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Publisher Taylor & Francis

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Journal of Vertebrate Paleontology

Publication details, including instructions for authors and subscription information:

<http://www.informaworld.com/smpp/title~content=t917000010>

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Online publication date: 21 March 2011

To cite this Article O'Keefe, F. Robin , Street, Hallie P. , Wilhelm, Benjamin C. , Richards, Courtney D. and Zhu, Helen(2011) 'A new skeleton of the cryptoclidid plesiosaur *Tatenectes laramiensis* reveals a novel body shape among plesiosaurs', Journal of Vertebrate Paleontology, 31: 2, 330 – 339

To link to this Article: DOI: 10.1080/02724634.2011.550365

URL: <http://dx.doi.org/10.1080/02724634.2011.550365>

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A NEW SKELETON OF THE CRYPTOCLIDID PLESIOSAUR *TATENECTES LARAMIENSIS* REVEALS A NOVEL BODY SHAPE AMONG PLESIOSAURS

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ABSTRACT—Current knowledge of plesiosaurs of clade Cryptoclidia is constrained by a lack of fossils from outside the Oxford Clay deposits of England. Recent fieldwork in the Sundance Formation of the Bighorn Basin, Wyoming, has resulted in the recovery of significant new fossils of cryptoclidid plesiosaurs, including the small-bodied form *Tatenectes laramiensis*. A new partial skeleton of this taxon is reported here; it is the most complete and best-preserved example of the taxon found to date, comprising a complete dorsal vertebral series, many ribs and gastralia, and a complete pelvic girdle. This skeleton illuminates several unique features of the taxon, including a novel pattern of midline pachyostosis in the gastralia. In addition, a range of both axial and appendicular morphological features reveals that *Tatenectes* had a body shape unique among known plesiosaurs, characterized by extreme dorsoventral compression, and modest anteroposterior reduction. The combination of the new skeleton with information from previous finds allows the first reconstruction of the taxon. *Tatenectes* had a dorsoventrally compressed, oblate spheroid body shape, with a high skeletal mass concentration in the ventral elements. We hypothesize that these features were adaptations for increased near-surface stability, perhaps allowing access to above normal wave base, inshore environments in the shallow Sundance Seaway.

INTRODUCTION

Current knowledge of the plesiosaurs of clade Cryptoclidia (Ketchum and Benson, 2010) rests largely on the Oxford Clay (Callovian) fauna from the United Kingdom (Andrews, 1910). At least three cryptoclidid genera are known from this formation (*Cryptoclidus*, *Muraenosaurus*, and *Tricleidus*), and plentiful, well-preserved fossils have allowed thorough morphological understanding of these taxa. Knowledge of the clade outside the Oxford Clay remains poor, despite evidence of a global distribution in the Late Jurassic (Cuba: Gasparini and Iturralde-Vinent, 2006; Svalbard: Druckenmiller et al., 2009; Wyoming: Mehl, 1912) and the Late Cretaceous (Argentina: Cabrera, 1941; Antarctica: Chatterjee and Small, 1989; New Zealand: Cruickshank and Fordyce, 2002). The morphology and relations of the Late Cretaceous taxa *Aristonectes* and *Kaiwhekea* are a long-standing problem; these taxa are very derived, and some contend they form a clade with less autapomorphic cryptoclidids from the late Jurassic (formalized as the family Aristonectidae; O'Keefe and Street, 2009). However, the large-scale phylogenetic analysis of Ketchum and Benson (2010) failed to recover this family as a monophyletic group, perhaps due to a pronounced lack of data for the directly relevant taxa. Consequently, this area of the Ketchum and Benson (2010) cladogram is labile, and further data on the taxa involved are obviously desirable. In alternative reconstructions *Aristonectes* falls within Elasmosauridae (Gasparini et al., 2003). Recent field work in the Jurassic Sundance Formation of Wyoming has been aimed at this ambiguity.

The Sundance Plesiosaur Project has increased our knowledge of the morphology and phylogenetic position of the cryptoclidid *Tatenectes laramiensis* (O'Keefe and Wahl 2003b; O'Keefe and Street, 2009; Street and O'Keefe, 2010), and of *Pantosaurus*

striatus (O'Keefe and Wahl, 2003a; O'Keefe et al., 2009; Wilhelm and O'Keefe, 2010). Neither taxon was included in the Ketchum and Benson (2010) phylogenetic analysis, nor did either appear in previous large-scale phylogenetic analyses of the Plesiosauria (O'Keefe 2001, 2004; Druckenmiller and Russell, 2008; Smith and Dyke, 2008). *Tatenectes* has appeared in the limited analyses of O'Keefe and Wahl (2003b) and O'Keefe and Street (2009), although it is still poorly known.

Here we report on a new partial skeleton of *Tatenectes laramiensis*, discovered in Sundance exposures north of the town of Shell, Wyoming. This skeleton is the most complete and best-preserved example of the taxon yet reported, comprising an articulated vertebral column, many ribs and gastralia, and a complete pelvis. However, the skeleton poses a paradox; its wealth of anatomical detail sheds little light on its phylogenetic relationships below the family level, explicable by a previous lack of diagnostic characters in the plesiosaurian thorax (Ketchum and Benson, 2010:suppl. 3). The pelvis does indicate a close relationship with the Oxford Clay cryptoclidids, in agreement with previous evidence. Beyond this, however, the skeleton is highly autapomorphic. Evidence from the vertebrae, ribs, and pelvic girdle indicate that the transverse section through the body of *Tatenectes* is very oblate, with anteroposterior reduction and extreme dorsoventral compression with lateral expansion. *Tatenectes* also displays a unique pattern of pachyostosis in its gastralia (Street and O'Keefe, 2010). These specializations yield a gross body shape and body mass distribution that are unique among the Plesiosauridae.

This paper has several goals. The first is a detailed description of the new partial skeleton, emphasizing unique features. This skeleton, when combined with previously known material, allows a complete body reconstruction for *Tatenectes*. The morphology of *Tatenectes* is then compared to those of the closely related Oxford Clay taxa *Cryptoclidus* and *Muraenosaurus* to emphasize its uniqueness. Lastly, we offer some conjectures that might explain this novel morphology.

Institutional Abbreviations—BMNH, Natural History Museum, London; USNM, National Museum of Natural History,

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Smithsonian Institution, Washington, D.C.; **UW**, University of Wyoming Museum of Geology, Laramie, Wyoming.

