2009

A study of the morphology of Tatenectes laramiensis, a cryptocleidoid plesiosaur from the Sundance Formation (Wyoming, USA)

Hallie P. Street

Recommended Citation
Street, Hallie P., "A study of the morphology of Tatenectes laramiensis, a cryptocleidoid plesiosaur from the Sundance Formation (Wyoming, USA)" (2009). *Theses, Dissertations and Capstones*. 1073.
http://mds.marshall.edu/etd/1073

A study of the morphology of *Tatenectes laramiensis*, a cryptocleidoid plesiosaur from the Sundance Formation (Wyoming, USA)

Thesis submitted to
the Graduate College of
Marshall University

In partial fulfillment of
the requirements for the degree of
Master of Science
in Biological Science

by
Hallie P. Street

Dr. F. Robin O'Keefe, Ph.D., Committee Chairman
Dr. Suzanne Strait, Ph.D.
Dr. Victor Fet, Ph.D.

Marshall University

May 2009

Abstract

A study of the morphology of *Tatenectes laramiensis*, a cryptocleidoid plesiosaur
from the Sundance Formation (Wyoming, USA)

By Hallie P. Street

Tatenectes laramiensis is a cryptocleidoid plesiosaur from the Late Jurassic Sundance Formation. This study primarily concerns a partial skeleton comprised of dorsal vertebrae, ribs, gastralia, and pelvic girdle. Even though the skeleton is incomplete, it is hypothesized that the preserved fossils are sufficient to indicate the overall body shape and also the preferred habitat of *Tatenectes*. Possibly the most notable of the novel characters is the pachyostotic state of the gastralia. In relation to the ribs and overall size of *Tatenectes,* in comparison to the gastralia in related taxa, these gastralia are disproportionately robust. The combination of these morphologies suggests a dorso-ventrally compressed body shape. A sub-cylindrical cross-section along with the low center of gravity indicated by the pachyostotic gastralia suggest that *Tatenectes laramiensis* inhabited shallow coastal regions.

Acknowledgments

I would like to extend my thanks to those who aided me in this research. Thanks particularly to my advisor, the head of my committee, Dr. F. Robin O'Keefe for his advice and guidance throughout the extent of this research. Thanks also to the other members of my committee, Dr.'s Suzanne Strait and Victor Fet. Thanks to Ben Wilhelm for assistance in the lab and in museum work. Thanks to Helen Zhu for her artistic reconstructions. Thanks to Dr. Hillary Ketchum of the Natural History Museum, London, for her help and knowledge of the collections in that museum. Thanks to Dr. Matt Carrano and preparators of the Natural History Museum, Smithsonian Institution. Thanks to National Geographic, the College of William and Mary Monroe fund, and EPSCoR for funding, which made this research possible.

Table of Contents

Table of Figures

Chapter I. Introduction

Plesiosaurs are secondarily marine diapsid reptiles that lived during the Mesozoic Era (250-65 Mya). Their fossils are known from Jurassic marine deposits in Europe and North America. Plesiosaurs achieved a worldwide distribution before dying off in the Cretaceous-Tertiary mass extinction event (Andrews, 1910; Brown, 1981). Despite living concurrently with the better-known reptile clade, the dinosaurs, plesiosaurs are not closely related to their terrestrial Mesozoic counterparts. Along with other ancestral marine reptiles, plesiosaurs form the outgroup to the clades of derived diapsids, including Testudines, Lepidosauria, and Archosauria (Hill, 2005).

During the Jurassic and Cretaceous, many regions of the current continents were flooded by shallow epicontinental seas. The species which is the focus of this research is known only from the Sundance Formation. This stratum, the final in the Jurassic marine sequence for this area, has been dated to the Early Oxfordian [~160 Ma (ICS, 2008)]. This age is well supported by ammonite biostratigraphy and by bentonite layers that have been radiometrically dated (Pipiringos, 1957). The Sundance Formation is extremely heterogeneous, both laterally and vertically (O'Keefe and Street, 2009). The degree of variation seen in this formation is most likely due to the fact that it represents the final regressive stage of the Sundance Seaway. The sediments of the Sundance Formation crop out in Montana, Wyoming, South Dakota, Colorado, and Utah (Kvale et al., 2001). All of the modern specimens have been found in the Bighorn Basin of Wyoming, near the towns of Shell and Greybull.

Taxonomy

Plesiosaurs are the most derived members of the subclass Sauropterygia (Brown, 1981). More basal members of this clade include placodonts, pachypleurosaurs, pistosaurs, and nothosaurs (Rieppel, 2000; O'Keefe, 2001). These taxa inhabited shallow marine environments and diversified throughout the Triassic. The more basal stem-group sauropterygians were likely amphibious, and even the more derived might have retained morphologies that would have allowed some degree of terrestrial locomotion. Contrastingly, the derived crown-group Plesiosauria, which underwent evolutionary radiation events during the Jurassic, appear to be obligatory aquatic animals (Rieppel, 2000).

Relationships among Plesiosauria are very complex (Figure 1.1). There has also been a great deal of disagreement about the various phylogenetic trees that have been proposed over the years. Much of the debates stems from he issue of whether various general body morphologies, such as pliosauromorphs or elasmosauromorphs, evolved once or multiple times in convergence. Based on research by O'Keefe (2001, 2004), general body shapes arose multiple times, and more complex features, such as palatal and braincase osteology, are better criteria for determining relationships among Plesiosauria. One such controversial clade is Cryptocleidoidea. The cryptocleidoid plesiosaurs are closely related to the extremely long-necked Elasmosauria. One clade of pliosauromorphs, Polycotylidae, in nested within Cryptocleidoidea. The original plesiosaurian taxon, *Plesiosaurus,* is an outgroup to these two clades. The other branch of Plesiosauria consists of two clades of pliosauromorphs, Pliosauridae and Rhomaleosauridae, along with other unresolved taxa (O'Keefe, 2001, 2004).

Smith's 2007 dissertation included a new cladistic analysis of Plesiosauria, with a focus on the pliosauromorph Rhomaleosauridae. In that study, the polycotylids were found to be the sister group to Leptocleididae, another pliosauromorph. These two lineages form a clade Leptocleidoidea, which is the sister group to Pliosauridae (Smith, 2007). However, no other members of Cryptocleidoidea were included in this study. Indeed, the entirety of the plesiosauromorphs is represented by just five taxa.

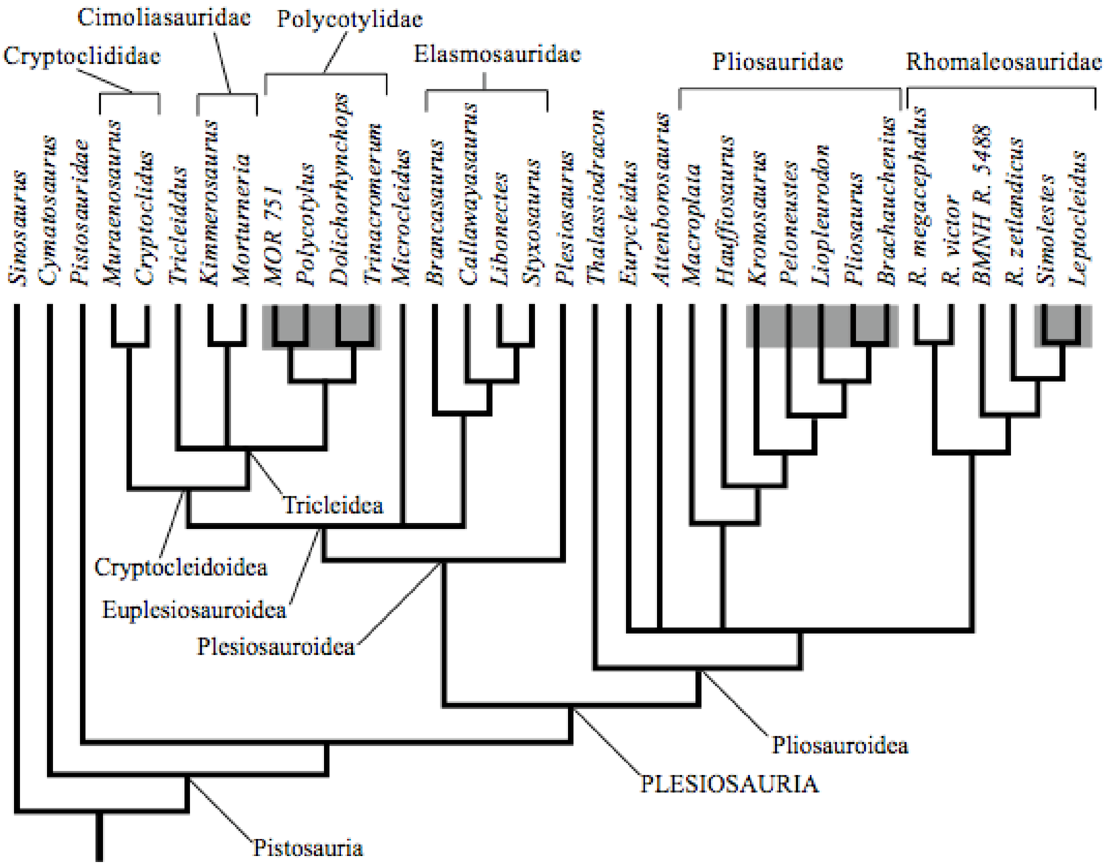

Figure 1. 1: Phylogenetic relationships among the Plesiosauria. Tatenectes laramiensis was not included in the study from which this cladogram was produced. Based on more recent phylogenetic analyses, Tatenectes is most closely related to Kimmerosaurus. From O'Keefe 2001, 2004.

Another recent phylogenetic analysis conducted by Druckenmiller and Russel (2008) hypothesizes alternative relationships. The results of their study find no relationship between Cryptocleidoidea and Polycotylidae. The cladograms generated in that study include Pliosauroidea and a highly unresolved Plesiosauroidea, which is a polytomy including Elasomosauridae. *Muraenosaurus* and *Cryptoclidus*, the only two non-polycotylid cryptocleidoids included, were found to be successive outgroups to Elasmosauridae. These differences can be attributed to variations in the way characters were coded and scored, along with new interpretations of the fossil material (Druckenmiller and Russel, 2008). This highlights just how little is known about plesiosaurian phylogeny and the importance of new systematic analyses.

These two phylogenetic analyses do not support the findings of O'Keefe (2001, 2004). However, due to the primary taxa of focus in each study, this is not surprising. Smith (2007) and Druckenmiller and Russell (2008), were both studying the phylogenetic position of one genus of pliosauromorph, *Rhomaleosaurus* and *Leptocleidus* respectively. The taxa lists for each study therefore contained many derived pliosauromorphs and few (Druckenmiller and Russell, 2008) if any (Smith, 2007) plesiosauromorphs. The inclusion of so many derived taxa at the expense of basal taxa will bias the analysis. Without ample representation of ancestral taxa, the derived similarities in the stem-group taxa will automatically group those taxa together. Plesiosauria desperately needs a new comprehensive phylogenetic analysis including basal, intermediate, as well as the derived forms.

