebrae.

**Referred Material**—USNM 536963, USNM 536965, UW 3, UW 5544, UW 15938.

**Stratigraphic Occurrence**—Upper Member of the Sundance Formation (“Redwater Shale” informal member), Upper 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 and the articular faces of the centra have well-ossified rims. 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.

### Description

**USNM 536963**—USNM 536963 preserves three posterior cervical vertebrae in articulation, and fragments of a fourth (Fig. 2). The centra are waisted and wider

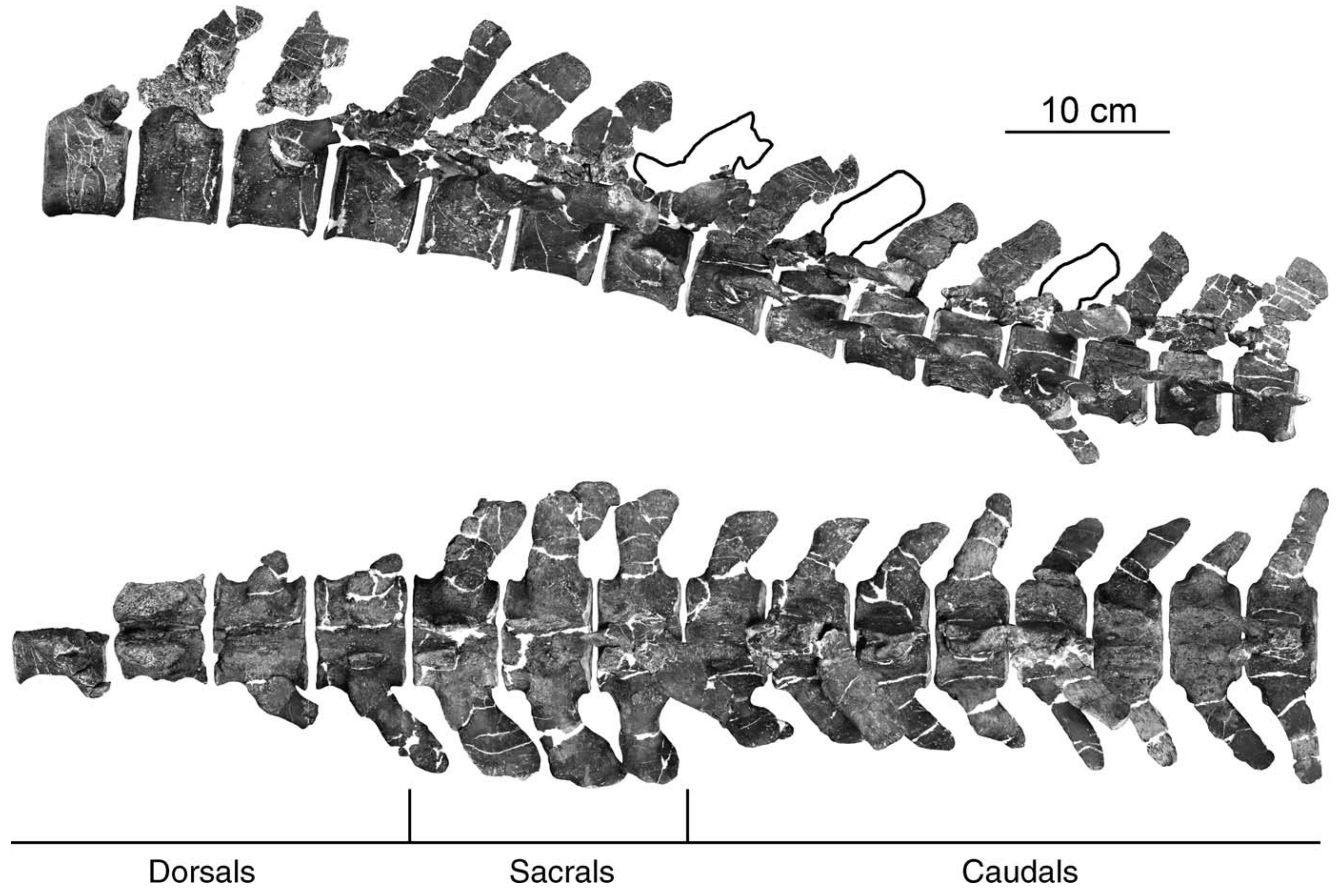


FIGURE 3. Axial column of USNM 536965 in left lateral and dorsal views. The lateral view is in articulation whereas the dorsal view is aligned to show the ribs without overlap.