MATERIALS AND DESCRIPTION

The partial skeleton of *Tatenectes laramiensis* described here was excavated from exposures of the Sundance Formation near Shell, Wyoming, during the summer of 2006 (for a geological review see O'Keefe and Street, 2009; for map of the field area see Wilhelm and O'Keefe, 2010). It was subsequently accessioned as USNM 536976 and prepared at the Smithsonian Institution. The skeleton consists of an articulated vertebral column of 22 vertebrae, comprising 16 dorsals, four sacrals, and two caudals. All six pelvic elements are preserved, as are numerous ribs and gastralia. All elements were closely associated with the articulated vertebral column, although not in life position. The skeletal elements and body shape of *Tatenectes* will be compared to those of the related cryptoclidids *Cryptoclidus eurymerus* Phillips, 1871, and *Muraenosaurus leedsii* Seeley, 1874. Material of these taxa was examined at the BMNH (*Muraenosaurus*: BMNH R. 2678; *Cryptoclidus*: BMNH R. 2860).

SYSTEMATIC PALEONTOLOGY

SAUROPTERYGIA Owen, 1860
 PLESIOSAURIA de Blainville, 1835
 CRYPTOCLIDIA Ketchum and Benson, 2010
 ARISTONECTIDAE O'Keefe and Street, 2009
TATENECTES O'Keefe and Wahl, 2003b

Type Species—*Tatenectes laramiensis*, by monotypy.

Diagnosis—As for species.

TATENECTES LARAMIENSIS (Knight, 1900)

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

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

Referred Material—UW 24215, USNM 536970, and USNM 536976.

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

Revised Diagnosis—A small (total body length less than 3 m) plesiosaur with an unknown number of cervical vertebrae. Teeth small and more narrow than in other plesiosaurs, with relatively long roots, and lightly ridged enamel all around; anterior interpterygoid vacuity present; pterygoids posterior to anterior pterygoid vacuity are developed into a deep block of bone projecting ventrally out of the plane of the palate; parasphenoid not visible in palatal view; overall body form oblately spheroid, due to extreme dorsoventral compression resulting from a low degree of dorsal concavity in the medial gastralia, pronounced curvature of the J-shaped lateral gastralia, and ribs articulating in a horizontal plane; presence of pachyostotic midline gastralia; cervical vertebrae much shorter than wide, not constricted at midcentrum, and with well-defined rib articulations that are not anteroposteriorly elongate; foramina subcentralia widely spaced; the rims of articular faces of cervical vertebrae are poorly defined and rounded; neural spines of dorsal vertebrae anticlinal; humerus with long, slender shaft and radial and ulnar articulations that are subequal in length; articulations for two supernumerary ossifications in the epipodial row; scapulae medial processes meet in

a median symphysis anterior to the pectoral fenestrae, but symphysis is relatively short, and the medial process of the scapula is short anteroposteriorly; short anterior extensions of the scapulae are separated on the midline by a deep notch, which is covered dorsally by a reduced, plate-like clavicle; angle of iliac articulation with ischium shallow.

Justification of Referral

The new skeleton (USNM 536976) is referred to the species *Tatenectes laramiensis* based on its possession of diagnostic pachyostotic midline gastralia, and lateral gastralia with an autapomorphic J shape (Street and O'Keefe, 2009). The anticlinal neural spines of the dorsal vertebrae illustrated here also appear in the previously referred partial skeleton UW 24215, although interpretation is equivocal due to lack of preparation and poor preservation.

Description

Previously Known Material—Over the past decade, several new partial skeletons of *Tatenectes*, along with various isolated elements, have been found and described. Previously described material includes cranial elements, cervical and dorsal vertebrae, ribs and gastralia, and the pectoral girdle (O'Keefe and Wahl, 2003b; O'Keefe and Street, 2009; Street and O'Keefe, 2010). Known cranial elements of *Tatenectes* include teeth, the squamosal, and the frontal, as well as the autapomorphic palate and basicranial elements. Many cervical vertebrae are known, including the atlas-axis complex; however, the complete length of the neck remains unknown (O'Keefe and Wahl, 2003b; O'Keefe and Street, 2009). Anterior dorsal vertebrae have been found but not described in detail. Two incomplete but complementary pectoral girdles have been described (O'Keefe and Wahl, 2003b; O'Keefe and Street, 2009). The ribs and gastralia have been discussed in a separate publication, emphasizing the unique pachyostosis found in the gastralia (Street and O'Keefe, 2010). Forepaddle elements, including humeri, epipodials, and phalanges, were originally described by Mehl (1912), and more isolated examples have since been found. No definite hindpaddle elements have been described.

Axial Skeleton—The preserved vertebral column of the new skeleton consists of 22 articulated vertebrae, starting at or about the first dorsal and continuing uninterrupted to the second caudal vertebra (Fig. 1). The first preserved vertebra is identified as a dorsal because the transverse process is carried entirely on the neural arch; this definition is the generally accepted one in treating the gradual transition from the pectoral to the dorsal series in plesiosaurs (Brown, 1981). The transverse process in the first dorsal is low on the neural arch, however, and this indicates that the preceding transverse process would have been carried at least partially on the centrum. We therefore identify the first preserved vertebra as the first dorsal. *Tatenectes* therefore had 16 dorsal vertebrae and four sacral vertebrae, with the last two preserved being the proximal caudals. The dorsal series is four to six vertebrae shorter than is typical for *Muraenosaurus* and *Cryptoclidus*, producing a correspondingly squat trunk; in contrast to the reduction of dorsals, four sacral vertebrae are typical of those taxa (Andrews, 1910; Brown, 1981).

The articular faces of the dorsal vertebral centra are round and nearly as tall as they are wide. The centra are shorter anterodorsally than the centra are tall or wide. These proportions of the vertebral centra are more similar to *Cryptoclidus* than to *Muraenosaurus* (Andrews, 1910); the centra in the latter taxon tend to have more symmetrical faces and to be relatively longer anteroposteriorly. The centrum dimensions in *Tatenectes* would result in further anteroposterior reduction of the thorax, at least relative to *Muraenosaurus*.