The specimen under examination in this study has been referred to the taxon *Tatenectes laramiensis* (O'Keefe and Wahl, 2003, a). It is a member of the clade Cryptocleidoidea (Figure 1.2). The group derives its name from the characteristically reduced nature of the clavicles and interclavicals. Due to the expansion of the scapulae anteriorly and toward the midline, the clavicles and

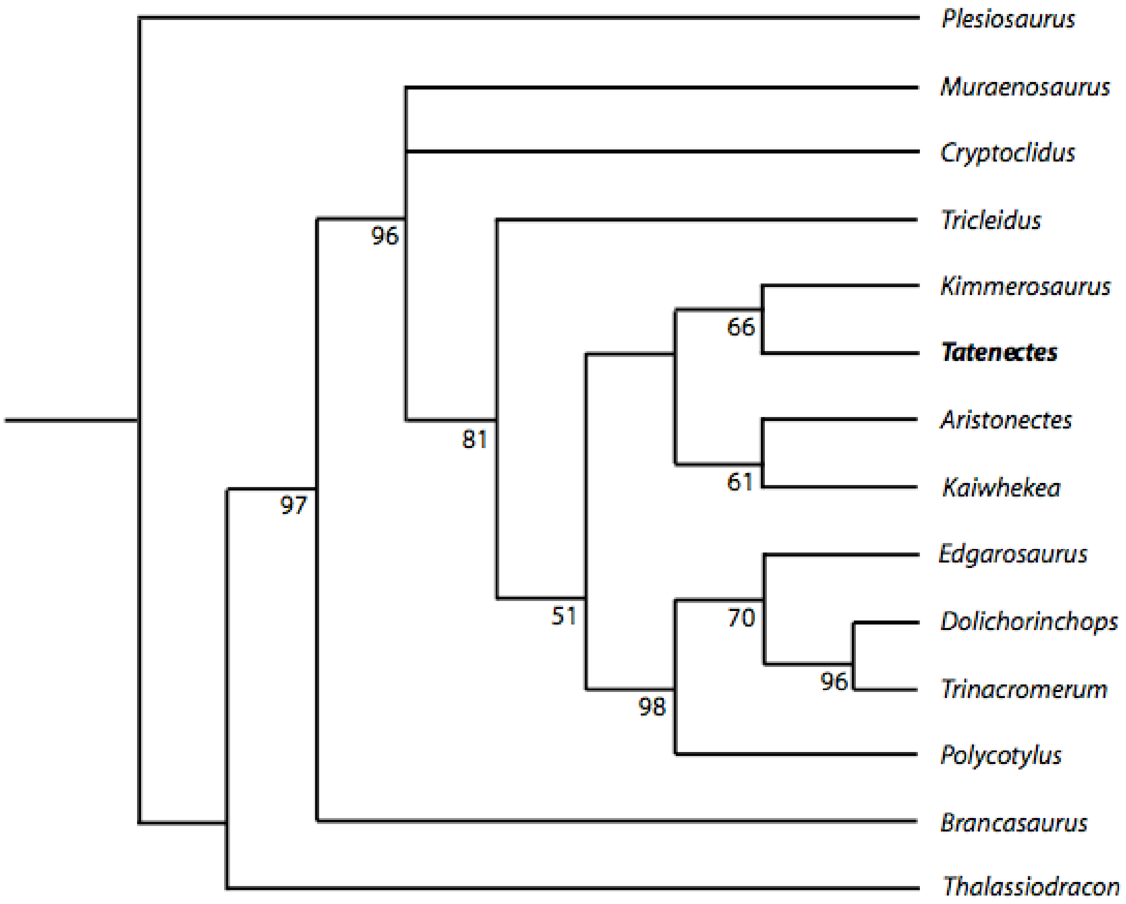

Figure 1. 2: Phylogenetic relationships within Cryptocleidoidea. Note that *Tatenectes* is the sister taxon to *Kimmerosaurus*. Note also that *Pantosaurus* (not shown) is likely closely related to *Muraenosaurus*. Bootstrap values of over 50 are indicated. From O'Keefe and Street, 2009.

interclavicals are located on the visceral surfaces of the scapulae (Andrews, 1910). The clavicles have thereby become hidden or 'cryptic'. Even though all cryptocleidoids share this trait of reduction of the clavicles and interclavicals, there is variation in the morphology of these dermal elements within the clade (Brown, 1981).

Cryptocleidoidea is an unusually diverse clade in that nearly all morphotypes of plesiosaurs are represented in this taxon. At one extreme, there are the polycotylids, one group of pliosauromorphs. Some taxa are relatively unspecialized. At the other end of the spectrum, there is *Muraenosaurus*, which had been placed within Elasmosauridae. Certainly, *Muraenosaurus* does have the long neck associated with elasmosaurids, however its palatal anatomy indicates that this taxon is actually an elasmosauromorph within the Cryptocleidoidea. According to the most recent phylogenetic analysis of Cryptocleidoidea (O'Keefe and Street, 2009), *Tatenectes laramiensis* is most closely related to the Kimmeridge Clay taxon *Kimmerosaurus langhami*. These two plesiosaurs, along with two closely related taxa from Cretaceous deposits of Australia, *Aristonectes* and *Kaiwhekea*, form the clade Aristonectidae. These crown-group cryptocleidoids are the sister group to the pliosauromorph clade within Cryptocleidoidea, Polycotylidae. Basal to these two groups is the taxon *Tricleidus*. The relationships within Cryptocleidoidea become less resolved basal to Tricleidea. A polytomy exists with this clade and the two genera *Muraenosaurus* and *Cryptoclidus* (O'Keefe and Street, 2009). Based on this cladistic analysis, *Tatenectes* should most closely resemble *Kimmerosaurus*. However, *Kimmerosaurus* is known only from cranial material, and little is known of the skull of *Tatenectes*. Preliminary observations of the postcranial skeleton suggest that *Tatenectes* shares some charters with *Cryptoclidus* and *Muraenosaurus*, particularly the former.

It is important to note that the phylogeny for Plesiosauria is in a state of flux. New descriptions, whether they represent a new taxon or merely a previously unpreserved feature of a well-known species add to the knowledge base from which phylogenetic analyses are derived. New interpretations of fossils also can lead to rearranging the phylogeny.

Morphology

The two most completely known cryptocleidoid plesiosaurs are *Cryptoclidus* and *Muraenosaurus*, each genus containing two species. These taxa, along with *Tricleidus*, are known from Upper Jurassic-aged sediments from the United Kingdom (Andrews, 1910). Nearly complete specimens have been discovered of *Cryptoclidus eurymerus* and *Muraenosaurus leedsi*, and each species is also known from examples of specimens of various ages as well. The skeleton of *Cryptoclidus* is relatively unspecialized. Its neck is comprised of about 32 vertebrae, followed by two or three pectoral vertebrae, 20 dorsal vertebrae, and three or four sacral vertebrae. The exact number of caudal vertebrae is still unknown, but it has been hypothesized to be around 30 (Andrews, 1910). *Muraenosaurus* has 44 cervical vertebrae, and the numbers of the rest of the vertebrae in the spinal column are about the same seen in Cryptoclidus. There are significant differences between the pectoral girdles of the two genera. Cryptoclidus has triangular clavicles and a greatly reduced interclavicals, whereas in Muraenosaurus, the oval-shaped interclavical is the more prominent dermal bone and the clavicles are reduced. The pectoral girdle of Cryptoclidus is widest at the posterior margin of the coracoids, due to laterally extending phalanges on these bones. Conversely the pectoral girdle of Muraenosaurus is relatively wider anteriorly (Andrews, 1910, Brown, 1981).

In order to fully understand the significance of unique skeletal features of Tatenectes, it is important to have a thorough knowledge of the morphologies of related taxa (Figure 1.3). These well-studied related plesiosaurs then serve as a

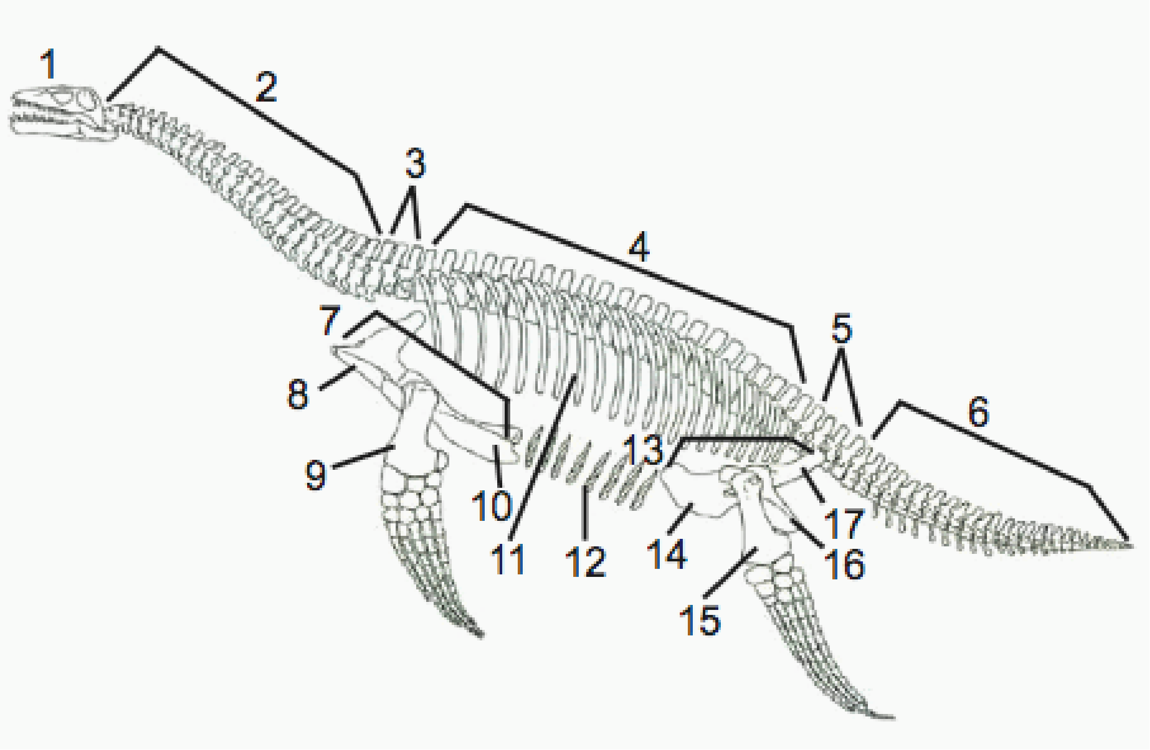

Figure 1. 3 General skeletal anatomy.

1. Skull
2. Cervical vertebrae
3. Pectoral vertebrae
4. Dorsal Vertebrae
5. Sacral vertebrae
6. Caudal vertebrae
7. Pectoral girdle
8. Scapula
9. Humerus
10. Coracoid
11. Dorsal ribs
12. Gastralia
13. Pelvic girdle
14. Pubis
15. Femur
16. Ishium
17. Illium

Image from wisegorilla.com

basis for comparison. In that vein, the published literature on Cryptoclidus, Muraenosaurus, and other cryptocleidoid plesiosaurs was studied for descriptions of skeletal elements from these taxa that are also known from *Tatenectes*.

Vertebrae

Vertebrae are separated into five regions along the spinal column: cervical vertebrae in the neck region, including the first two vertebrae posterior to the skull, which are known as the atlas and axis; the vertebrae in the shoulder region are known as pectoral vertebrae; the vertebrae of the back are the dorsal vertebrae; sacral vertebrae are those of the hip region, and the vertebrae of the tail are the caudal vertebrae. These distinctions are largely made due to the location of the articular facets for the ribs (Brown, 1981). In the cervical vertebrae, the ribs articulate with the lateral faces of the vertebral centra. These articulations are located near the ventral margin of the vertebrae. Moving posteriorly, the rib articular facets move up the lateral faces of the vertebral central till there is a transition to the ribs articulating with the transverse processes. That transitionary phase marks the pectoral vertebrae, and the transverse processes carrying the articulation marks the dorsal vertebrae. There is a similar transition between the dorsal and caudal vertebrae a well. The sacral vertebrae are those where the rib articulation facets have descended from the transverse processes and are once again on the lateral faces of the vertebral centra. The caudal vertebrae have rib articulation facets on the lateral faces and chevron facets on the ventral faces (Andrews, 1910, Brown, 1981).

The centra of the cervical vertebrae of *Muraenosaurus* are wider laterally than they are long anterio-posteriorly. The difference between these dimensions increases posteriorly. The height of the centra is intermediate between the length and width. The cervical rib head articular facets are anterio-posteriorly elongated with an irregularity on the dorsal margin. The articular facets between the vertebral centra are nearly circular in the dorsal series, and once again the centra width exceeds the height in the sacrals and caudals (Andrews, 1910). In *Cryptoclidus*, the centra are never longer than they are wide (Brown, 1981). The cervical centra width is however greater than the height, and the cervical rib articulation facets are subequal in length and height (Andrews, 1910). *Tricleidus* has cervical vertebrae that are wider than they are high and dorsals that are subcircular (Andrews, 1910).