than they are tall and long. The vertebral length indexes (Brown, 1981; O’Keefe and Hiller, 2006) for the three complete vertebrae, from anterior to posterior, are 84.9, 88.4, and 79.7. Comparisons of their dimensions to those of other Oxfordian plesiosaurs are not diagnostic, because the dimensions of posterior cervical centra tend to be similar in plesiosauroid plesiosaurs (O’Keefe and Hiller, 2006). The rib facets are single headed, blade-like, and carried on a pedestal, with a dorsal excursion for a tubercle of the cervical rib. These facets resemble those of *Muraenosaurus leedsi*, which has a similar dorsal excursion. The neural spine preserved is posteriorly angled, as in the holotype of *Pantosaurus*, but unlike the upwardly directed spines of other Oxfordian cryptocleidoids. The anteroventral and posteroventral edges of the centra do not bear the short anteriorposterior striations seen in the anterior cervical vertebrae of the *Pantosaurus* holotype and *Muraenosaurus*.

Their presence in the posterior cervical vertebrae of these taxa is unknown; the condition in *Muraenosaurus* is not mentioned by Andrews (1910).

**USNM 536965**—USNM 536965 preserves four dorsal, three sacral, and eight caudal vertebrae (Fig. 3; Table 1). The centra are waisted and wider than tall, and taller than long. The articular faces are amphicoelus and bear a notochordal pit slightly dorsal to center. The articular faces of the caudal vertebrae have more rounded edges than those in the sacrum. When the centra are articulated in life position, there is a slight downward bend of the tail beginning at the fourth caudal. As with the cervical vertebrae of the *Pantosaurus* holotype and USNM 536963, the dorsal, sacral, and caudal neural spines are posteriorly directed. These spines shorten in the anterior caudals, but then begin to lengthen again after the fifth caudal. Anterior zygapophyses are well developed and extend beyond the anterior face of the centra, whereas the posterior zygapophyses are reduced.

The preserved dorsal vertebrae bear short ribs that are completely fused to the transverse processes. These ribs angle dorsally, becoming more horizontal in successively posterior vertebrae. They are widest at the point of attachment, dorsoventrally flattened, and swept-back posteriorly. The sacral vertebrae bear stout sacral ribs that lie at a 90° angle to the neural spine. They are constricted at their midpoint and then widen again at the distal end. Each bears a facet for cartilaginous articulation with the ilia. The second sacral ribs extend dorsal to the more posterior ribs, which are notched to allow them to articulate. The ribs of the anterior caudal vertebrae are angled slightly downward behind the sacral ribs, and then begin to angle upward again. These ribs are not as wide as those of the sacral vertebrae and are angled more posteriorly. In ventral view (Fig. 4), the articular faces of the last preserved caudal vertebra are not parallel, but are at a slight angle to each other. This centrum is well preserved and free of compression, so this feature is likely real. If the subsequent vertebrae had similar angles between the articular faces, there would have been a permanent bend of the tail to the left.

Pedestals for chevrons begin on the ventral surface of the second caudal, and distinct facets begin on the fourth caudal. The sizes of the facets are quite variable, but articulated chevrons are similar in size despite disparity in the size of their facets. Twenty-two chevrons are preserved, more than can articulate with the vertebrae present. Following Andrews (1910) in placing chevrons with one articular facet anterior to those with two, it appears that the chevrons are quite short anteriorly, and then become longer as the chevrons begin articulating between adjacent centra, and then rapidly shorten again. The chevrons of USNM 536965



TABLE 1. Measurements (in mm) of vertebral centra preserved in USNM 536965.