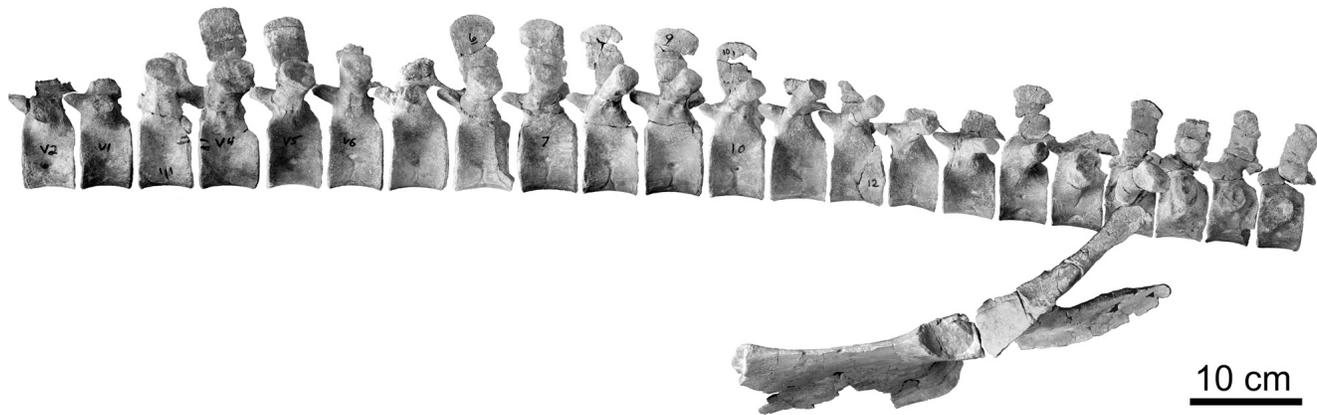


FIGURE 1. Articated vertebral column and pelvis of *Tatenectes laramienseis*, USNM 536976, in left lateral view. The column is comprised of 22 vertebrae, with the first preserved inferred as the first dorsal. The resulting vertebral counts are 16 dorsals, four sacrals, and two preserved caudals. The subtle 'lumbar' curve beginning at dorsals 15–16 and recumbent rib articulations are unique to this taxon. The ilium and the ischium shown here are anatomically right, and their photographs have been reversed for this composite.

The neural arches are well ossified to the centra with nearly obliterated lines of fusion, indicating that this individual, although small, was a mature adult. The first fully preserved neural spine is the fourth dorsal. It is tall and blade-like, as are those on more posterior vertebrae to the eleventh dorsal. The twelfth and consequent dorsals display a precipitous decline in height, so that those in the sacral region are low and blade-like. Neither *Muraenosaurus* nor *Cryptoclidus* display this decrease in spine height, and it is therefore autapomorphic in *Tatenectes* (Andrews, 1910; Brown, 1981). The neural spines also display another unique feature; they are anticlinal, or angled anteriorly rather than having edges parallel to the centrum face as is typical for other cryptoclidids (Andrews, 1910), or in derived plesiosauroids in general (Ketchum and Benson, 2010). Vertical or posteriorly angled neural spines occur in all other known plesiosaurs (character states in O'Keefe, 2001; Ketchum and Benson, 2010). Although it is possible that the anteriorly angled neural spines are an artifact of distortion during preservation, this does not seem likely. The angle is consistent over the length of the entire column, and there is no evidence of anteroposterior (or any other) deformation in the vertebral centra or transverse processes.

The vertebral column was found in articulation, allowing a confident reproduction of the arch of the spine (Fig. 1). This arch is much lower than is typical for other cryptoclidids (Andrews, 1910; Brown, 1981). This flattening of the back is achieved both by a lack of arching in the articulation of consecutive centra, and by a shortening of the neural spines on the posterior vertebrae. Lastly, the articulated dorsal series does not form a gentle, ventrally concave arch into the sacrum; instead, the column flattens out anterior to, and within, the sacrum. This subtle 'lumbar' curve arises from the rhomboidal centrum shape of dorsals 15 and 16, and of sacral 1.

The transverse processes differ greatly among the anterior and middle dorsals and the posterior-most dorsals. Along the entirety of the series the ventral surfaces of the transverse processes are concave, but the processes take on an increasing caudal curvature, similar to *Muraenosaurus* (Andrews, 1910), after the tenth dorsal (Fig. 1). They also bear a marked ventral tuberosity that matches a similar excrescence on the ventral face of each rib (Fig. 2C). This feature is vaguely reminiscent of the condition in *Cryptoclidus*, but is both more strongly developed and more ventrally directed. Anteriorly the transverse processes are more robust. The distal ends of the anterior transverse processes are slightly expanded at the rib articulation. In the posterior dorsal

vertebrae the transverse processes are shorter and considerably more gracile, with little distal expansion. Another marked difference between the posterior dorsals and those more anterior is the change in the dorsoventral angle of the transverse processes relative to the neural spine. For the anterior-most dorsals, the transverse processes make an approximate 70° angle to the sagittal plane. This angle decreases slightly in succeeding posterior vertebrae, but there is a sharp increase in transverse process angle beginning at the fourteenth vertebra; this angle is nearly 90°, just anterior to the sacrum (dorsals 14–16). This feature does not exist in *Cryptoclidus* or *Muraenosaurus* (Brown, 1981; Andrews, 1910).

The orientation of the rib articular facets on the transverse processes is a very distinctive feature of *Tatenectes* (Fig. 2). The ventral tuberosities on the distal ends of the transverse processes, and the corresponding structures on the ventral surfaces of the rib heads mentioned above, provide confidence in the reconstruction angles presented here. Anteriorly, the angle of the rib articulation is about 28° to the horizontal, and this angle continues back to the eleventh vertebra. The angle then decreases further, from 24° in vertebra 12° to 13° in dorsals 15 and 16. These angles are extremely low relative to other cryptoclidid taxa; for instance, the angle of the rib facets averages about 45° in *Cryptoclidus* across all dorsals, and actually increases to about 55° in more posterior vertebrae (Brown, 1981:fig. 2). In *Muraenosaurus* this angle is uniform throughout the dorsal series and approaches 90° (Andrews, 1910). These differences in angle have an enormous impact on thorax shape; the ribs of *Muraenosaurus* trend ventrally, whereas those of *Cryptoclidus* trend posteroventrally. The ribs of *Tatenectes* trend more posteriorly than ventrally, and the tips of most ribs do not descend past the ventral margin of the vertebral column. This unusual morphology results in an exceptionally dorsoventrally compressed thorax compared to related taxa.

There are four vertebrae in the sacrum of *Tatenectes* (Fig. 3). This number is typical for cryptoclidid plesiosaurs (*Cryptoclidus*: Brown, 1981; *Muraenosaurus*: Andrews, 1910; *Pantosaurus*: Wilhelm and O'Keefe, 2010). The centra of the sacral vertebrae are shorter than the dorsal vertebrae, both anteroposteriorly and dorsoventrally. The neural spines are shorter both actually and proportionately than those of the dorsals, and they angle backward (Fig. 1). The sacral ribs articulate directly to the centra with very large facets, the outlines of which vary from vertebra to vertebra; this condition is typical for cryptoclidid plesiosaurs.

