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EVIDENCE OF PACHYOSTOSIS IN THE CRYPTOCLEIDOID
PLESIOSAUR *TATENECTES LARAMIENSIS* FROM THE
SUNDANCE FORMATION OF WYOMING

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INTRODUCTION

In this paper we present evidence for pachyostosis in the cryptocleidoid plesiosaur *Tatenectes laramiensis* Knight, 1900 (O'Keefe and Wahl, 2003a). Pachyostosis is not common in plesiosaurs and is particularly rare in non-pliosaurian plesiosaurs, although enlarged gastralgia were first recognized in *Tatenectes* by Wahl (1999). This study aims to investigate the nature of the disproportionately large gastralgia of *Tatenectes* in greater depth, based on new material. A recently discovered partial skeleton consisting of a dorsal vertebral series, ribs, gastralgia, and a complete pelvic girdle was collected from the Jurassic-aged Sundance Formation of the Bighorn Basin in Wyoming during the summer of 2006. The gastralgia of this specimen are disproportionately large considering the small size of the taxon (about 3 meters total length), and we therefore investigated the size of these elements quantitatively. Polished cross-sections were also prepared to explore the histology of the ribs and gastralgia. The ribs of *Tatenectes* are not pachyostotic, whereas the gastralgia exhibit a novel condition of pachyostosis while lacking osteosclerosis.

Skeletal tissue modification is common among secondarily marine tetrapods. These modifications can follow one of two major trends: toward a lighter skeleton or toward a lighter skeleton. The skeleton can be made lighter by reduction in number or size of skeletal elements. Bones themselves can also be reduced in density (de Buffr nil et al., 1990; de Ricql s and de Buffr nil, 2001). This condition, known as osteoporosis, occurs when the cortical bone layer, usually the most compact and dense region of a bone, is reduced, and the marrow cavity or regions of cancellous bone are increased (de Ricql s and de Buffr nil, 2001). Osteoporosis is a common pathology in humans, but in secondarily marine tetrapods the osteoporosis is adaptive, having occurred in several lineages including ichthyosaurs, pliosaurs, and cetaceans (de Buffr nil et al., 1990; de Ricql s and de, Buffr nil, 2001).

At the other end of the spectrum, the skeleton of secondarily marine tetrapods can become heavier. Bones can become enlarged via pachyostosis. Pachyostosis is another adaptive condition through which the periosteal cortex of the bone undergoes hyperplasy (Francillon-Viellot et al., 1990). In such cases hyperplasy indicates that the cortical bone layer grows to a greater thickness, either through increased amount of time in the growth stage, or accelerated growth rate. The periosteal cortex of the bone is therefore thicker, thus enlarging the entire bone (de Ricql s and de Buffr nil, 2001). The total weight of the skeleton can also be multiplied through increased bone density. Osseous tissue may also become more dense via a condition termed osteosclerosis. This condition involves disruption of endochondral ossification, resulting in less resorption of endochondral tissue and a lack of endosteal development. Therefore, cancellous bone tissue or marrow cavities do not form and the bones are instead filled with dense calcified cartilage. Pachyostosis and osteosclerosis can occur concurrently, and this combined condition is known as pachyosteosclerosis (Taylor, 2000; de Ricql s and de Buffr nil, 2001). Varying degrees of these

conditions are seen in basal sauropterygians, primitive cetaceans, and sirenians, among others (de Buffrénil et al., 1990; Domning and de Buffrénil, 1991; Taylor, 2000; de Ricqlès and de Buffrénil, 2001).

Pachyostosis is uncommon among plesiosaurs. The extant literature contains no mention of possible pachyostosis in other cryptocleidoid plesiosaurs other than that of Wahl (1999), although detailed descriptions of ribs and gastralia are rare in the literature (Andrews, 1910; Brown, 1981). Currently, *Pachycostasaurus dawni* Cruickshank et al., 1996, is one of the few plesiosaurs described as exhibiting some degree of pachyostosis. This small pliosauromorph (~3m long) displays marked pachyostosis of the dorsal vertebrae, ribs, and gastralia. The pachyostosis of these skeletal elements is accompanied by an increase in tissue density as well, resulting in a pachyosteosclerotic state (Cruickshank et al., 1996). It has also been hypothesized by Wiffen et al. (1995) that the condition of plesiosaurian bone tissue changes throughout ontogeny. Their research on Late Cretaceous elasmosaurs and pliosaurs indicates a possible trend from osteosclerosis in immature individuals to an osteoporotic state in adults (Wiffen et al., 1995). It should be noted that the specimen under consideration in this study, USNM 536076, is a fully mature adult. All known *Tatenectes* specimens, including the relatively common juvenile specimens, exhibit pachyostosis of the gastralia (Wahl, 1999, 2006).