	Field vertebra no.	W	H	L	VLI
I	12	X	X	X	X
II	9	69	53	54	88.5
III	10	70	59	54	83.7
IV	11	71	59	54	83.1
V	13	69	58	54	85.0
VI	14	68	55	50	81.3
VII	15	69	52	48	79.3
VIII	8	70	51	48	79.3
IX	7	69	51	47	78.3
X	6	69	49	47	79.7
XI	5	68	49	45	76.9
XII	4	67	48	46	80.0
XIII	3	65	49	45	78.9
XIV	2	64	47	43	77.5
XV	1	64	46	43	78.2

Roman numerals are the order of vertebrae from anterior to posterior. Arabic numbers are field numbers. Vertebral length index (VLI) calculated following Brown (1981) and O’Keefe and Hiller (2006).

are also unusual in the degree to which they curve inward below the tail (Fig. 5). Moving posteriorly down the column, the chevrons begin to curve inward until they point ventrally from the centra, almost parallel to the sagittal plane.

A number of ribs and gastralia that belong to segments anterior to the vertebrae present are preserved (Fig. 6). The ribs and gastralia are similar in thickness and do not show any signs of pachyostosis in cross-section, unlike the Sundance taxon *Tatenectes* (Street and O’Keefe, 2010). Two bifid gastralia are present. Similar pathologies have been observed in other Oxford Clay skeletons (Wilhelm, pers. observ., 2008).

USNM 536965 preserves a nearly complete pelvic girdle (Figs. 7, 8). The fragmentary left pubis is not figured, because its position cannot be determined due to poor preservation and asymmetries in the pelvic girdle. When articulated, the pubes and ischia are at an angle of 25° above horizontal. The pelvic girdle is wider than it is long, with a width to length ratio of 1.28. This ratio is more similar to that of *Cryptoclidus* (1.35) than it is to *Muraenosaurus* (1.08) (Andrews, 1910). The

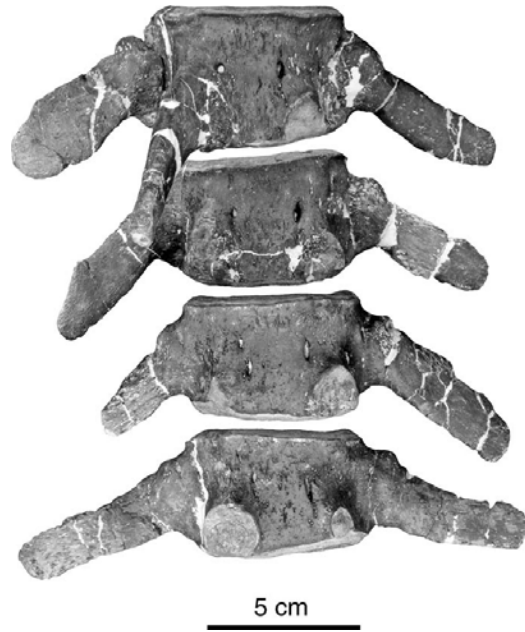


FIGURE 4. Last four preserved caudal vertebrae of USNM 536965 in ventral view, showing the angle between the articular faces on the last preserved centra and variable sizes of the chevron facets.

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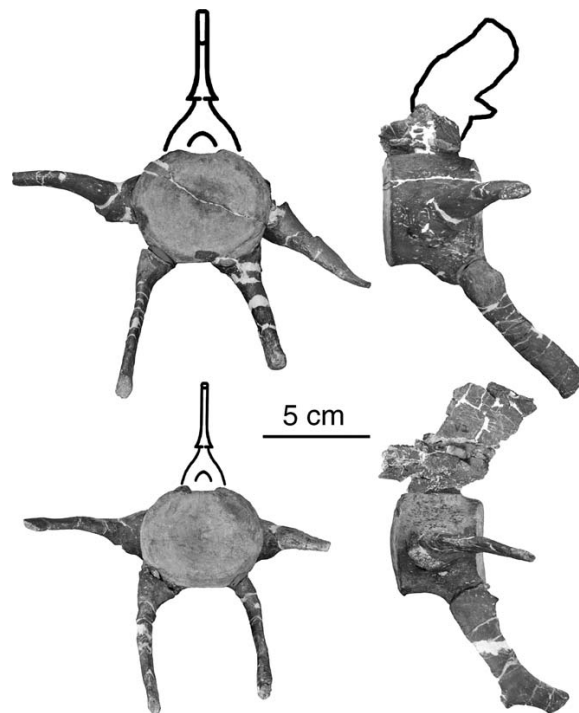