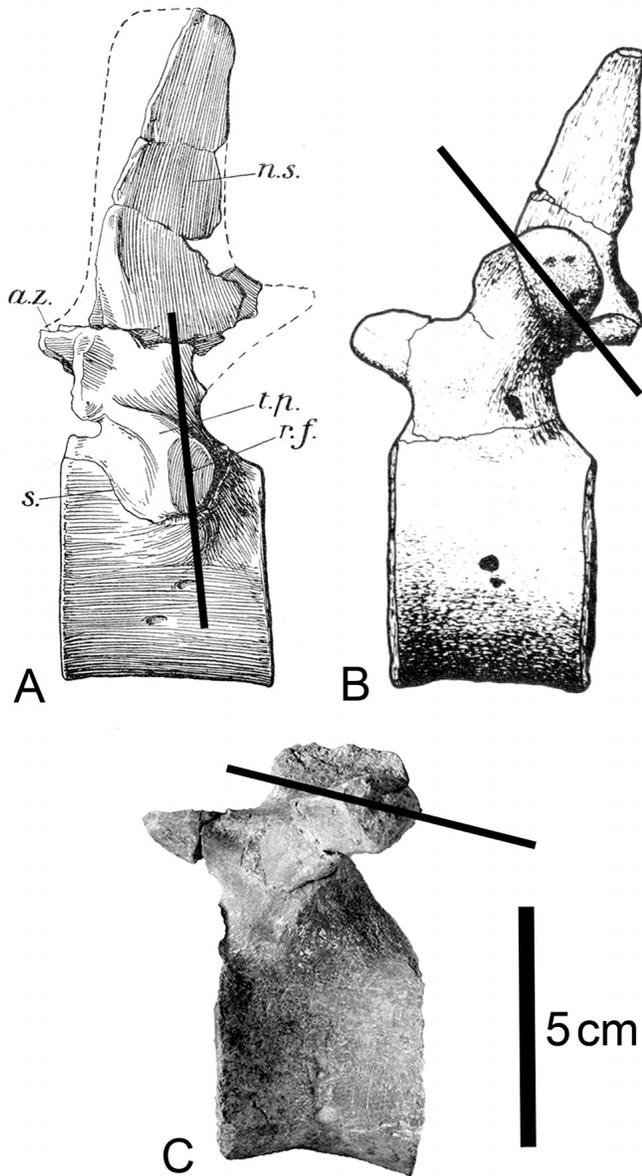


FIGURE 2. Posterior dorsal vertebrae of *Muraenosaurus* (A), *Cryptoctidus* (B), and *Tatenectes* (C). The figure of *Muraenosaurus* is taken from Andrews (1910), and the exact location of the vertebra is not given. The vertebra of *Cryptoctidus* is the twentieth dorsal (modified from Brown, 1981), whereas the vertebra of *Tatenectes* is the fifteenth. The lines across the rib articulations show the approximate angle of rib head articulation. The scale bar refers to *Tatenectes*; the other vertebrae are slightly larger but are scaled down to equal size.

Among cryptoctidids, *Cryptoctidus* is unique in that the first sacral rib is robust, with a correspondingly large articular surface on the sacrum and large roughened area on the tip for cartilaginous articulation with the ilium. In *Tatenectes*, the first sacral rib is gracile, with a small articular facet on the centrum, and a small cartilaginous attachment. *Pantosaurus* and *Muraenosaurus* share this condition. The first two caudal vertebrae are also preserved; they possess short, backward-pointing neural spines. The caudal centra are compressed anteroposteriorly, and the caudal ribs are gracile and short compared to those of the sacrum.

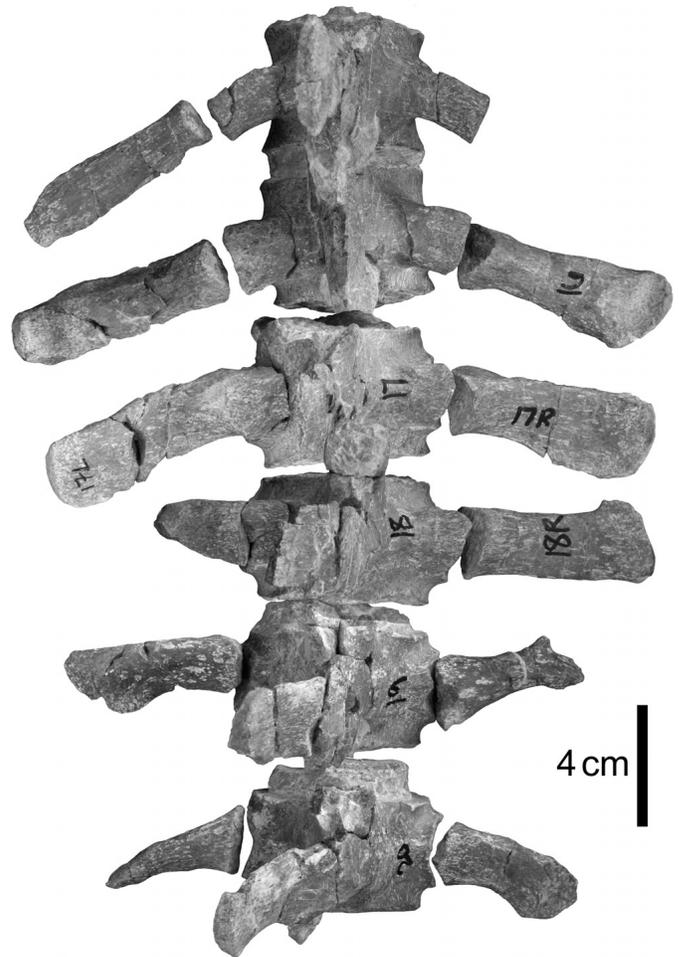


FIGURE 3. Sacrum and proximal caudals of *Tatenectes laramiensis*, USNM 536976, in dorsal view.

The ribs and autapomorphic gastralia of *Tatenectes* are described in detail in Street and O'Keefe (2010), and therefore will be discussed briefly here. The dorsal ribs (Fig. 4A) are gracile and very similar in overall form to those of *Cryptoctidus* and *Muraenosaurus* (Andrews, 1910). The rib heads are oval and slightly compressed. However, due to the posterior slant of the articular facets, this compression is not anteroposterior, as described for *Muraenosaurus* by Andrews (1910), but is instead obliquely dorsoventral. Each rib carries a low ridge on its ventral surface that extends a short way along the shaft; this ridge is the ventral process that articulates with the ventral excursion of the tip of the transverse process described above. More posterior ribs shorten pregressively, until the ribs in the 'lumbar' region are much reduced, as is the case in other cryptoctidids. These ribs are also compressed dorsoventrally, giving them a blade-like appearance. The sacral ribs are short, though longer than the final dorsal ribs, and extremely robust (Fig. 3). Their distal ends are expanded, presumably for an extensive cartilage structure at the ilial articulation. There is little consistency between the sacral ribs from vertebra to vertebra, and even a lack of symmetry between the two ribs of any one sacral vertebra. This asymmetry is common among cryptoctidids; Andrews (1910) remarked on the difficulty of accurate reconstruction of the sacrum of *Muraenosaurus* due to similar inconsistencies.