In marine tetrapod taxa displaying pachyostosis that is not pervasive throughout the entire skeleton, the enlargement of bones is often concentrated within the thoracic region (de Ricqlès and de Buffrénil, 2001). This is expected if the increase in bone mass serves as ballast. For maximal maneuverability and stability, the most buoyant region of an aquatic tetrapod, the lungs, and the densest region, skeletal pachyostosis, should both be near the anteroposterior midpoint of the organism (Domning and de Buffrénil, 1991). The new partial skeleton of *Tatenectes* does appear to have this pattern and we describe in here. Unlike what is seen in *Pachycostasaurus*, the only bones in the new skeleton that exhibit pachyostosis are the gastralia, as mentioned briefly in O'Keefe and Street (2009) and Wahl (1999). In comparison to the dorsal ribs, the gastralia of *Tatenectes* appear to be disproportionately robust. The gastralia are also noticeably thicker than those of *Pantosaurus*, another, larger Sundance cryptocleidoid. It is the goal of this research to determine if the gastralia of *Tatenectes laramiensis* do indeed exhibit pachyostosis, and if so whether the histologic condition is pachyostotic or pachyosteosclerotic.

MATERIALS AND METHODS

This study focuses on the axial morphology and histology of the cryptocleidoid plesiosaur *Tatenectes laramiensis*. We also present comparative material from three related taxa: *Pantosaurus striatus* Marsh, 1891, *Cryptoclidus eurymerus* Phillips, 1871; and *Muraenosaurus leedsii* Seeley, 1874. Specimens were examined from the Natural History Museum, London (NHM), the National Museum of Natural History, Smithsonian Institution (USNM), and the University of Wyoming (UW).

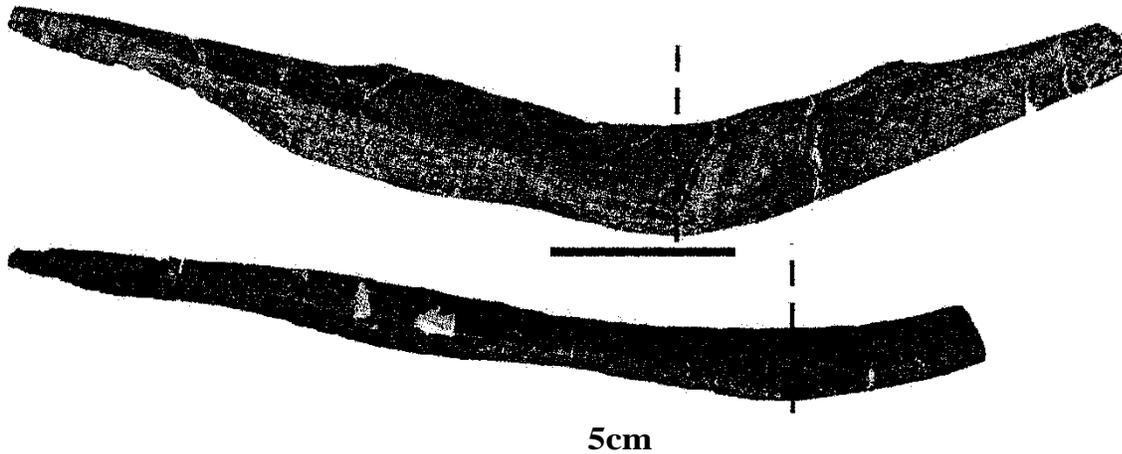


FIGURE 1. Examples of midline gastralia of *Tatenectes* (top) and *Pantosaurus* (bottom) in dorsal view with anterior toward the bottom. Dashed line represents midline.