FIGURE 5. Fifth (top row) and seventh (bottom row) caudal vertebrae of USNM 536965 in posterior and left lateral views showing the inward curving chevrons.

width of the pubis is increased by a prominent anterolateral horn, more similar to those of *Cryptoclidus*, but not lacking in the pubis of *Muraenosaurus* (Andrews, 1910). The acetabular margin of the pubis is more concave than in *Cryptoclidus* and *Muraenosaurus*. The lateral-posterior edge of the ischium is more concave than it is in *Muraenosaurus* or *Cryptoclidus*. In life position, the symphyseal margin of the right pubis crosses the sagittal plane. There is no deformation of the pubis, so this asymmetry is probably real. The posterior portion of the ischium also has a posterolateral horn, more prominent than that seen in *Cryptoclidus*, and not present in *Muraenosaurus*. The neck of the left ischium is bent slightly ventrally, whereas the right ischium it is much flatter. Both ischia are free of compression, so this asymmetry appears to be pathological.

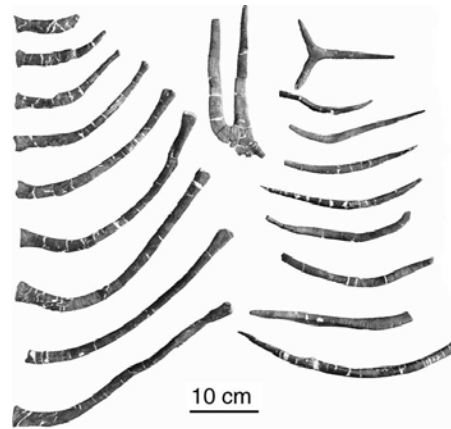


FIGURE 6. Ribs (left), pathological gastralia (top middle and right), and normal gastralia (right) of USNM 536965.

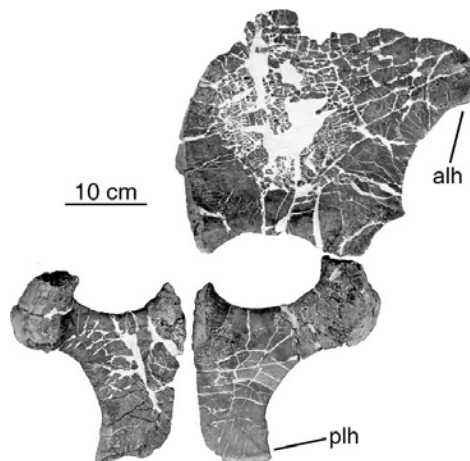


FIGURE 7. Dorsal view of the pubis and ischia of USNM 536965 in life position. Angle of elements from horizontal is  $25^\circ$ . The partial left pubis is not figured as its exact position is uncertain. Anterolateral horn indicated by alh, posterolateral horn indicated by plh.