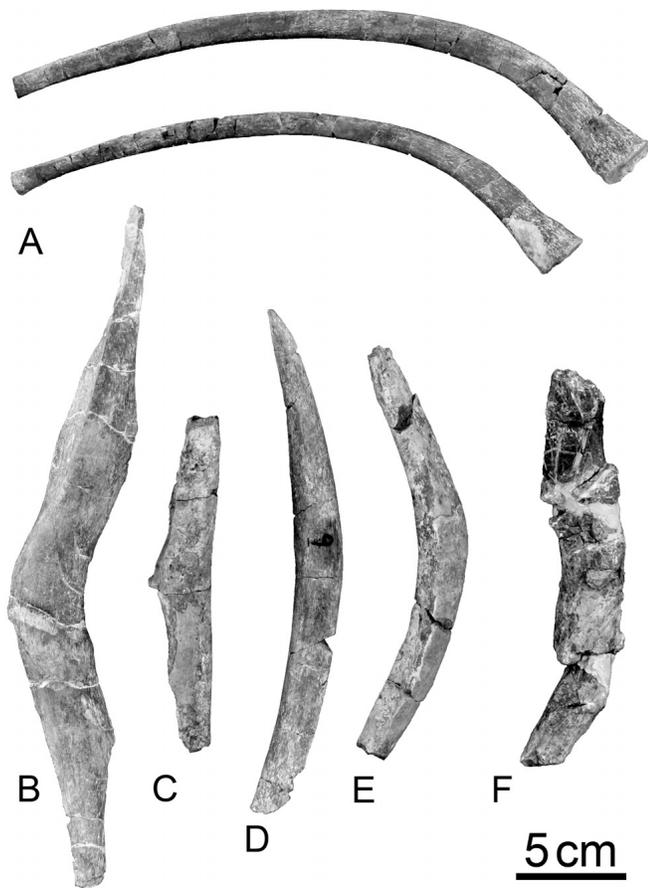


FIGURE 4. Representative ribs and gastralia of *Tatenectes laramiensis*, USNM 536976. The ribs (A) are typical of cryptoclidids except for the triangular cross-section of the articulation for the transverse process. The gastralia are pachyostotic to varying degrees; those from the midline (B, C) are large and possess thick cortices, whereas more lateral gastralia are more gracile with normal histology (D, E) (Street and O'Keefe, 2010). Gastralium in E is a 'J-bend' lateral element. Element in F is two fused pachyostotic gastralia fragments from another *Tatenectes* partial skeleton (UW 24215). The referral of the present skeleton rests partially on this morphology.

Whereas the ribs of *Tatenectes* are not unusual save for the ventral ridge along the medial shaft, the gastralia are very robust for such a small plesiosaur (Fig. 4B–F). This disparity was first noted by Wahl (1999) and discussed by O'Keefe and Street (2009), and is examined in detail in Street and O'Keefe (2010). The last study determined that the gastralia, particularly the median gastralia, are pachyostotic, achieved through thickening of the cortical bone, thus enlarging the size of each gastralium. The gastralia are arranged in multiple segments consisting of one central gastralium with three lateral gastralia to each side, a configuration diagnostic of Plesiosauria (Andrews, 1910; Ketchum and Benson, 2010). The number of gastralia segments is unknown due to lack of articulation of the gastralia basket in the skeleton, but due to the volume of fragments preserved, the total would be at least seven or eight, as figured for *Cryptoclidus* and *Muraenosaurus* (Andrews, 1910; Brown, 1981). The morphology of the gastralia differs between *Tatenectes* and the Oxford Clay taxa. The midline and lateral gastralia of *Cryptoclidus* and *Muraenosaurus* all display dorsoventral curvature. In contrast, the midline and first two sets of lateral gastralia in *Tatenectes* display very little curvature. Only the lateral-



FIGURE 5. Pelvis of *Tatenectes laramiensis*, USNM 536976, in ventral view. The presence of the complete lateral horn on the left pubis indicates that the element was not significantly longer than the preserved portion. The right ischium and ilium are essentially complete. Note the ventral dish of the pubes, presumably to accommodate pelvic viscera within the compressed lumbar region.

most gastralia are greatly curved in *Tatenectes*, and these take on a distinct 'J-bend' morphology (Fig. 4E). This lack of curvature in the medial gastralia basket contributes to dorsoventral compression of the thorax.

Pelvic Girdle—All six bones of the pelvis were recovered, although only the right ischium and ilium are complete (Fig. 5). The left pubis lacks only the anteromedial margin and preserves an anterolateral horn, so the anterior edge of the pubis was not significantly longer than the preserved portion. It is therefore estimated that the pubes are subequal in length and width, and that the entire pelvic girdle is wider than it is long. In this respect *Tatenectes* is very similar to *Cryptoclidus*; the girdle in *Muraenosaurus* is significantly longer than it is wide, due to relative lengthening of both the pubis and the ischium (Andrews, 1910).

The pubis is the typical broad, thin plate of bone diagnostic of Plesiosauria (O'Keefe, 2001). As in *Cryptoclidus*, there is a distinct notch in the lateral end of the anterior margin (Fig. 5), forming an anterolateral horn. However, the horn is broader in *Tatenectes* and does not project as sharply posteriorly as that in *Cryptoclidus*. The anterolateral horn is a diagnostic feature present in cryptoclidids (Andrews, 1910) and polycotyliids (Williston, 1903). The intact portions of the two pubes indicate that these bones articulated to form a flat sheet of bone; the pubes, however, dish ventrally to form a unique bowl-shaped depression on the visceral surface. They also meet at a relatively shallow angle at the midline (as do the ischia); the pelvic region in *Tatenectes* was therefore less rounded than in other taxa.

The ischium has a thick acetabular process that thins medially to the symphysis, and gives rise to the thin posterior ramus. The length and width of the ischium are nearly equal (Fig. 5). In shape, the ischium of *Tatenectes* is more similar to that of *Muraenosaurus* than that of *Cryptoclidus* in that the posterior ramus

is relatively broad, and does not taper. This posterior process is proportionately shorter anteroposteriorly and wider mediolaterally in *Tatenectes* than in *Muraenosaurus* (Andrews, 1910). The ischium is thick anteriorly where it forms the posterior margin of the thyroid fenestra, but this border is not as deeply concave as is seen in *Cryptoclidus* or *Muraenosaurus*. The posterior ramus becomes slightly concave viscerally, similar to the anterior portion of the pubis. The head of the ischium, bearing the articular facet of the acetabulum, is the thickest portion of the bone. The facets for the pubis and the acetabulum meet at a nearly 90° angle. In overall morphology, the pubis and ischium closely resemble those of *Cryptoclidus* save for the depressions on the visceral surface and their relatively shallow angle of midline articulation.