Girdles

The pectoral girdles are comprised of coracoids, scapulae, and dermal elements that are paired across the longitudinal midline. Whereas in more basal taxa the clavicles, interclavicles, scapulae, and coracoids would span the body cavity with the dermal elements dorsal and the scapulae and coracoids ventral, in plesiosaurs, all the elements have shifted to lie in the ventrum of the animal (Andrews, 1910). The scapulae and coracoids fuse in the glenoid fossa and in the scapulo-coracoid midline bar. As mentioned in the description of Cryptocleidoidea, the clavicles and interclavicles are greatly reduced and often fused to the scapulae. In some cases, one of the dermal elements will be reduced to a narrow splint of bone that lies on the midline between the scapulae. In *Muraenosaurus*, the anterior rami of the scapulae do not meet at the midline, the scapulae and coracoids join about midway along the scapulo-coracoid bar, and the widest part of the pectoral girdle is formed by the dorsal rami of the scapulae (Brown, 1981). Conversely, in *Cryptoclidus*, the anterior rami of the scapulae do meet along most of their midline length, the scapulae and coracoids join in the anterior portion of the scapulo-coracoid bar, and the lateral rami of the posterior termini of the coracoids are greatly extended, surpassing the width of the scapulae. The anterior rami of the scapulae of *Tricleidus* do not meet on the midline. They are separated by a wide v-shape, as opposed to the narrow u-shape separating the anterior rami of the scapulae of *Muraenosaurus*. The scapulae and coracoids join in the anterior portion of the scapulo-coracoid bar. The lateral rami of the posterior termini of the coracoids are expanded laterally, though not to the extent seen in *Cryptoclidus*, and there are distinct posterior rami just lateral to the midline suture along the posterior termini of the coracoids (Andrews, 1910; Brown, 1981). Of these taxa, *Tricleidus* has the relative deepest pectoral girdle. The dorsal rami of the scapulae extend nearly vertically, and the paired scapulae form a deep u-shaped body cavity. The scapulae of *Cryptoclidus* form a v-shaped body cavity with the dorsal rami of the scapulae extending at a much shallower angle.

The pelvic girdles are composed of three sets of paired elements. The most anterior are the pubes, with the ischia extending posteriorly. The illia, which join the pelvic girdle to the spinal column, articulate with the ischia only. The pubes are broad elements, which are thickest were they form the anterior margin of the acetabula and where they meet at the midline. The ischia are usually described as having a hachet-shaped morphology. Similar to the pubes, the ischia are thickest where they form the posterior margin of the acetabula and join with the illia. They are also slightly thicker along the midline. The illia are elongate, rather than platy, wider where they join with the ischia than at the end where they join with the sacral ribs. This articular surface is compressed medio-laterally (Andrews, 1910).

The pelvic girdle of *Muraenosaurus* is relatively longer than that of *Cryptoclidus*. The width of the pubes exceeds their lengths in both taxa, but that difference is greater in *Cryptoclidus*. This is partially due to the more prominent antero-external angle of the pubes of the later taxon. The ischia are also relatively longer in *Muraenosaurus* than in *Cryptoclidus*. The illia of *Muraenosaurus* are relatively straight, with a concave anterior surface and an anterio-posteriorly expanded articular surface for the sacral ribs (Andrews, 1910). The illia of *Cryptoclidus* are quite similar in morphology, but there are differences in the angles of articulation between the illia and ischia. The illia articulate with the ischia in *Muraenosaurus* at a nearly vertical angle. This makes the body cavity quite deep in this region. The angle between both pubes is also more pronounced in this taxon. In *Cryptoclidus*, the pubes articulate at a shallower angle, producing a broader, shallower body cavity. A more oblate body shape for *Cryptoclidus* is also supported by the shallower angle of articulation between the illia and ischia in *Cryptoclidus*. Only one pubis in known from *Tricleidus*. Its length and width dimensions are subequal, with the length being perhaps a little greater (Andrews, 1910).

Tatenectes laramiensis

As mentioned above, this study focuses on a cryptocleidoid plesiosaur known as *Tatenectes laramiensis*. This taxon was originally described in 1900 by Knight. At that time, the plesiosaur was assigned to the now invalid genus *Cimoliosaurus*. Mehl (1912) transferred the taxon to the genus *Tricleidus*. At some point the holotype specimen was lost. O'Keefe and Wahl (2003) later discovered a new specimen that matched the Knight's original description. That specimen was designated as the neotype (O'Keefe and Wahl, 2003, a). However, upon further examination, it became evident that the species did not belong within the genus *Tricleidus*, so the new genus *Tatenectes* was erected. After these taxonomic revisions the taxon's correct appellation is *Tatenectes laramiensis* (Knight 1900) (O'Keefe and Wahl, 2003, a). The current specimen is referred to this taxon due to the similarities of the skeletal elements that overlap with known specimens of *Tatenectes*. Also, only two cryptocleidoid plesiosaurs are known from the Sundance formation, and the other, *Pantosaurus striatus*, is considerably larger than this specimen (O'Keefe and Wahl, 2003, b).

Prior to the excavation of this specimen, *Tatenectes laramiensis* was known from three partial skeletons and various other isolated elements (Figure 1.4). The holotype, described by Knight (1900), has been lost, but based on his description it comprised axial skeleton elements and most of the bones of one forelimb (O'Keefe and Wahl, 2003, a). O'Keefe and Wahl (2003, a) described a new specimen consisting of similar elements along with a pectoral girdle and other axial components such as ribs, which is now the neotype of the species. Another specimen, which consists of articulated vertebrae, a pectoral girdle, and

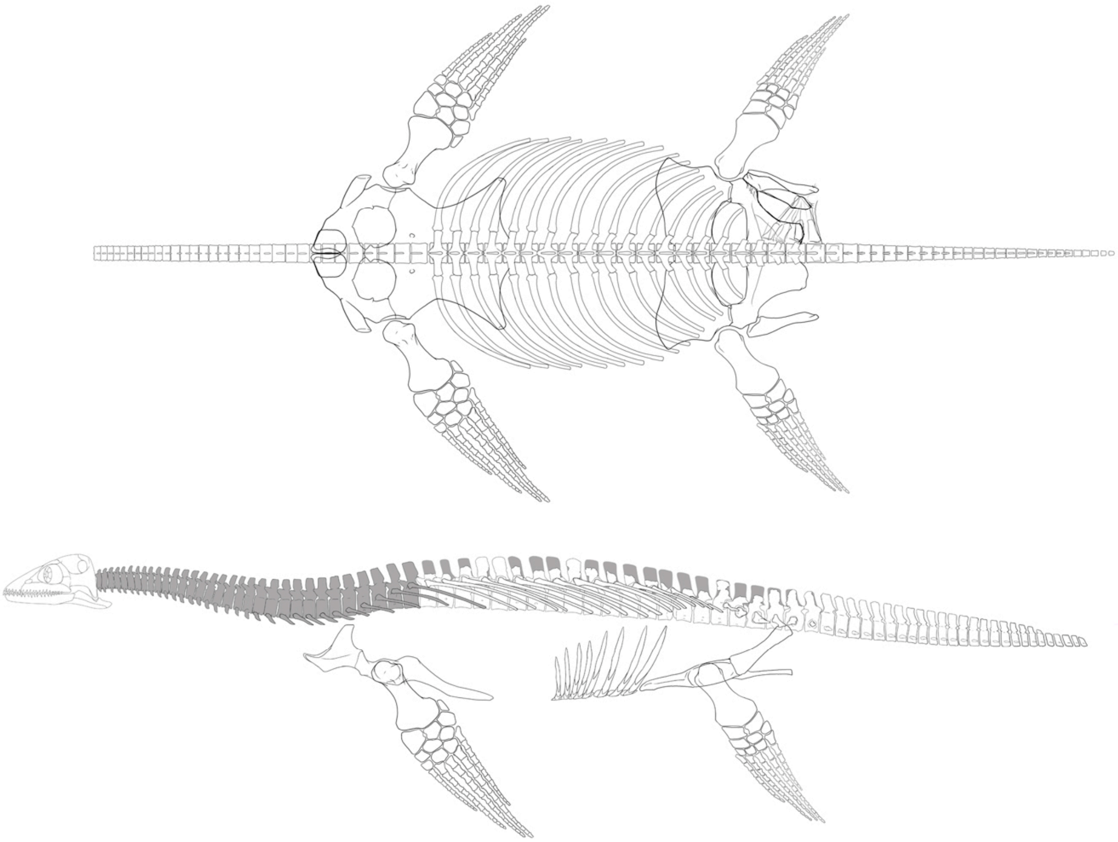

Figure 1. 4: Artist reconstruction of *Tatenectes laramiensis* in dorsal view (top) and lateral view (bottom). Dark gray areas represent material that remains unknown or broken portions of known elements.

fragments of cranial material, has since been referred to the taxon (O'Keefe and Wahl, 2003, a). The pectoral girdle of this specimen was described by O'Keefe and Street (2009). In total the previously known material comprises skull, braincase, and palatal bones, cervical vertebrae, dorsal vertebrae, ribs, and pectoral girdle elements.

The skull of *Tatenectes* is known from fragmentary elements. Among these are isolated teeth, which are striated around their lingually curving, slender crowns. The midline portion of the left frontal was also preserved (O'Keefe and Wahl, 2003, a). Both the left and right squamosals are known, and though neither is complete, different processes are preserved in each. The left squamosal was preserved with the articulations to the quadrate and the right squamosal, which is on a gracile process, intact. The length of the dorsal process indicates that the temporal fenestra is relatively deep, similar to the conditions of *Tricleidus* and *Kimmerosaurus* (O'Keefe and Wahl, 2003, a). The right squamosal also has the quadrate articulation, and the anterior process, which is unusually deep dorso-ventrally, is better preserved on this side (O'Keefe and Street, 2009). The pterygoids are unusual in *Tatenectes* in that the site where they fuse posteriorly to the anterior interpterygoid vacuity is very thick dorso-ventrally and obstructs the regions where one would expect to find the posterior interpterygoid vacuities. The articulations for elements of the basioccipital are preserved on the posterior portions of these bones (O'Keefe and Wahl, 2003, a).

Vertebrae are known from nearly all regions of the spine. The cervical vertebral series is currently represented by isolated anterior and posterior elements. These vertebrae are quite compressed anterio-posteriorly, and they are wider than they are tall. (O'Keefe and Wahl, 2003, a; O'Keefe and Street, 2009). The cervical ribs on the anterior cervicals are also compressed dorso-ventrally (O'Keefe and Street, 2009). Since a complete cervical series has not yet been found for this taxon, the exact number of cervicals is unknown. However, it is unlikely that the cervical count would be as high as is seen in

Muraenosaurus. The dorsal vertebrae are longer than the cervical vertebrae, though they are not as long as those of *Muraenosaurus*. The transverse processes of the dorsal vertebrae angle slightly dorsally, and the articular facets for the dorsal rib head are angled posteriorly. There are four sacral vertebrae in the spinal column of *Tatenectes*. The length of the tail is also unknown. Ribs and relatively large gastralia are known from fragments in these described specimens.

Two different pectoral girdles have been described. Neither is complete, but there is enough evidence to estimate a reconstruction. The pectoral girdle described by O'Keefe and Wahl (2003, a) is most likely a juvenile. Its immature status led to some erroneous original interpretations. The description of the second, more mature, pectoral girdle indicates that the scapulae do indeed meet at the midline. One of the most distinct features of the pectoral girdle of *Tatenectes* is how short it is anterior to the pectoral fenestrae. The scapulae and coracoids join near the midpoint of the scapulo-coracoid bar. The complete dimensions of the pectoral girdle are as yet unknown, but based on reconstructions, the widest part of the girdle is formed by the lateral rami of the coracoids, but this width only slightly exceeds the width from the dorsal ramus of one scapula to the other (O'Keefe and Street, 2009). Only one dermal element is known, and the degree to which it was fused to the scapula has made it difficult to determine if it is a clavicle or interclavical (O'Keefe and Street, 2009). This dermal element is sub-rectangular in shape and appears to be one of a set of paired bones that would have met on the midline. Considering that the full extent of the dorsal rami of the scapulae have not yet been preserved, it is difficult to know how deep the body cavity would have been, but the preserved regions are quite flat.