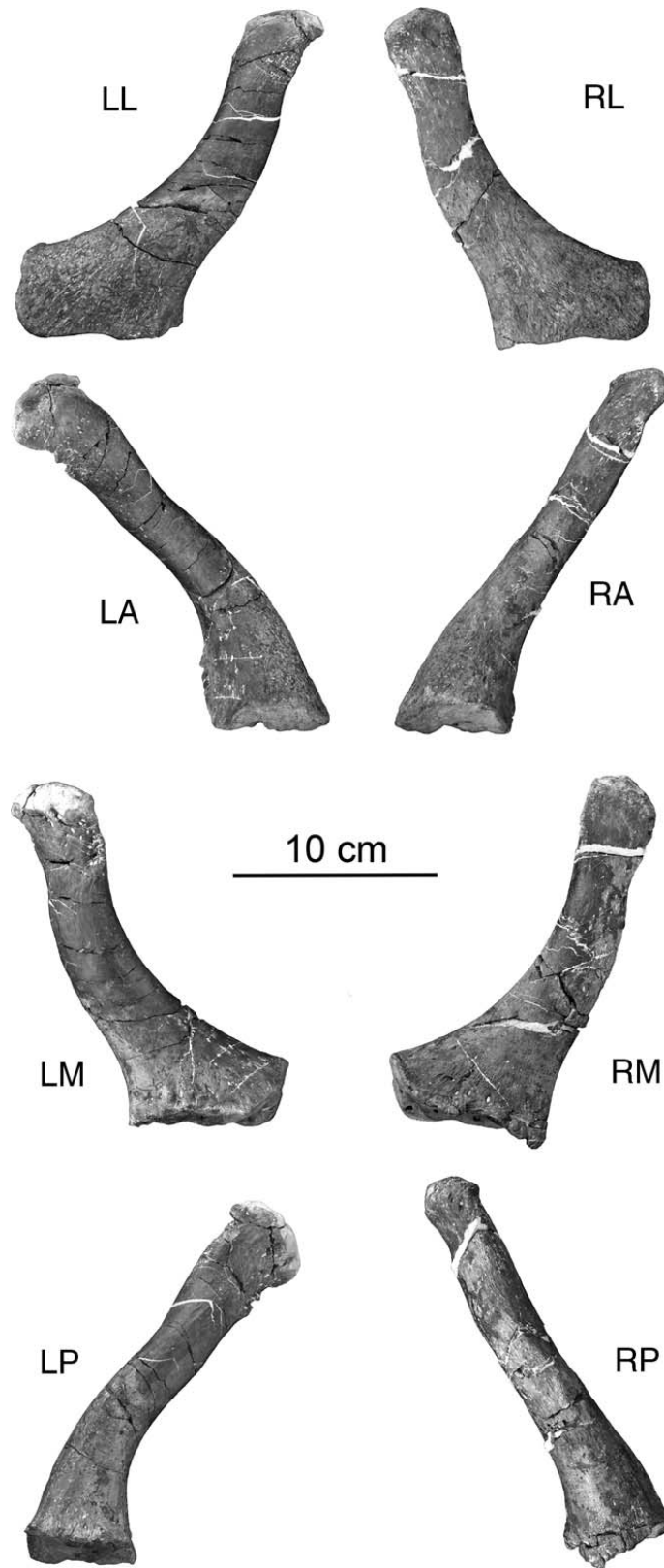


FIGURE 8. Left and right ilia of USNM 536965. Views are top row, lateral; second row, anterior; third row, medial; bottom row, posterior.

The ilia of USNM 536965 (Fig. 8) differ markedly from that of *Muraenosaurus* and *Cryptoclidus*, and from all other plesiosaurs. Both *Muraenosaurus* and *Cryptoclidus* have ilia that are straight along their posterior edges and concave on their anterior edges (Andrews, 1910); the iliac blades are also flared and wider than the shafts. In contrast, the ilia of USNM 536965 are widest at the acetabular end and approximately the same width at the midpoint of the shaft and the iliac blade. The posterior edges are also much more curved than those of *Muraenosaurus*. The left and right ilia differ significantly, with the blade of the left ilium being twisted clockwise. Like the ischia, the ilia are free of deformation, so this feature appears to be pathological.

## DISCUSSION

Taxonomic assignment of the fossils reported here is difficult due to the lack of overlap of this material with the *Pantosaurus* holotype, and the fact that the holotype is a juvenile. The specimens were compared to four cryptocleidoid taxa: *Muraenosaurus* and *Cryptoclidus* from the Oxford Clay, and *Pantosaurus* and *Tatenectes* from the Sundance Formation. The plesiosaurs of the Jagua Formation of Cuba were examined from the literature. They are of doubtful relevance because they are represented mainly by cranial and disarticulated postcranial material. Pliosaurus, such as *Peloneustes* from the Oxford Clay (Andrews, 1913) and *Megalneusaurus* from the Sundance Formation (Knight, 1898), were excluded from study because USNM 536963 lacks the double headed cervical ribs and USNM 536965 lacks the large pelvis typical of pliosaurs.

USNM 536963, the short cervical series, shares several characters with the *Pantosaurus striatus* holotype. Both have rib facets carried on a pedestal and with a dorsal excursion for a tubercle of the cervical rib, and posteriorly directed neural spines. Although the rib facets also resemble those of *Muraenosaurus*, posterior cervical vertebrae with posteriorly directed neural spines appear to be unique to *Pantosaurus* among cryptocleidoids from the Sundance Formation and Oxford Clay. For this reason, we refer USNM 536963 to *Pantosaurus*. USNM 536963 does lack the anterior-posterior striations seen in the anterior cervical vertebrae of the *Pantosaurus* holotype, but the presence of these striations in the posterior cervicals is unknown; and may vary ontogenetically. The lack of these striations does not preclude the referral of USNM 536963 to *Pantosaurus*, because these striations may be found only in the anterior cervical vertebrae or lost in the adult.