The ilium of *Tatenectes* is shorter and more gracile than that of either *Cryptoclidus* or *Muraenosaurus* (Andrews, 1910). The relative slenderness is achieved via narrowing of the proximal end of the ilium. Without expansion at this end of the bone, the ilium also appears more straight than those in related cryptoclidids. The sacral end of the ilium is obliquely dorsoventrally compressed, and this compression continues nearly one-third the length of the bone. The shaft of the ilium is narrow and oval in cross-section. The bone is thickest where it contributes to the acetabulum, and assumes a triangular cross-section in this region. The ilium of *Tatenectes* articulates with the ischium at an acute angle in lateral view (Fig. 6C), more similar to the morphology seen in *Cryptoclidus* than the nearly 90° angle between the ischium and ilium of *Muraenosaurus* (Andrews, 1910). The ilium in *Tatenectes* forms an extremely shallow angle with the ischium relative to other taxa. Because the ilium of *Tatenectes* is straight, it also articulates with the sacral ribs at an acute angle, whereas the bend in the ilium of *Cryptoclidus* indicates that the angle of articulation with the sacral ribs in this taxon is more obtuse. The exact morphology of the articulation of the ilium with the sacral ribs remains uncertain due to the large amount of cartilage and other soft tissue that contributed to this joint. Together these features result in a shallow, dorsoventrally compressed girdle relative to related taxa.

DISCUSSION

Body Shape

Previous plesiosaur descriptions rarely discuss thoracic geometry, perhaps due to the presumed lack of diagnostic variety among taxa. However, there is growing awareness that body shape does vary. In his study of buoyancy and lung position in plesiosaurs, Henderson (2006) included digital wire-frame models of the plesosaurid *Liopleurodon ferox*, the cryptoclidid *Cryptoclidus oxoniensis*, and the elasmosaur *Thalassomedon haningtoni*. These models depict a circular transverse section for *Thalassomedon*, a sub-circular one for *Liopleurodon*, and an oblate one for *Cryptoclidus* (Henderson, 2006). This last model was influenced by Brown's (1981) comments on his reconstruction, saying that the Andrews (1910) *Cryptoclidus* reconstruction was unnaturally tall and narrow. Although this is true, we believe that Henderson's *Cryptoclidus* cross-section may be a bit too oblate based on our study of *Cryptoclidus* thoracic material (Fig. 7). The radical degree of thoracic compression in *Tatenectes*, however, is unique among plesiosaurs, yielding a novel body profile (Figs. 7, 8).

Overall thoracic geometry is determined both by the morphologies of the constituent skeletal elements and their manner of articulation. Individual dorsal vertebral centra influence body shape primarily by their number, and the relatively small number of dorsals in *Tatenectes* indicates a short thorax. The articulated spine of *Tatenectes* also displays little dorsoventral curvature; reconstructions of *Cryptoclidus* by Andrews (1910) and Brown (1981) show a greater degree of spinal curvature, whereas that of *Muraenosaurus* is more curved still (Andrews, 1910). The posterior 'lumbar' curve is unique to *Tatenectes*, having no analog

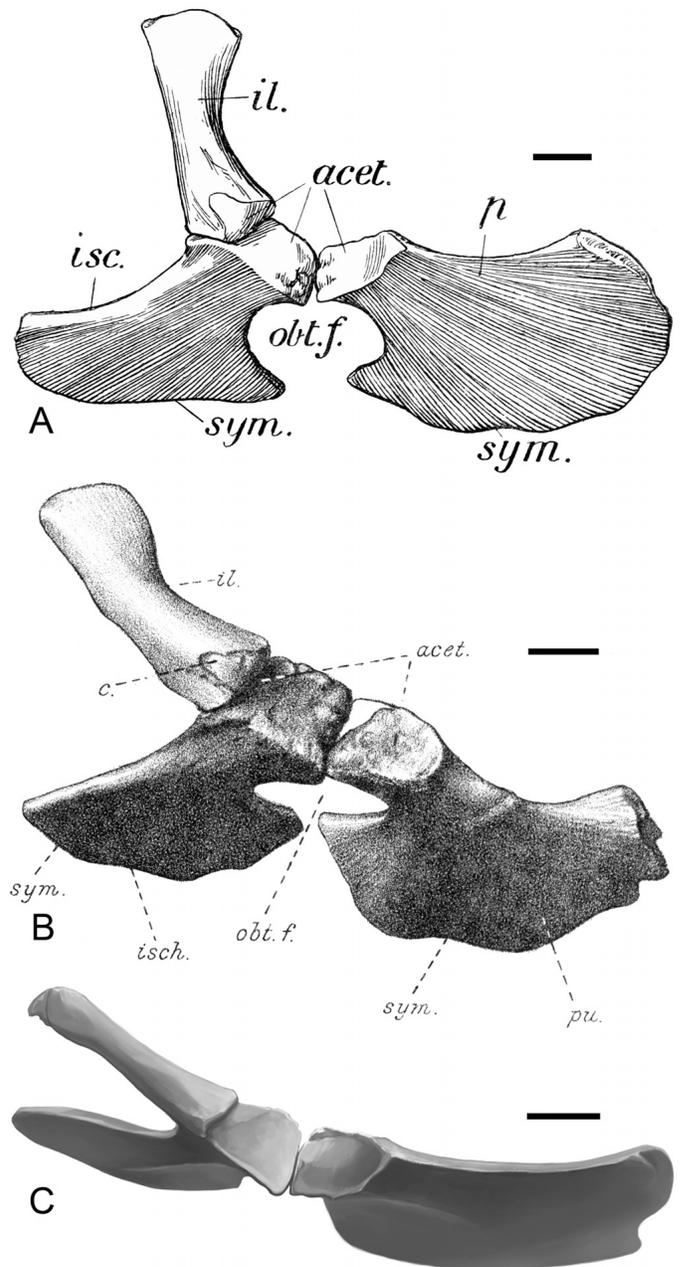


FIGURE 6. Reconstructed pelves of *Muraenosaurus* (A), *Cryptoclidus* (B), and *Tatenectes* (C). A and B taken from Andrews (1910). Scale bars equal 5 cm.

in any known plesiosaurian. The lack of dorsoventral curvature and the presence of a flattened 'lumbar' region markedly reduce the depth of the body in lateral profile (Fig. 8).

Although spinal curvature has a significant impact on thoracic depth, the orientation of the ribs has a greater effect. The pronounced posterior slant of the costal articular facets indicates that the ribs were recumbent, with the distal ends of the ribs approximately even with the ventral surface of the vertebral centra (Fig. 8). The distal ends of the longest ribs, associated with the anterior dorsal region, span five vertebrae posterior to the vertebra to which the rib articulates. These nearly horizontal ribs greatly reduce the depth of the body relative to other taxa (Figs.