This fossil of *Tatenectes laramiensis* was originally discovered near the town of Shell, Wyoming, during the 2005 field season but not excavated at that time. During the following field season, June 2006, the specimen was relocated and excavated. After removing the overburden and surrounding sediments until bone was exposed on all sides of the remaining matrix blocks, the specimen was removed in two large plaster casts. The casts were transported to the Natural History Museum of the Smithsonian Institution, Washington, D.C. for preparation.

The specimen under current consideration, USNM 536974, preserves the posterior region of *Tatenectes laramiensis* for the first time. This specimen consists of a vertebral column of twenty-two articulated vertebrae from the anterior dorsal region through the first two caudals. Many dorsal ribs and gastralia were also preserved in a mass. Finally, all six pelvic elements were also found in various states of fragmentation. This discovery of the hip region of *Tatenectes* is scientifically significant in that it greatly adds to what is known about this species and provides greater overlap between this taxon and its closest relatives.

Tatenectes laramiensis is diagnosed by several autapomorphies. One of the most unusual is the anterior slant of the neural spines. This is not seen in any other plesiosaur. There is one possible reference to a similar condition as cited by Hulke (1870). However, the terminology used by Hulke is ambiguous and old-fashioned and the vertebrae in question are not figured. The neural spines of that specimen were not located during a search of the Natural History Museum, so the assertion could not be confirmed. It also appears that the vertebral column articulates to produce less curvature than is seen in other cryptocleidoids such as *Cryptoclidus* and *Muraenosaurus*. The final unique character of the vertebrae of *Tatenectes* is the posteriorly slanting to nearly horizontal facets on the transverse processes for the articulation of the rib heads. The ribs themselves, therefore have an extreme posterior slant, greatly contributing to the reduction in depth of the trunk of *Tatenectes*. Possibly the most evident autapomorphy of *Tatenectes* is the pachyostosis of the gastralia. A final unique trait is the angle produced by the articulation of the illium to the ischium. While the illia in *Muraenosaurus* are nearly vertical, and those of

Cryptoclidus are more posteriorly slanted, the illia in *Tatenectes* articulate at an even more exaggerated posterior angle, also reducing the depth of the trunk in this region.

The purpose of this study is to closely examine the morphology of the postcranial skeleton of *Tatenectes laramiensis*, as known from this specimen. This material is compared to corresponding elements from related cryptocleidoids. Regarding the gastralia, it is hypothesized that the gastralia of *Tatenectes* are pachyostotic and possibly pachyosteosclerotic. It is also hypothesized that *Tatenectes* has a body shape that is greatly reduced in depth, compared to related taxa.

Chapter II. Pachyostosis

Some degree of skeletal tissue modification is quite common among secondarily marine tetrapods. These modifications fall into one of two general types: toward an overall lightening of the skeleton, or toward a more robust skeleton. Lightening the skeleton, either by reducing overall bone volume or density through non-pathologic osteoporosis, appears to favor deeper diving and faster swimming (de Ricqlès and de Buffrénil, 2001). Heavier skeletons can be achieved either through increasing bone volume, a condition known as pachyostosis, through increasing bone density through non-pathologic osteosclerosis, or a combination of the two, called pachyosteosclerosis (de Buffrénil et al., 1990). Pachyostosis and osteosclerosis are seen more commonly in organisms that favored near-shore shallow marine environments such as lagoons or even estuaries (de Ricqlès and de Buffrénil, 2001). The added density serves multiple purposes, such as stabilizing an animal passively and reducing the effects of waves, providing negative buoyancy, or maintaining neutral buoyancy even as the lungs enlarge (Taylor, 2000; de Ricqlès and de Buffrénil, 2001).

Pachyostosis and osteosclerosis result from the alterations of rates of natural processes of bone formation or maintenance. The actions of osteoblasts and osteocytes, the types of cells that produce bone tissues, and osteoclasts and chondroclasts, which resorb osseous and cartilaginous tissues respectively, are involved to different degrees in the two conditions (Hall, 2005). At the level of the organism, pachyostosis is the enlargement of the bones in the body relative to the bones of a related taxon, or the thickening of parts of the skeleton relative to the rest of the body. It is most common for pachyostosis not to be present throughout an entire organism but to be confined to particular regions of the skeletal system. At the histological level, pachyostosis results from the hyperplasy of the periosteal cortex (Francillon-Viellot et al., 1990). An osteosclerotic state can develop through multiple processes (Ricqlès and de

Buffrénil, 2001). Skeletons can become denser if the spongiosum or marrow cavity of the bones is occluded by hypertrophied deposition of endosteal bone. Deep cancellous bone tissue can also be replaced though Haversean substitution (de Ricqlès and de Buffrénil, 2001). The most common processes that lead to osteosclerosis result from masses of calcified cartilage, which can result from the disruption of the resorption/deposition balance of both cartilaginous and osseous tissue (Francillon-Viellot et al., 1990). When chondroclastic and osteoblastic activities are reduced but the rates of deposition of bone are not reduced, the density of tissues will increase without the overall size of the bone changing. Through such processes *globuli ossei* can be formed. These dense accretions form around existing Haversean systems, taking up the space that another, more highly vascularized, Haversean system would form (de Buffrénil et al., 1990, and de Ricqlès and de Buffrénil, 2001). Previous studies have investigated the evidence of these ontogenetic processes on the skeletons of sirenians, archaeocetes, and some plesiosaurians (de Buffrénil et al., 1990, Wiffen et al., 1995 and de Ricqlès and de Buffrénil, 2001). An example of the latter is the plesiosaur *Tatenectes laramiensis*, which seems to display system level pachyostosis of the gastralia at the very least (O'Keefe and Street, 2009), and it is the purpose of this research to determine if the morphology of these particular skeletal elements were the result of pachyostosis, osteosclerosis or a combination of the two processes.

Both of these skeletal modifications tend to occur in the same lineage. One of the prime examples is in Cetacea. Primitive archaeocetes exhibit pachyosteosclerosis, most notably in the ribs (de Buffrénil et al., 1990). However, modern cetaceans have reversed this body-weighting trend and reduced skeletal mass to a great extent. This has been achieved both through the reduction of unnecessary skeletal elements such as the pelvic girdle and hind limbs, and through extensive osteoporosis (de Ricqlès and de Buffrénil, 2001). Sauropterygia also includes both osteosclerotic and osteoporotic taxa (Wiffen et al., 1995). In the cases of both these lineages, increased skeletal mass, through increases in volume and/or density, is seen in ancestral taxa (de Ricqlès and de Buffrénil, 2001). These taxa would have been struggling to adapt to the new demands of a marine habitat and would have been limited to shallow marine environments. Pachyostosis or osteosclerosis would have been beneficial to newly aquatic organisms, which would not have yet evolved characters typical of strong swimmers. However, as millennia passed and the archaeocetes and sauropterygians evolved and became more adept in an open marine environment, the original usefulness of a dense skeleton (passively maintaining trim, assisting in diving, counteracting the increased buoyancy of expanding lungs) would instead become a hindrance by preventing the faster swimming, precise movements, and increasing the difficulty of returning to the surface to breathe (Taylor, 2000). More derived taxa, often thought not always interpreted as being pursuit predators, therefore have developed osteoporosis as is seen in ichthyosaurs, some derived plesiosaurs, and modern cetaceans (Wiffen et al., 1995 and de Ricqlès and de Buffrénil, 2001).

Pachyostosis and osteosclerosis are seen in few modern taxa, but are common among secondarily marine tetrapods, both mammalian and reptilian (Francillon-Viellot et al., 1990). Modern and fossil sirenians display pachyostosis and osteosclerosis throughout their skeletons (Domning and de Buffrénil, 1991). Evidence of pachyostosis and osteosclerosis has previously been found within Sauropterygia. A combination of both conditions has been noted throughout the skeletons of basal sauropterygians including nothosaurs and pachypleurosaurs (Taylor, 1993; Wiffen et al., 1995; Ricqlès and de Buffrénil, 2001; Cheng et al., 2004). Within the more derived Plesiosauria, pachyostosis and osteosclerosis have been studied both in an ontogenetic context and as being diagnostic of the species *Pachycostasaurus dawni* (Wiffen et al., 1995). The conditions also serve as evidence of heterochronies in Late Cretaceous elasmosaurids and pliosaurids from New Zealand (Wiffen et al, 1995; Cruickshank et al., 1996). A study by de Ricqlès and de Buffrénil (2001) included a table of the occurrences of pachyostosis and osteosclerosis among secondarily marine tetrapods.

Pachycostasaurus dawni is known from the prolific marine reptile deposits of the Oxford Clay Formation of the United Kingdom. The taxon is a small pliosaur, unique in its pachyostotic ribs and vertebrae, particularly those of the lumbar region of the trunk. Both the ribs and the gastralia have the banana-like morphology that is seen in pachyostotic marine mammals. Based on histological sections taken of the pachyostotic elements, it was determined that the bones are osteosclerotic as well (Cruickshank et al., 1996). The degree of pachyosteosclerosis would have provided *Pachycostasaurus* with a great deal of ballast.

Wiffen et al. (1995) studied ontogenetic effects on bone density in plesiosaurians from New Zealand's Late Cretaceous Mangahouanga Stream site. The taxa they used cannot be identified to the genus level, but represent a taxon of elasmosaur and one of pliosaur. In their research, they compared the tissue formations in conspecific juveniles and adults. The skeletal elements observed included limb elements as well as vertebrae and ribs. Their findings, which were consistent for both taxa across the various skeletal elements, indicate an ontogenetic trend among these derived plesiosaurs from osteosclerosis in juveniles to osteoporosis in adults (Wiffen et al., 1995).

While the observed osteosclerosis in the New Zealand elasmosaurids and pliosaurids seems to be an artifact of their ontogenetic stage, this does not appear to the the case for *Pachycostasaurus*. The degree of osteosclerosis seen in the New Zealand taxa is not as extreme as that which is diagnostic of *Pachycostasaurus*. Even though the specimen of *Pachycostasaurus* described by Cruickshank et al. (1996) appears to be a juvenile or sub-adult, its age is probably not solely responsible for the unusual bone structures.

The maintenance of buoyancy, the ability to float, the sustaining of trim, and the resistance to roll around the body axes are necessary for any marine animal. Passively maintaining buoyancy is especially important for secondarily marine tetrapods who must return to the surface to breathe. Having to work hard to reach the surface would be very energy expensive and evolutionarily maladaptive. Buoyancy is provided by the expanded, dorsally-oriented lungs of secondarily marine tetrapods (Domning and de Buffrénil, 1990). Various forms of counterweights, known collectively as ballast, have been developed by marine tetrapods. Increasing skeletal volume or density through pachyostosis and osteosclerosis respectively are developmental methods of adding ballast. A behavioral method is the ingestion of stones or sand as gastroliths. The exact purpose of these gastroliths, whether they are ingested merely for maintaining trim or if they have a digestive purpose, has been debated (Taylor, 1993). It is interesting to note that the other cryptocleidoid plesiosaur known from the epicontinental Sundance Seaway, *Pantosaurus striatus*, has been found with associated gastroliths (O'Keefe et al., in press). However, it is unknown at this time whether the sediments and small pebbles were ingested on purpose for the maintenance of trim or if they were ingested accidentally during benthic feeding. According to Domning and de Buffrénil (1990), the most efficient arrangement for both surfacing and submerging is to locate the center of gravity of the organism more anteriorly and ventrally than the center of buoyancy.

Hypotheses developed here regarding the development of pachyostosis as a method of bone ballast are speculative at the present time. As stated by Domning and de Buffrénil (1990), rigorous testing of such hypotheses requires accurate knowledge as to the position of the center of gravity of the animal. No complete skeletons of *Tatenectes laramiensis* have yet been found. The lack of a complete cervical column in particular makes any guesses as to overall neck length complete conjecture. However, if the conclusions derived in the study by Domning and de Buffrénil (1991) can be applied to other taxa, the center of gravity, in the case of *Tatenectes* augmented by the enlarged gastralia, should be only slightly ventral to the center of buoyancy, provided by the lungs.