Referral of USNM 536965 is more difficult, because material from the posterior axial column of *Tatenectes* and *Pantosaurus* is limited (although unreported *Tatenectes* material does exist; Street and O’Keefe, 2009). This specimen can be excluded from *Tatenectes*, because it lacks the pachyostotic gastralia diagnostic of the genus (Street and O’Keefe, 2010). Although similar in some ways to *Cryptoclidus* and *Muraenosaurus*, the pelvic girdle of USNM 536965 is distinct in its autapomorphic ilium. This ilium is unique in that the iliac blade is approximately the same width as the midpoint of the shaft. In *Cryptoclidus* and *Muraenosaurus*, the iliac blade is flared and wider than the shaft.

Despite the lack of overlapping material, some evidence suggests that USNM 536965 may be referable to *Pantosaurus*. The dorsal, sacral, and caudal neural spines of USNM 536965 are posteriorly directed, as are the cervical neural spines of *Pantosaurus striatus*. Posteriorly directed neural spines are uncommon in Oxfordian plesiosaurs, being seen only in the anterior cervicals of ‘*Picrocleidus*’ *beloclis* (Andrews, 1913: pl. VII, fig. 5) and the posterior caudals of *Cryptoclidus*. In *Cryptoclidus*, this feature appears to be associated with dermal structures in the distal portion of the tail (Wilhelm, pers. observ., 2009). The posteriorly directed neural spines in ‘*Picrocleidus*’ are problematic, because this genus was synonymized with *Muraenosaurus* (Brown, 1981), which lacks posteriorly directed anterior cervical neural spines. This suggests that *Picrocleidus* may not be synonymous with *Muraenosaurus*. Because posteriorly directed neural spines are rare, we tentatively refer USNM 536965 to *Pantosaurus*. It remains possible, however, that this specimen represents a third, currently unknown cryptocleidoid taxon from the Sundance Formation.

The morphology of the caudal region of USNM 536965 indicates that it may have played a role in locomotion. The articular faces of the caudal vertebrae are more rounded than those of the sacral vertebrae immediately antecedent, indicating greater flexibility in the proximal tail. This flexibility would have allowed for the tail to be moved laterally, possibly acting as a rudder. If the tail was used in such a manner, it might explain some of the pathologies seen in the partial skeleton. The left ilium and ischium are rotated compared to their counterparts on the right side, and the tail appears to be bent to the left. If this individual had a missing or damaged flipper on its right side, it is possible that the tail was bent to the left side to provide drag to counteract the bilateral imbalance of propulsion. A dermal tail fin could be used to create increased drag and would make the tail a more effective rudder. The presence of a dermal tail fin in plesiosaurs has been suggested before (Dames, 1895; Tarlo, 1957; Smith, 2007), but no osteological evidence has been described for its presence in cryptocleidoid plesiosaurs. The imbalance of forces

acting on the two sides, and habitual asymmetric behaviors resulting from this, could eventually lead to the distortion seen in the left girdle elements and in the axial column. Distortion due to habitual asymmetric swimming behaviors is seen in captive bottlenose dolphins, which tend to swim in a primarily counterclockwise direction around their tanks. This behavior results in a permanent leftward turn of the dorsal fin (Ridgway, 1990).

## CONCLUSIONS

USNM 536963 and USNM 536965 are significant new specimens given the paucity of cryptocleidoid plesiosaur material from the Sundance Formation. USNM 536963 is referable to *Pantosaurus* due to the posteriorly directed neural spines and cervical rib articulation morphology. USNM 536965 is also referred to *Pantosaurus* for the former reason, although this referral is tentative because posteriorly directed neural spines sometimes appear in other Oxfordian plesiosaurs. This specimen is excluded from all other Oxfordian plesiosaur genera on the basis of its autapomorphic ilium. The caudal vertebrae and pelvic girdle of USNM 536965 are also notable because they suggest the tail may have been used as a rudder. The role of the tail during plesiosaur locomotion warrants further examination.

## ACKNOWLEDGMENTS

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