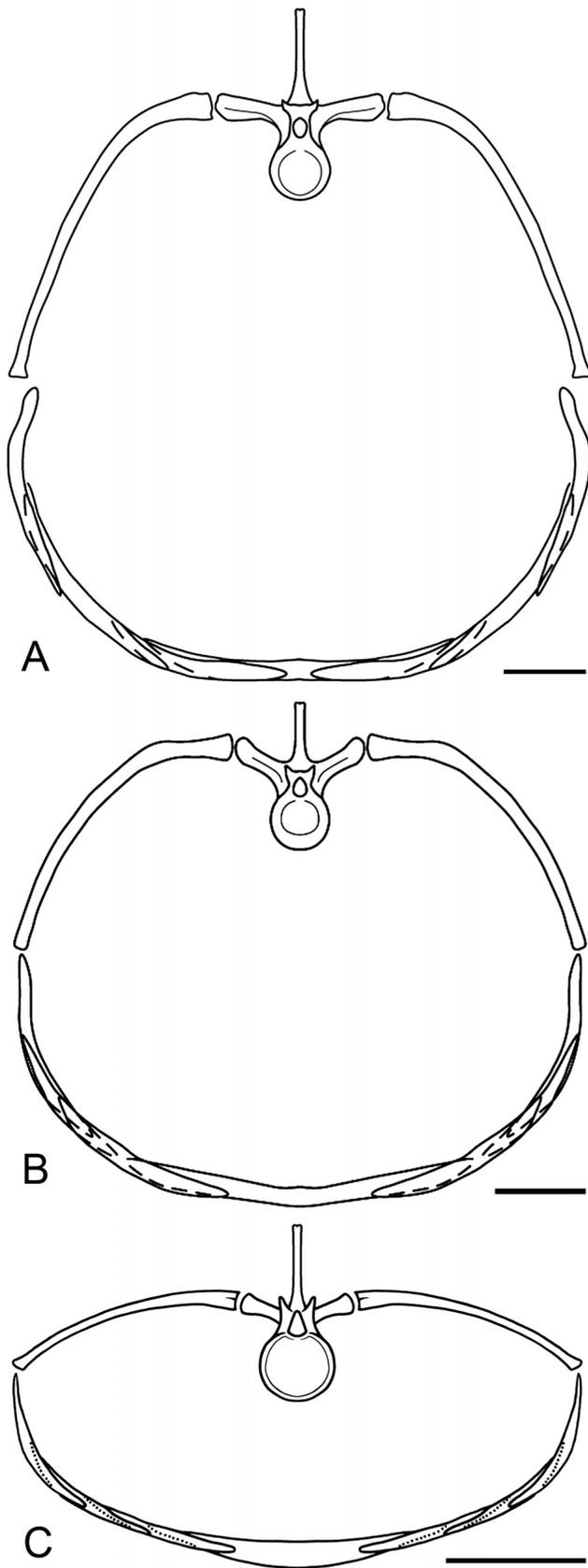


FIGURE 7. Cross-sections through the mid-thoracic region of cryptoclidid plesiosaurs *Muraenosaurus* (A), *Cryptoclidus* (B), and *Tatenectes* (C). Reconstruction in A is based primarily on examination of BMNH R. 2678; that in B is based on reinterpretation of the mounted specimen BMNH R. 2860. Scale bars equal 10 cm.

7, 8). The morphology of the gastralia produces further relative compression in the thorax of *Tatenectes*. By comparison, the gastralia of *Muraenosaurus* are the most curved; the gastralia of *Cryptoclidus* are less curved than those of *Muraenosaurus*, but in *Tatenectes*, the ventrum is nearly flat (Fig. 7). The central gastralia of *Tatenectes* have relatively little curvature, with curvature being confined to the lateral-most (J-bend) members of each segment. The morphology of the thoracic cage of *Tatenectes* gives the transverse section a very shallow, almost boxy appearance (Fig. 7), one that contrasts greatly with those of related taxa.

The morphology of the pelvis also affects body shape. The orientation of the ilium contributes to body shape because the angle of articulation with the ischium dictates how far ventral to the vertebral column the pelvic girdle is located. The ilium of *Tatenectes* is not disproportionately short, but does articulate with the ischium at a shallow angle (Fig. 6). Therefore, the overall depth of the pelvic region is reduced because the vertical distance between the spinal column and pelvic girdle is shortened. Given the same consideration, the pelvis of *Cryptoclidus* is deeper than that of *Tatenectes*, but not as deep as the pelvis of *Muraenosaurus*. The right and left hemipelves also articulate at a relatively shallow angle along the midline, another feature flattening the ventrum. The unique depressions seen in the visceral surface of the pelvic girdle may provide space for the pelvic viscera. Incidentally, because the ilium of *Tatenectes* is not disproportionately short, the entire pelvic girdle is shifted anteriorly, reducing the distance between the girdles and the limbs they carry.

The range of vertebral, distal thoracic, and pelvic adaptations described here have a clear theme, and that is extreme compression of the thorax dorsoventrally, and foreshortening anteroposteriorly. The body cross-section is also derived in being vaguely box-shaped rather than round; the dorsum is relatively flat, both in the anterior-posterior axis due to the low degree of curvature in the spine, and in the mediolateral axis due to the horizontal ribs. The ventrum also lacks curvature mediolaterally due to the presence of flat medial and J-bend lateral gastralia, as well as a shallow pelvis. Taken together, these features create a shouldered elipsoid thoracic morphology that is unique among plesiosaurs (Fig. 8).

Ecological Implications

Inference concerning the function of the novel body shape in *Tatenectes* must also consider the highly unusual pachyostotic midline gastralia possessed by the taxon (Street and O'Keefe, 2010). Pachyostosis in general is a method of passive buoyancy control (de Buffrénil et al., 1990; de Ricqlès and de Buffrénil, 2001), and its presence is generally correlated with life in shallow water (Gray et al., 2007). Pachyostosis in the skeleton of secondarily marine tetrapods seldom occurs in fast swimming, highly maneuverable taxa (Taylor, 2000), or in habitually deep-water forms (Gray et al., 2007). The added mass of pachyostotic bones acts as ballast to help the animal resist the dragging or buffeting effects of the turbulent environment at or near the water surface (de Ricqlès and de Buffrénil, 2001). Street and O'Keefe (2010) therefore postulated that pachyostosis in *Tatenectes* evolved as an adaptation for added stability in a shallow marine habitat. The distribution of pachyostotic bone is also significant; it is concentrated on the ventral midline, creating a heavy longitudinal core of bone. When added to the bone mass of the girdle elements, *Tatenectes* had a significant mass of heavy bone concentrated ventrally and medially in the thorax. This is unusual given that pachyostotic bone is more evenly distributed in most taxa possessing it (Domning and de Buffrénil, 1991; Gray et al., 2007), including the one other known pachyostotic plesiosaur (*Pachycostasaurus dawni*: Cruickshank et al., 1996). One other consideration is relevant, and that is the placement of the lungs within the body cavity. Air-filled lung tissue is obviously low in density and hence buoyant near the surface, and the lungs are dorsally located