Ribs and gastralia from two partial skeletons of *Tatenectes laramiensis* were observed for this study. One specimen, UW 24215, was described in O'Keefe and Wahl (2003, a) and O'Keefe and Street (2009). As mentioned in that study, the rib material of that skeleton is highly fragmentary; however, there are a few gastralia complete enough on which to base observation (Figure 2.1). There is very little overlap between the two skeletons, dorsal vertebrae and gastralia being the only elements they share.

Methods and Materials.

To investigate the histology of the ribs and gastralia of *Tatenectes laramiensis*, fragmentary gastralia from USNM 536974 were either polished with a rock polisher or sawed with a rock saw to produce even surfaces for comparisons to the published literature. The schematic of a skeletal transverse section through the posterior abdomen of *Tatenectes laramiensis* shows the approximate places were the cuts were made (Figure 2.2). Since the gastralia and ribs sacrificed were not complete it is difficult to say exactly where the fragmentary elements would have fit. The fragmentary nature of the material used for cross-sections also makes it unlikely that the skeletal elements represent the same axial segment.

Basic morphology of the skeletons, particularly the gastralia, of various cryptocleidoid plesiosaurs were also studied. *Pantosaurus striatus* USNM 536965 (Figure 2.3), *Cryptoclidus eurymerus* NHM R. 2860, *Muraenosaurus leedsi* NHM R. 2863, and *Tricleidus seeleyi* NHM R. 3539 were observed for comparative purposes. These specimens were all photographed with digital cameras and the photos were processed in PhotoShop. Measurements were taken of the relative widths of the gastralia to the ribs in these taxa. The lengths of the ribs or gastralia were measured, then the widths of the skeletal elements were measured using electronic calipers either at their midpoint (ribs) or at their widest central point (central gastralia). The way the specimens were stored in the Natural History Museum also made it difficult to ensure that rib and gastralia

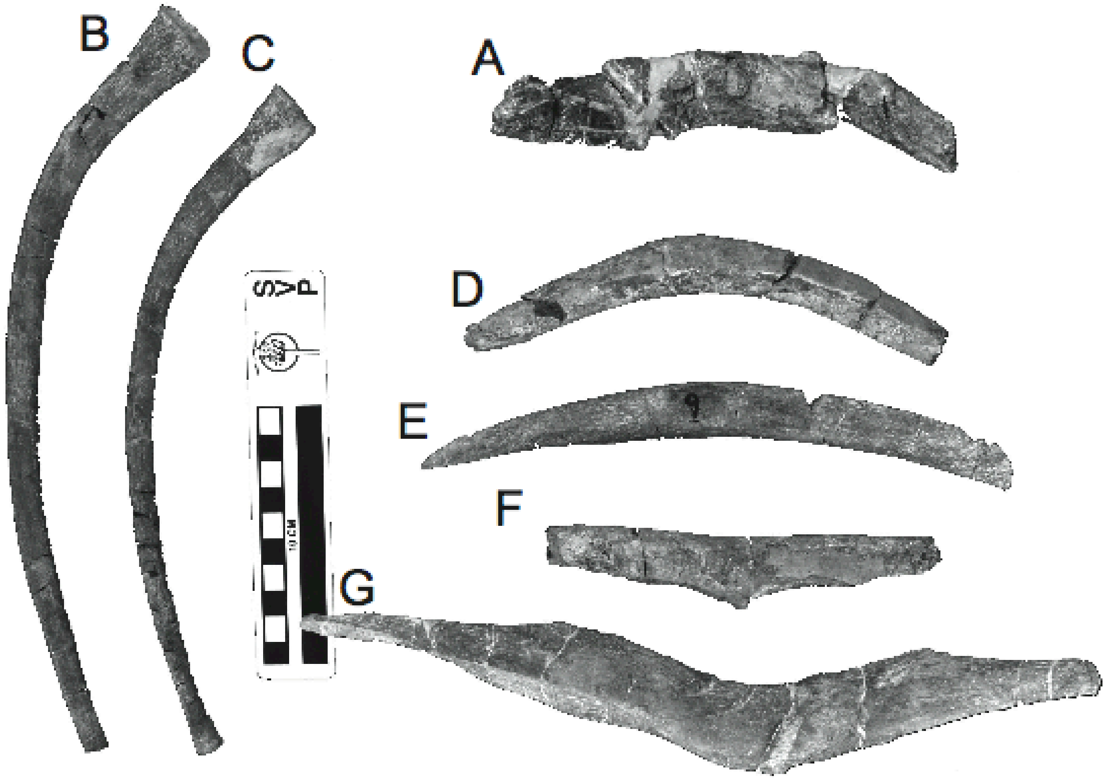

Figure 2. 1: An assemblage of dorsal and ventral ribs of *Tatenectes laramiensis*. Element C is a pair of fused gastralia from specimen UW 24215, serving as referral material. The other elements are from USNM 536974. B and C are dorsal ribs. D is a distal “j-bend” gastralium. E is an intermediate median gastralium, and F and G are central gastralia.

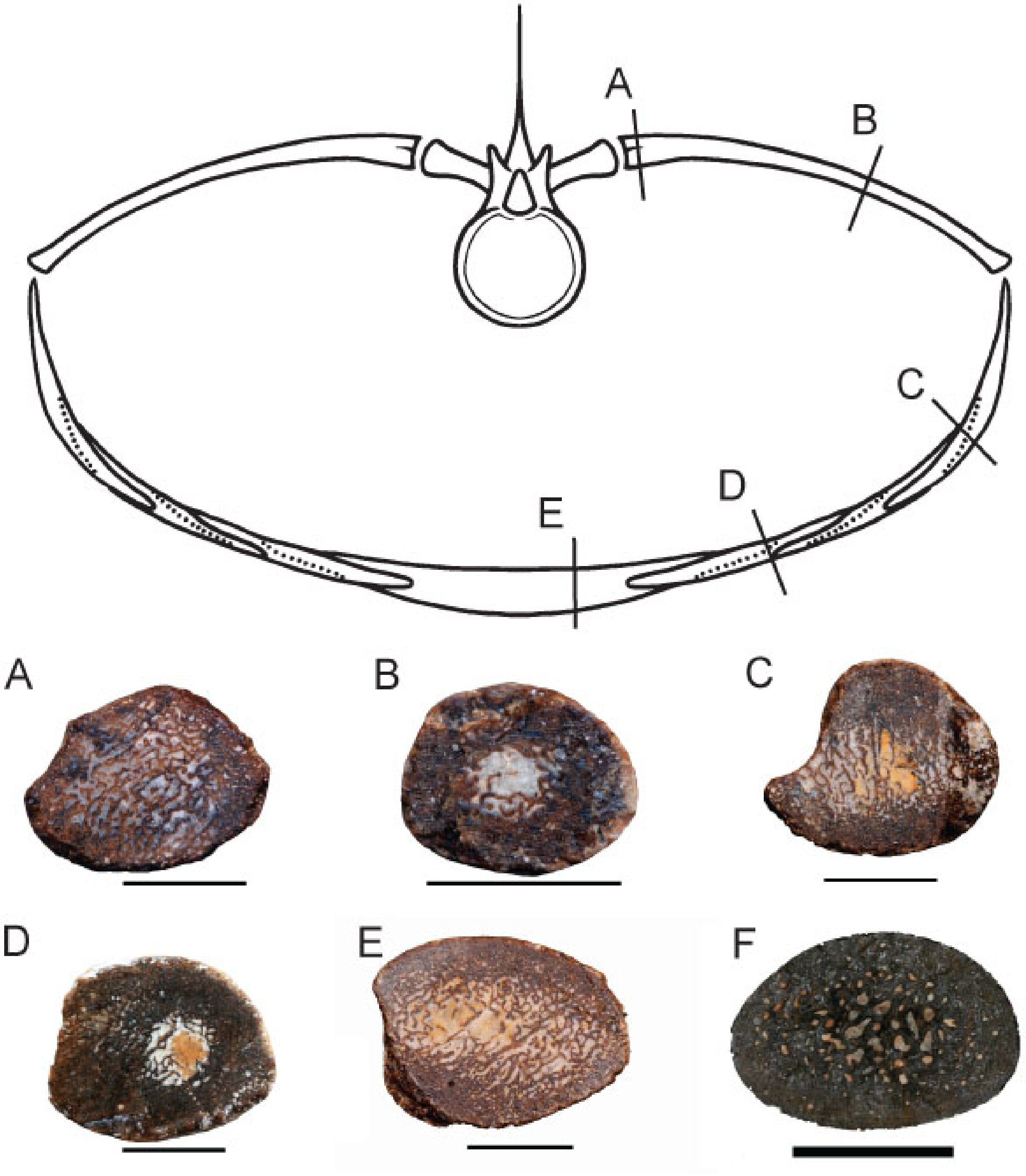

Figure 2. 2: Schematic transverse section through abdomen of *Tatenectes laramiensis*, anterior view (top). A-E: Cross-sections through ribs and gastralia of USNM 536974. F: Cross-sectional view of a rib of *Pantosaurus striatus* USNM 536965. Letters and bars in top image indicate approximations where corresponding cross-sections were made. Scale bars represent one centimeter.

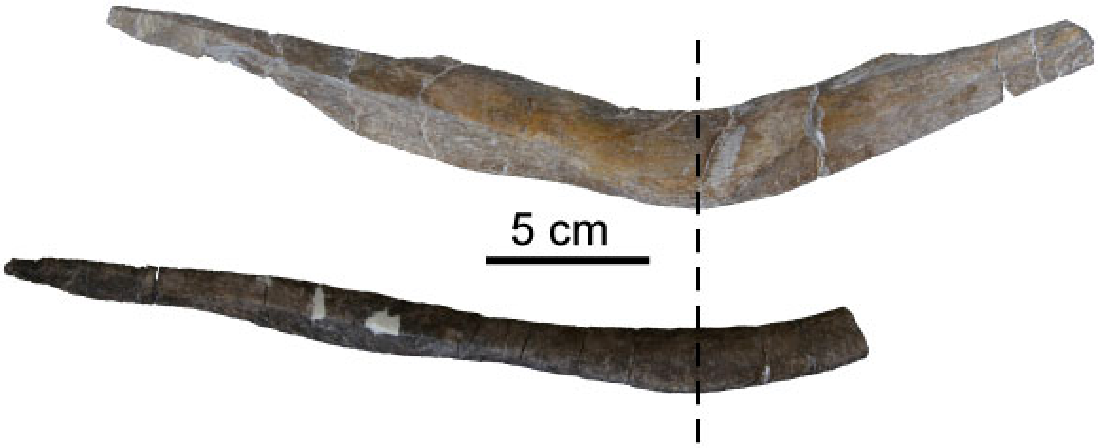

Figure 2. 3: Dorsal view of central gastralia of *Tatenectes laramiensis* USNM 536974 (top) and *Pantosaurus striatus* USNM 536965 (bottom). Anterior toward bottom. Dashed line represents midline.

measurements came from the same segment. The ratio of gastralia width to rib width was calculated two different ways. The first merely involved dividing the average gastralia width by the average rib width for each taxon

$$\frac{\text{Mean gastralia width (cm)}}{\text{Mean rib width (cm)}}$$

(Figure 2.4).

The other involved dividing each gastralium width by the average rib width for the taxon

$$\frac{\text{Individual gastralium width (cm)}}{\text{Mean rib width (cm)}}$$

(Figure 2.5).

Also, in order to determine the significance of differences between ratios of gastralia:rib width measurements, an analysis of variance (ANOVA) statistical test was performed. Due to the small sample size and the possibility of the data being non-paramentric, a Mann-Whitney U test was also completed.