When first prepared, the gastralia of a new partial skeleton of *Tatenectes* appeared to be disproportionately large. In order to determine if this size difference is statistically significant relative to closely related plesiosaurs, gastralia and ribs of each of the above taxa were measured so that statistical tests could be calculated. Using digital calipers, the widths of the midline gastralia were measured anteroposteriorly on the midline, and these measurements were recorded in centimeters to the nearest one-hundredth of a centimeter. Measurements are reported in Table 1. The width of the midpoint of the shaft of the dorsal ribs were also measured. The rib chosen for comparison was a rib close to the thoracic segment containing the most posterior gastralium. This particular rib was chosen in an attempt to standardize the comparison across taxa. One partial skeleton each for *Tatenectes* and *Pantosaurus* (USNM 536976 and USNM 536965, respectively) were examined. Multiple specimens of *Cryptoclidus* (NHM R.2860, NHM R.2862, and NMH R.8575) and *Muraenosaurus* (NHM R.2421 and NHM R.2863) were also examined. However, due to fixture to mounts or poor preservation, it was only possible to take accurate measurements from one specimen each of these taxa as well (NHM R.2860 and NHM R.2863, respectively). Due to the incomplete fusing of the neural arches to the vertebral centra, both of these specimens are considered to be sub-adult individuals. It should be noted that it was impossible to know exactly from which segment each measured gastralium or rib originated. However, care was taken to measure elements from similar segments as far as was possible.

From these measurements a ratio was calculated to remove the impact of body size differences among taxa. No complete specimen of *Tatenectes* has been found, but it is estimated that an adult would likely have been approximately 2 m long. *Muraenosaurus* measures between 4.5 and 5.5 m (Brown, 1981), *Pantosaurus* is about 4.5 m (O'Keefe and Wahl, 2003b), and *Cryptoclidus* is around 4 m (Brown, 1981) in length. Comparing ratios, as opposed to raw gastralium size, is especially important considering the relatively small size of *Tatenectes*. The ratio compared the midline gastralium width to the dorsal rib width for each taxon:

$$\frac{\text{Gastraliumwidth (cm)}}{\text{Ribwidth (cm)}}$$

These ratios were analyzed with a Mann-Whitney U test in the program JMP to account for the small size of the data set and the possibility of the data being non-normal.

The second goal of this study was to determine if the unusually large gastralgia of *Tatenectes* display pachyostosis or pachyosteosclerosis. We studied cross-sections of ribs and gastralgia to investigate histology. Several fragmented ribs and gastralgia of *Tatenectes* USNM 536976 were sliced with a rock saw and/or smoothed with a rock polisher to produce flat surfaces for observation and comparison to descriptions in the literature. A fragmentary rib of *Pantosaurus* was also used for comparison.

RESULTS

The gastralgia of *Tatenectes laramiensis* are found to be relatively larger than the gastralgia of the comparison taxa (Fig. 1), and this difference is statistically significant. The gastralgia width: rib width ratio for *Tatenectes* averages 2.30, whereas none of the other taxa studied average a gastralgia:rib ratio above 1.50. The taxon with the next-largest gastralgia is *Cryptoclidus* (1.44). The ratio for *Pantosaurus* is 1.35, and there is the least difference in size between the gastralgia and ribs of *Muraenosaurus* (1.26). The difference between the ratios of *Tatenectes* and the other taxa is particularly interesting due to the fact that the difference in size is due completely to the size of the gastralgia; the ribs of *Tatenectes* are not unusually slender. Figure 2 illustrates the range of gastralgia:rib widths for the measured central gastralgia for each taxon. There is no overlap between the ranges for *Tatenectes* and the other related cryptocleidoid plesiosaurs studied. A non-parametric Mann-Whitney U test was run for these data, and a statistically significant P-value (0.01) was found between the *Tatenectes* ratios and the pooled ratios of other taxa. The gastralgia of *Tatenectes* are therefore proportionately larger than those of related taxa, and this size increase is attributed to pachyostosis.