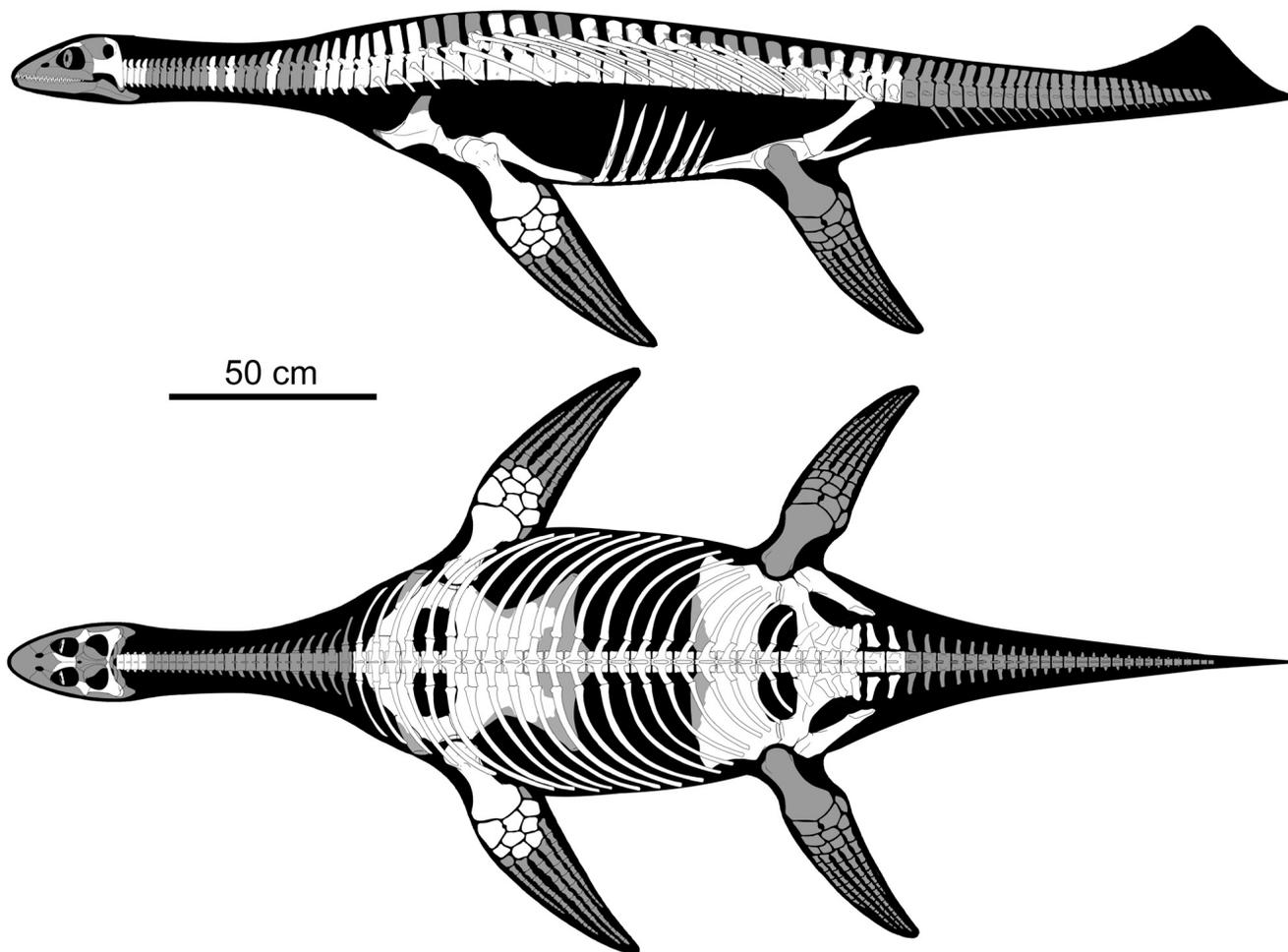


FIGURE 8. Full-body reconstruction of *Tatenectes laramiensis*, from the Upper Sundance Formation (Oxfordian) of Wyoming. Total reconstructed body length is just under 3 m, although uncertainty concerning the length of the neck makes this estimate conjectural. Neck length is based loosely on that of *Kaiwhekea* (Cruikshank and Fordyce, 2002). The presence and size of the tailfin is inferred from the condition in *Cryptoclidus* (Wilhelm, 2010). White indicates known material, and gray indicates missing elements or estimated edges of incomplete elements.

in most reptilian taxa, particularly aquatic ones like crocodylians and sea turtles (Henderson, 2006). A similar pleural location in *Tatenectes*—above the mid-coronal plane—would place a region of low density above a region of high density.

The oblate thoracic morphology of *Tatenectes*, when coupled with its ventrally heavy mass distribution, results in a body we hypothesize would be extremely stable at or near the surface of shallow water, particularly in the roll axis. This increased stability may have allowed access to the more turbulent regions above wave base in shallow, inshore environments not accessible to larger, deeper-bodied, less stable plesiosaurs. Although this is an adaptive inference, it seems a sensible one given its simplicity and ability to explain the panoply of novel morphological details displayed by the taxon.

There is no evidence to suggest that *Tatenetes* was a bottom feeder, unlike the elasmosaur fossils described by McHenry et al. (2005), whose gut contents primarily comprised benthic macroinvertebrates such as mollusks and echinoderms. In contrast, stomach contents associated with fossils of *Tatenectes* contain abundant cephalopod remains and hybodont shark material (Wahl, 2005, 2006).

The Sundance Seaway was also generally shallow, less than 40 m, during this geological interval (Wahl, 2006; O'Keefe and Street, 2009, and references therein), and adaptations to shal-

low water would make sense ecologically. Specht and Brenner (1979) describe pervasive winnowing of sediments of the upper Sundance Formation, indicating that the entire seaway was near or above storm wave base. Regions of the seaway were certainly shallower than the maximum depth of 40 m, and therefore likely above normal wave base. Such shallow water habitats would be easier to access and negotiate by animals with increased stability at the water surface, particularly in the roll axis. Lastly, the inference that the novel body shape of *Tatenectes* was adaptive via an increase in stability is open to test, via computer modeling using the methods pioneered by Henderson (2006).

ACKNOWLEDGMENTS

We thank M. Carrano for curatorial assistance and K. Reich for skilled preparation at USNM. D. Hanson at the Wyoming BLM has been a great help throughout the Sundance Plesiosaur Project. We thank E. Love, S. Peters, and E. Kvale for help with field work and C. and R. Manual for hospitality and other assistance. Thanks also to H. Ketchum for assistance to HPS during a study visit to NHM. Funding for this study was provided by National Geographic Society grant CRE 7627-04, and an NSF EPSCoR Grant to Marshall University.



FIGURE 9. Reconstructions of the cryptoclidid plesiosaur *Tatenectes Laramienseis* swimming in shallow water, its inferred environment. Morphology based on skeletons found in the Upper Member of the Sundance Formation, Bighorn Basin, Wyoming. The belemnite cephalopod is *Pachyteuthis densus*, the most common fossil in the formation. Art by Helen Zhu.

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Submitted June 22, 2010; accepted October 27, 2010.

Handling editor: Sean Modesto.