Results

At first glance, it is obvious that the gastralia of *Tatenectes laramiensis* are unusually robust. One of the most complete gastralia is a midline gastralium, presumably from the posterior end of the dorso-ventral series. It is 29.8 cm long with a circumference of 9.1 cm at the midline. It has a recurved shape with deep lateral fossa for the articulation of the next lateral gastralium in the segment (Figure 2.3). One segment of gastralia in this and other cryptocleidoids, appears to be made up of nine bones, including one symmetrical midline element, two similar and relatively gracile lateral elements to each side, and finally one more robust and “j-bend” lateral-most element per side (Andrews, 1910) (Figure 2.6). The odd number of gastralia per segment actually represents a derived state. In the primitive state, such as in sphenodon, the gastralia are all paired and none cross the midline (Jollie, 1962). The presence of an unpaired midline gastralium is a synapomorphy of Cryptocleidoidea. The distal-most gastralia are dorso-ventrally compressed with deep fossae where they articulate with the next-medial elements in the segment, but become anterio-posteriorly compressed at their

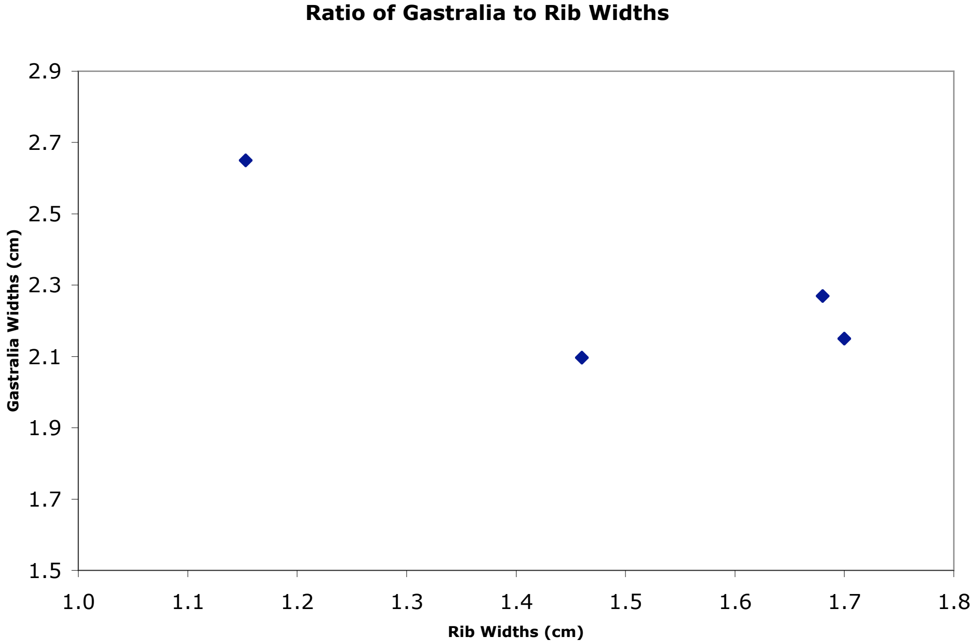

Figure 2. 4: Graph of ratios of gastralia to rib widths. The point farthest to the left represents *Tatenectes*, the point near the middle represents *Cryptoclidus*, and the two points grouped at the right represent *Muaenosaurus* and *Pantosaurus*.

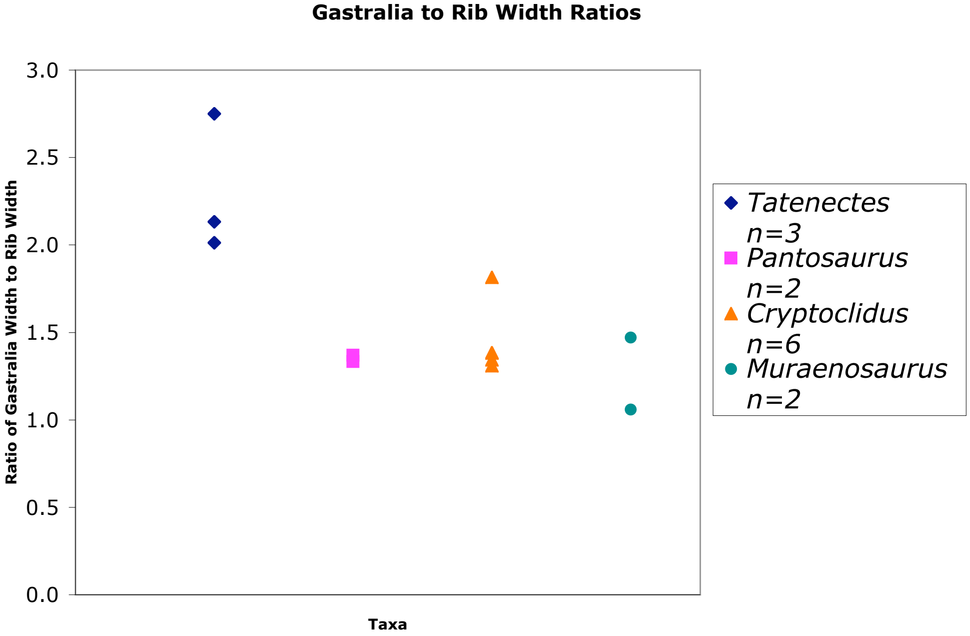

Figure 2. 5: Graph comparing the gastralia:rib width ratios for the various gastralia measured for each of the taxa.

Figure 2. 6: Posterior view of right lateral-most ("j-bend") gastralium of *Tatenectes laramiensis* USNM 536974.

distal tips as they extend into the lateral body walls. There is no clear rib articulation. However, due to the jumbled arrangement in which the gastralia were found, and the extent to which the gastralia and ribs were fragmented, an exact reconstruction of life position of these elements is difficult. The current reconstruction is based on previous reconstructions of related cryptocleidoids such as *Cryptoclidus* and *Muraenosaurus* (Andrews, 1910; Brown, 1981). The length of the ventral rib elements is shorter than what is seen in other cryptocleidoids, which is fitting for *Tatenectes*' relatively diminutive size. The midline and next two sets of lateral gastralia give very little curve to the ventral surface of *Tatenectes*. The greatest amount of curvature is provided by the "j-bend" distal-most gastralia.

The description of cross-sections made of ribs and gastralia and whole bone examples of these elements similar to those cross-sectioned from *Tatenectes* USNM 536974 will begin ventrally and proceed dorsally up the lateral body wall. The cross-section of the midline gastralium, taken slightly lateral of the true midline, is surprisingly osteoporotic. If the purpose of the pachyostosis was to act as ventral midline ballast, we would have expected these bones to be particularly dense. However, it should be noted that the midline gastralium that was cross-sectioned was presumably much more anterior than the robustly pachyostotic midline gastralium whose morphology was described earlier. The next cross-section, through one of the two middle gastralia, appears to have a small free marrow cavity in another asymmetric band of osteoporotic tissue, though in this case, the osteoporosis is less pronounced. The cross-section of the j-bend gastralium (showing on the left the fossa where the next-medial gastralium would articulate) has an asymmetric band of osteoporotic tissue surrounded dorsally and ventrally by hyperplasic cortical bone. Moving dorsally up the body wall to the ribs, it is found that the ribs are gracile, in common with other cryptocleidoids (Andrews, 1910; Brown, 1981). In cross section, there is a free marrow cavity surrounded by relatively dense cortical bone. The rib heads are not pachyostotic, and seem to be osteoporotic in cross section. The degree of variability of bone density seen in these cross-sections presumably continues throughout all the gastralia. It is therefore possible that the more robust posterior central gastralia are less osteoporotic than the cross-sectioned gastralia. It should also be noted that while these cross-sections were described as if they were all from the same body segment, it is highly unlikely that this is the case. The elements that were selected were chosen from the assortment of broken pieces so as not to destroy one of the more complete fossils in this incomplete skeleton. The cross-section of the *Pantosaurus* rib looks very different (Figure 2.2, F). The cortex appears to be more vascularized than that of *Tatenectes*, but the medullary cavity is less hollow, possibly indicating a lesser degree of reworking.

The proportions of the gastralia to the ribs indicate that the gastralia of *Tatenectes* are relatively large. When compared to gastralia:rib width measurements of *Cryptoclidus eurymerus*, *Pantosaurus striatus*, and *Muraenosaurus leedsii*, the ratio for *Tatenectes* is noticeably different. The average ratios for *Pantosaurus*, *Muraenosaurus*, and *Cryptoclidus* are 1.35, 1.26, and 1.44 respectively. The mean ratio for *Tatenectes* is 2.30 (Figure 2.5). When all the ratios were analyzed using ANOVA, a statistically significant difference was found to exist. Upon ovserving the data, it does appear that the difference occurs between *Tatenectes* and the other cryptocleidoids studied. There is sufficient evidence (P=0.003) to reject a null hypothesis that all the ratios are the same. The Mann-Whitney U test corroborates this finding (P=0.01).

Discussion

The dorsal ribs of *Tatenectes laramiensis* are not osteosclerotic or pachyostotic, but the gastralia seem to exhibit a slightly pachyostotic state. This would have resulted from hyperplasy of the periosteal cortex, perhaps due to a prolonged growth phase. The gastralia are not as pachyostotic as the ribs of *Pachycostasaurus dawni*, nor to the degree seen in sirenians or primitive archaeocetes. The gastralia of *Tatenectes* do not have the more typical pestleor banana-like morphology seen in other pachyostotic taxa but still have the same general shape as is seen in related cryptocleidoid plesiosaurs. The relative width is merely greater in *Tatenectes* (Figure 2.3). The data do not support the hypothesis that the gastralia are osteosclerotic as well as being pachyostotic. The cross sections of the ribs and gastralia of *Tatenectes laramiensis* show that these skeletal elements are not abnormally dense (Figure 2.3). The cross section of the rib shaft shows a free marrow cavity, and one of the gastralia also appears to have a free marrow cavity, albeit somewhat reduced. All the gastralia possess cancellous bone tissues, which run in an asymmetrical band across the width of the elements. The fact that these bands of cancellous tissue reach nearly to the cortices of the bones make these regions of the gastralia appear more osteoporotic than osteosclerotic; however, there is thick periosteal bone dorsally and ventrally adding significant density along with the increase in volume. This formation of pachyostosis is nothing like nothing else seen on other taxa. The bands of pachyostotic cortical bone surrounding an asymmetirical marrow cavity, which is nearly oteoporotic, is a novel tissue arrangement. It is possible that this histological condition is partially due to the age of the specimen. From the degree to which the neural arches are fused to the vertebral centra, it is known that this specimen was a fully-grown adult at the time of its death. During life, osteous tissue is resorbed and redeposited. It is possible that the ostoporotic tissue is due to asymmetrical resorbtion and redeposition.

It is the specific arrangement of pachyostotic bones within *Tatenectes* that would have contributed to the overall stability of the animal. The concentration of the increase in bone volume to the ventral region of the organism would have helped to make *Tatenectes* bottom-heavy. The middle two elements in each side of a segment of gastralia are not as massive as the central gastralia or the distal-most gastralia. This means that the greatest increases in volume are localized on the midline and, to a lesser extent, at the sides, where the gastralia bend dorsally. The pachyostosis at the midline would have served as a keel in the broad, flat ventral surface of *Tatenectes* (Figure 2.2). The slight degree of pachyostosis in the j-bend gastralia might also have provided the animal with increased stability. The need for greater mass in the ventral region of the body is presumably to offset the buoyancy provided by the lungs, which in secondarily marine tetrapods tend to run dorsally (Domning and de Buffrénil, 1991). In sum, the rib structures gave *Tatenectes* a flat, nearly boxy body, which is bottom heavy and apparently resistant to roll.

The evidence of pachyostosis, along with the geologic evidence from the site where specimen USNM 536974 was excavated (oyster shoals, localized coarse-grained sand in an otherwise fine-grained silt, located near the top of the formation) suggest that *Tatenectes laramiensis* lived in a shallow water environment. The increased mass provided by the pachyostotic gastralia would have lowered the center of buoyancy and helped *Tatenectes* maintain trim, even in more turbulent waters. Even if the low degree of pachyostosis exhibited by *Tatenectes laramiensis* would have had only a nominal effect on the organism’s overall density, the enlargement of the bones would have to have had some effect on overall body shape, possibly also aiding in maneuvering a shallow lagoonal, occasionally turbulent marine environment.

Chapter III. Body Shape

Despite all the literature about variations in plesiosaur neck length, and all the characters that accompany the long- and short-necked morphotypes, very little has been written about plesiosaur thorax shape. Presumably, this is based on the assumption that there is little to no important variation of body shape within Plesiosauria. For the most part, this may in fact be the case. Prominent reconstructions in the literature show nearly all plesiosaurs as having round to sub-round transverse sections. *Tatenectes laramiensis*, however, is an exception to this apparent rule.

Though not specifically studying body shape, Henderson (2006) developed virtual three-dimensional models of three different taxa of plesiosaur. Various views of these models indicate the shape of the trunk region. The three taxa he modeled were *Cryptoclidus oxoniensis*, *Liopleurodon ferox*, and *Thalassomedon haningtoni*. *Thalassomedon*, an elasmosaur, had the most nearly circular transverse section. The pliosaur *Liopleurodon* was sub-circular, and *Cryptoclidus* was significantly dorso-ventrally compressed (Henderson, 2006). This study provides some basis for this research in that it depicts *Cryptoclidus* as not having a barrel-like trunk. In the current study, *Tatenectes laramiensis* was compared with other cryptocleidids, including *Cryptoclidus eurymerus*, *Muraenosaurus leedsi*, and *Tricleidus seeleyi*. Based on skeletal morphology, it would be expected that *Cryptoclidus* and *Tricleidus* to have similar sub-round transverse sections and for *Muraenosaurus*, an elasmosauromorph cryptocleidoid, to be more nearly circular. *Tatenectes* is expected to be the most compressed of all the taxa compared due to its unique morphology.

Osteological clues illuminating the over-all body shape come from axial skeletal elements, as well as the limb girdles. Many of the most salient features can be found on the vertebrae. The curvature of the spine, when the dorsal vertebrae are articulated in life position, indicate the profile of the back. The angle of the transverse processes relative to the neural spines, along with the orientation of the rib head articulation facets and the curvature of the ribs, contribute greatly to the dimensions of the body. The morphology and articulations of the gastralia exert control over the shape of the ventrum of the animal. Angles between articulated girdle elements, whether corresponding bones across the midline or the various bones on each side, also affect the shape of the trunk.

Reconstructions of *Cryptoclidus eurymerus* and *Muraenosaurus leedsi*, such as those illustrated in Andrews (1910) and Brown (1981), show varying degrees of curvature of the spine. Brown's reconstruction of *Cryptoclidus* has less dorsal curvature than does the older version by Andrews, which was based primarily on the mounted specimen NHM R. 2860. Despite the slight differences in degree of convexity between the two reconstructions, both are consistent in that the highest point in the spine is approximately at the midpoint of the dorsal vertebrae series, caudal to the posterior terminus of the coracoids. *Muraenosaurus* is depicted by Andrews, based on NHM R. 2678, with an even more convex profile, and again the highest point of the back is near the midpoint in the dorsal vertebrae series, posterior to the terminus of the pectoral girdle.

Conversely, in *Tatenectes laramiensis*, the overall profile of the back is much flatter. Instead of exhibiting a gentle, convex dorsal curve, the spine has a faint s-curve (Figure 3.1). The highest point of the back is much farther anterior in *Tatenectes*, forming a slight hump in the first seven dorsal vertebrae preserved in this specimen, dorsal to the pectoral girdle. The rest of the dorsal series, progressing caudally, trends nearly horizontally, with perhaps a slight ventral slope. The fifteenth vertebra of the dorsal series is potentially rhomboid in shape. It is in this region, anterior to the pelvic girdle, that the dorsal series jogs ventrally, to continue nearly horizontally again through the sacral region toward the caudal series where there is a faint dorsal recurve. This combination of a reduced and anteriorly displaced dorsal hump, slight ventral slope of the posterior dorsal vertebral column, and faint s-curve generated by the possible

Figure 3. 1: Articulated vertebral column of *Tatenectes laramiensis*. Anterior to the left.

rhomboid vertebra anterior to the sacrum give *Tatenectes* a very low lateral profile.

The angle the transverse processes of the vertebrae make to the neural spine contribute to body shape by dictating how the ribs articulate. Assuming an identical vertebral centrum, neural spine, transverse process, and rib size, along with identical rib to transverse process articulation angle, the smaller the angle between the transverse processes and the neural spine, the broader and flatter the back of animal is in transverse section (Figure 3.2). Of course, these aspects of the vertebrae and ribs are not identical across taxa, but vertebral morphology is conserved enough that variation in transverse process angle does change the transverse section of various cryptocleidoids. In *Muraenosaurus*, the transverse processes are nearly perpendicular to the neural spines. They are not completely flat, and the angle is slightly reduced posteriorly. The angle between the neural spines and the transverse processes is smaller in *Cryptoclidus*. However, opposite what is seen in *Muraenosaurus*, that angle increases posteriorly. The angle appears to be even more reduced in *Tricleidus seeleyi*, and seems relatively consistent throughout the dorsal series. *Tatenectes* is similar to *Cryptoclidus* in that the transverse processes are at a reduced angle anteriorly, and that the angle increases posteriorly. From these comparisons and the assumptions stated above, it would seem that *Tricleidus* should have the flattest back of these taxa, but the other features of the vertebrae and ribs do vary, so conclusions cannot be based on the angle of the transverse processes alone.

Possibly having a greater impact on transverse section shape than the angle the transverse process makes to the neural spine is the orientation of the rib head articulations. Generally among plesiosaurs, including cryptocleidoids, there is a single rib head articulation, which is oval in shape. In *Muraenosaurus*, this oval has a slight posterior slant in the anterior dorsal vertebrae and is nearly vertical in the posterior dorsals. In *Tricleidus*, the articulation is sub-circular anteriorly, but

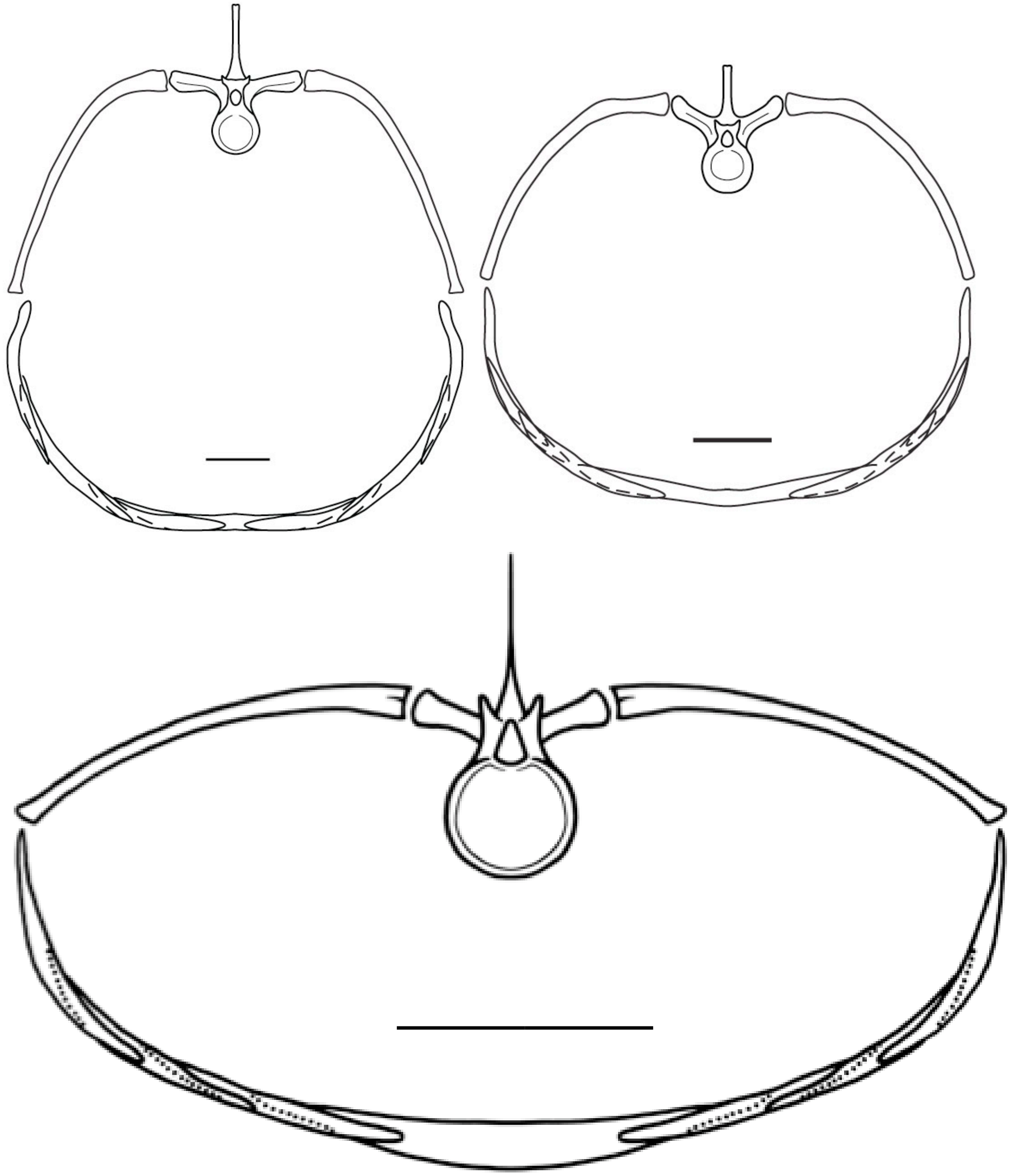

Figure 3. 2: Transverse sections Top left: *Muraenosaurus*. Top right: *Cryptoclidus*. Bottom: *Tatenectes*. Scale bars equal ten centimeters.

the long axis of the facet is nearly vertical. The articular facet is more compressed posteriorly and takes on a slight posterior slant. For *Cryptoclidus*, the articulations are slanted posteriorly throughout the dorsal column. The posterior slant is most exaggerated in *Tatenectes*. Moving posteriorly down the dorsal vertebral series the articular facets become nearly horizontal. The orientation of the rib head articulation mimics the orientation of the ribs themselves. Where the rib head articulations are vertical, the ribs run vertically though the lateral body walls, nearly perpendicular to the axis of the spine. The greater the posterior slant of the articular facets, the greater the posterior slant of the ribs. Posteriorly slanting ribs can have two effects on body shape. Primarily, the rotation of the ribs from a vertical to a sub-horizontal orientation greatly reduces body depth. Secondarily, as the body becomes flatter and the length of the ribs is not reduced, the back will necessarily become broader. The composite effects of the reduced angles of the transverse processes and the posterior slant of the rib head articular facets and ribs are a resulting broader, flatter back and great reduction in trunk depth.

The above discussion of axial skeleton elements illustrates variations primarily in the dorsal profile of a plesiosaur. The ventral profile is governed by the gastralia and the girdles. The more curved each of the individual gastralia, the rounder the articulated gastralia complex. In *Tatenectes*, the midline gastralia are slightly curved, and the distal-most gastralia are distinctly curved. The two middle gastralia have very little curve. When an entire segment of gastralia are articulated, the transverse section has a broad and gently curved bottom. At the lateral end of the segments, the j-bend gastralia angle sharply dorsally, giving the animal a box-like shape. The gastralia of other cryptocleidids, such as *Muraenosaurus*, have more evenly round, or barell-like morphologies.

The pectoral girdle perhaps contributes to body shape less than the pelvic girdle, but it still has some degree of impact. The angle between the two lateral halves of either girdle can indicate whether the plesiosaur was broad and flat or deeper and more barrel-like. A few of the specimens observed at the Natural History Museum in London appeared to have been mounted at exaggerated angles. When other conspecific girdles were articulated, more interpretations, hopefully more accurate, became possible. The pectoral girdle of *Tricleidus* is surprisingly deep. When the two lateral halves were articulated, the dorsal processes of the scapulae are nearly vertical. The lateral processes of the coracoids do not reach as far dorsally, but they do extend well beyond the level of the midline suture. The dorsal processes of the scapulae of *Cryptoclidus* are not nearly as steep as is seen in *Tricleidus*. The angle between the two lateral halves of the pectoral girdle appears to be slightly over 90 degrees. The lateral processes of the coracoids are much longer in this taxon, and while they do angle dorsally to a degree, they are not nearly as extreme as *Tricleidus*, thereby giving *Cryptoclidus* a shallower, broader transverse section. A complete pectoral girdle of *Tatenectes* has yet to be found, therefore the full dorsal extent of the dorsal processes of the scapulae or the lateral processes of the coracoids is unknown. However, from the known pectoral girdle material, it appears that *Tatenectes* much more closely resembles *Cryptoclidus* than *Tricleidus*. The pectoral girdle is quite flat with no strong dorsal processes, even at the lateral-most regions of the known elements.

The pelvic girdle elements can provide an even more precise estimation of body shape considering how the illia articulate directly with axial skeleton elements. Articulating the illia of the pelvis to the sacral ribs from the sacral vertebrae can provide the exact depth of the skeleton in the pelvic region. Of the pelvic girdle elements, the ischia are the most horizontal, or the ones most parallel to the spine. The pubes angle ventrally, and the illia angle dorsally to contact the sacral ribs. The degree to which the illia angle dorsally or posteriorly indicates how deep the skeleton would have been in life. In *Muraenosaurus*, the illium extends nearly vertically from the acetabulum to the sacral ribs. There is more of a posterior slant to the illium of *Cryptoclidus*, while it is nearly horizontal in *Tatenectes*. Therefore there is not as much distance between the bottom of the vertebral centra and the midline of the pelvic girdle. Reconstructing the pelvic girdle cannot determine the complete depth of the animal. In a living plesiosaur, there would have been cartilage caps on the ends of the neural spines, along with skin, muscle, and connective tissue around all the bones. However, comparing the articulated pelvic girdles across taxa can indicate relative dimensions. All of the skeletal features examined here combine to provide robust support for the hypothesis that *Tatenectes laramiensis* has a dorsoventrally-flattened morphology, to a degree which is unique among cryptocleidoid plesiosaurs.

Conclusions

The pachyostotic gastralia and the broad flat body shape could have served similar functions in *Tatenectes*. It is possible that the two are adaptations for greater stability when living in shallow water. As stated in the previous chapter, the pachyostotic gastralia might have served as ballast. The distribution of pachyostotic bone, concentrated on the ventral midline, and the ventral corners of the lateral body walls, around this dorso-ventrally compressed organism would seem to be beneficial for a secondarily marine animal living in shallow water. The morphology or histology alone would be insufficient to firmly support a hypothesis of a near-shore habitat for *Tatenectes*, but the combination of these traits strengthens such a premise. The additional sedimentological and invertebrate faunal data provide even more support for this idea. Examples of invertebrate fossils include burrows, belemnites, and bivalves. The most abundant bivalve fossils were *Ostrea*, which had been preserved in shoals.

The ventral surface of *Tatenectes* is comprised nearly entirely of bone. The large girdles comprise most of this region. In most cryptocleidoids, there is a sizable gap between the pectoral and pelvic girdles, which is filled in by the gastralia. The distance between the two girdles is reduced in *Tatenectes*. The horizontal orientation of the illia in *Tatenectes* has the net effect of shifting the entire pelvic girdle anteriorly as well as making the body less deep. The illia are not proportionately shorter in *Tatenectes* than in other cryptocleidoids, and they articulate with the spine in the same place as in related taxa. Even thought the complete number of dorsal vertebrae in *Tatenectes* remains unknown, a reasonable estimate is a total of eighteen, which is two fewer than is seen in *Cryptoclidus* or *Muraenosaurus*. Based on these consistencies, the change in the angle means that the connected pelvic bones must swing forward. The reduced gap between the girdles is filled in more densely than in related taxa due to the pachyostosis of the gastralia. The total number of segments of gastralia remains unknown for *Tatenectes*. *Cryptoclidus* and *Muraenosaurus* are reconstructed with eight sets of gastralia. It is possible that *Tatenectes* also has eight sets, but it is not unreasonable to assume that an increased number of segments of gastralia evolved along with the increased size of the bones. Whether *Tatenectes* has the same number or more segments of gastralia than are in other cryptocleidoids their increased size in a decreased space leads to the formation of a nearly solid bony “sled” in the ventral region of this plesiosaur. This broad, relatively flat expanse of bone could likely have provided ballast and stability to an animal living in turbulent waters.

Works Cited

Andrews, C.W. 1910. A descriptive catalogue of the marine reptiles of the Oxford Clay, Part I: British Museum (Natural History), London, England, 205 pp.

Brown, D.S. 1981. The English Upper Jurassic Plesiosauridea (Reptilia) and a review of the phylogeny and classification of the Plesiosauria, Bulletin of the British Museum of Natural History 35(4): 253-347.

de Buffrénil, V., A. de Ricqlès, C.E. Ray, and D.P. Domning. 1990. Bone histology of the ribs of the Archaeocetes (Mammalia: Cetacea). Journal of Vertebrate Paleontology 10: 455-466.

Chatterjee, S. and B.J. Small. 1989. New plesiosaurs from the Upper Cretaceous of Antarctica. Geological Society, London, Special Publications 47: 197-215.

Cheng, Y., X. Wu, and Q. Ji. 2004. Triassic marine reptiles gave birth to live young. Nature 432: 383-386.

Cruickshank, A.R.I. and F.R. Ewan. 2002. A new marine reptile (Sauropterygia) from New Zealand: further evidence for a Late Cretaceous Austral radiation of cryptoclidid plesiosaurs. Palaeontology 45(3): 557-575.

Cruickshank, A.R.I., D.M. Martill, and L.F. Noe. 1996. A pliosaur (Reptilia, Sauropterygia) exhibiting pachyostosis from the Middle Jurassic of England. Journal of the Geological Society of London 153: 873-879.

Domning, D.P. and V. de Buffrénil. 1991. Hydrostasis in the Sirenia: quantitative data and functional interpretations. Marine Mammal Scince 7(4): 331-368.

Drukenmiller, P.S., and A.P. Russel, 2008. A phylogeny of Plesiosauria (Sauropterygia) and its bearing on the systematic status of *Leptocleidus*, Andrews, 1922. Zootaxa 1863. Auckland. Magnolia Press, 120 p.

Francillon-Vieillot, H., V. de Buffrénil, J. Casranet, J. Géraudie, F.J. Meunier, J.Y. Sire, L Zylberberg, and A. de Ricqlès. 1990. Microstructure and mineralization of vertebrate skeletal tissues. Skeletal biomineralization: patterns, proccesses and evolutionary trends. Volume I. New York. Van Nostrand Reinhold.

Hall, B.K. 2005. Bones and Cartilage: developmental skeletal biology. Amsterdam. Elsevier, 792 p.

Henderson, D.M. 2006. Floating point: a computational study of buoyancy, equilibrium, and gastroliths in plesiosaurs. Lethaia 39: 227-244.

Hill, R.V. 2005. Integration of morphological data sets for phylogenetic analysis of Amniota: the importance of integumentary characters and increased taxonomic sampling. Systematic Biology 54(4): 530-547.

Hulke, J.W. 1870. Kimmeridge plesiosaurian remains. Proceedings of the Geological Society 26: 611-622.

International Commission on Stratigraphy. 2008. International Straigraphic Chart.

Jollie, M. 1962. Chordate Morphology. New York. Reinhold Publishing Corporation, 478 p.

Knight, W. C. 1900. Some new Jurassic vertebrates. American Journal of Science, Fourth Series 10 (whole number 160): 115–119.

Kvale, E. P., G. D. Johnson, D. L. Mickelson, K. Keller, L. C. Furer, and A. W. Archer. 2001. Middle Jurassic (Bajocian and Bathonian) dinosaur megatracksites, Bighorn Basin, Wyoming, U.S.A. Palaios16: 233–254.

Mehl, M. G. 1912. *Muraenosaurus? reedii*, sp. nov. and *Tricleidus? laramiensis* Knight, American Jurassic plesiosaurs. Journal of Geology 20(4): 344–352.

O'Keefe, F. R. 2001. A cladistic analysis and taxonomic revision of the Plesiosauria (Reptilia:Sauropterygia). Acta Zoologica Fenica 213: 1–63.

O'Keefe, F. R. 2004. Preliminary description and phylogenetic position of a new plesiosaur (Reptilia:Sauropterygia) from the Toarcian of Holzmaden, Germany. Journal of Paleontology 78(5): 973–988.

O'Keefe, F.R. and H.P. Street. 2009. Osteology of the cryptocleidoid plesiosaur *Tatenectes laramiensis*, with comments on the taxonomic status of the Cimoliasauridae. Journal of Vertebrate Paleontology 29: 10p.

O'Keefe, F.R. and W. Wahl, Jr. 2003, a. Preliminary report on the osteology and relationships of a new aberrant cryptocleidoid plesiosaur from the Sundance Formation, Wyoming, Paludicola 4(2):48-68.

O'Keefe, F.R. and W. Wahl, Jr. 2003, b. Current taxonomic status of the plesiosaur Pantasaurus striatus from the Upper Jurassic Formation. Wyoming. Paludicola 4(2): 37–47.

Pipiringos, G.N. 1957. Stratigraphy of the Sundance, Nugget and Jelm Formations in the Laramie Basin, Wyoming. The Geologic Survey of Wyoming Bulletin 47: 1-63.

de Ricqlès, A. and V. de Buffrénil. 2001. Bone histology, heterochronies and return of tetrapods to life in water: where are we? Secondary adaptation of tetrapods to life in water. 289-310.

Rieppel, O. 2000. Sauropterygia I. Placodontia, Pachypleurosauria, Nothosauria, Pistosauria. Encyclopedia of Paleoherpetology Part 12A. Kuhn, O. and P. Wellnhofer (eds.) Verlag Dr. Friedrich Pfeil, Munich, Germany. 134 p.

Smith, A.S. 2007. Anatomy and systematics of the Rhomaleosauridae (Sauropterygia: Plesiosauria). Doctorate thesis, School of Biology and Environmental Science, National University of Ireland, University College Dublin.

Taylor, M.A. 1993. Stomach stones for feeding or buoyancy? The occurrence and function of gastroliths in marine tetrapods. Philosophical Transactions of the Royal Society of London 341: 163-175.

Taylor, M.A. 2000. Funtional significance of bone ballast in the evolution of buoyancy control strategies by aquatic tetrapods. Historical Biology 14: 15-31.

Wiffen, J., V. de Buffrénil, A. de Ricqlès, and J. Mazin. 1995. Ontogenetic evolution of bone structure in Late Cretaceous Plesiosauria from New Zealand. Geobios 28: 625-640.

Table of the taxa mentioned in the text

Taxon	Formation	
	Age	Location
Aristonectes parvidens	Maastrichtian 71-65 Ma	Antarctica
Cryptoclidus eurymerus	Callovian 165-161 Ma	United Kingdom
Kaiwhekea katiki	Maastrichtian 71-65 Ma	New Zeland
Kimmerosaurus langhami	Kimmeridgian 156-151 Ma	United Kingdon
Leptocleidus	Berriasian 146-140 Ma	United Kingdon
Liopleurodon ferox	Callovian 165-161 Ma	United Kingdom
Muraenosaurus leedsii	Callovian 165-161 Ma	United Kingdom
Pachycostasaurus dawni	Callovian 165-161 Ma	United Kingdom
Pantosaurus striatus	Oxfordian 161-156 Ma	USA
Rhomaleosaurus	Toarcian 183-175 Ma	Germany
Tatenectes laramiensis	Oxfordian 161-156 Ma	USA
Thalassomedon haningtoni	Cenomanian 100-93 Ma	USA
Tricleidus seelyi	Callovian 165-161 Ma	United Kingdom

Table of Museums/Institutions mentioned in the text

Institution	Code
The Natural History Museum, London	NHM
National Museum of Natural History, Smithsonian	USNM
University of Wyoming	UW