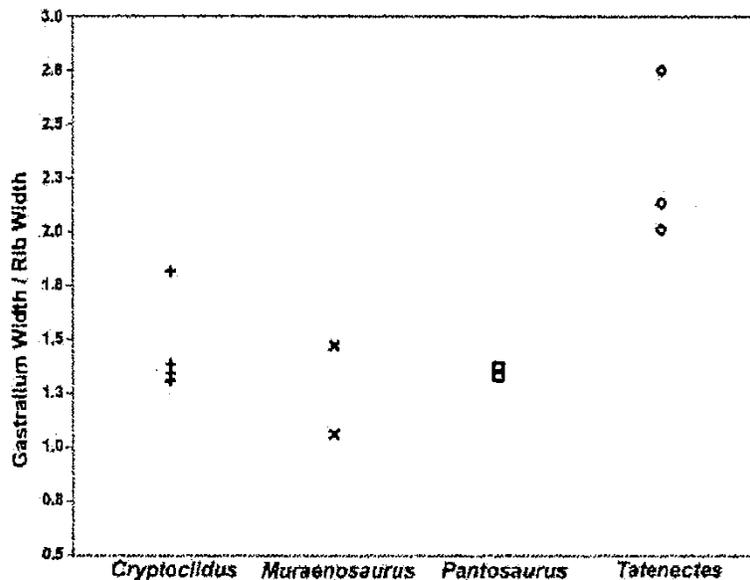


FIGURE 2. Graphs plotting gastralgia/rib widths for four taxa of cryptocleidoid plesiosaurs. Each data point represents a midline gastralgium divided by a rib width.

Examination of the histology of the cross-sections of the ribs and gastralium of *Tatenectes* revealed unexpected results (Fig. 3). That the ribs (Fig. 3A, B) of *Tatenectes* are not osteosclerotic was unsurprising because this is not typical of plesiosaurs in general; but the histologic condition of the gastralium was unanticipated. If the purpose of the gastralium is to serve as ballast, it was thought that the distribution of mass throughout the gastralium would have been constant or graded from most pachyostotic or pachyosteosclerotic at the midline to least massive or dense in the lateral-most elements. None of the elements that were crosssectioned show any evidence of osteosclerosis. Instead there appear to be regions of osteoporotic tissue in the gastralium. Also contrary to what was expected, the tissue conditions are neither constant, nor do they display a smooth gradient. The midline gastralium (Fig. 3E) has thick and dense cortical regions. However, the element is bisected by an asymmetrical band of osteoporotic tissue similar to that seen in the rib head (Fig. 3A). This conformation of cancellous osseous tissue reaches completely to the edges of the gastralium and suggests of osteoporosis. Figure 3D is a cross-section through a middle gastralium. This element also has thick cortical bone and an asymmetrical band of osteoporotic tissue. However, this gastralium appears to have some degree of a free marrow cavity, somewhat similar to what is seen in the rib shaft (Fig. 3B). Finally, the lateral-most gastralium (Fig. 3C) is more similar to the midline element with an asymmetric band of osteoporotic tissue surrounded by thick layers of cortical tissue. A cross-section from a rib of *Pantosaurus* (Fig. 3F) has also been included to serve as an example from a plesiosaur that does not exhibit pachyostosis. This arrangement of pachyostotic and osteoporotic tissue does not conform to other descriptions of either pachyostosis or osteoporosis found in the literature, either for plesiosaurs or any other taxon. In summary, *Tatenectes* displays a novel conformation of osteoporotic bone sandwiched between two layers of thick pachyostotic cortical tissue, and cannot be described as osteoporotic or osteosclerotic. The gastralium are clearly pachyostotic in terms of overall size, but their histology indicates that their unit density might not have differed much compared to more normal gastralium.

TABLE 1. Data of midline gastralium and rib widths used in plotting Figure 2.

Taxon	Gastralium width, cm	Rib width, cm
<i>Tatenectes</i>	2.32	1.153
<i>Tatenectes</i>	3.17	
<i>Tatenectes</i>	2.46	
<i>Pantosaurus</i>	2.3	1.68
<i>Pantosaurus</i>	2.24	
<i>Cryptoclidus</i>	2.02	1.46
<i>Cryptoclidus</i>	2.65	
<i>Cryptoclidus</i>	1.91	
<i>Cryptoclidus</i>	2.02	
<i>Cryptoclidus</i>	2.02	
<i>Cryptoclidus</i>	1.96	
<i>Muraenosaurus</i>	1.8	1.7
<i>Muraenosaurus</i>	2.5	

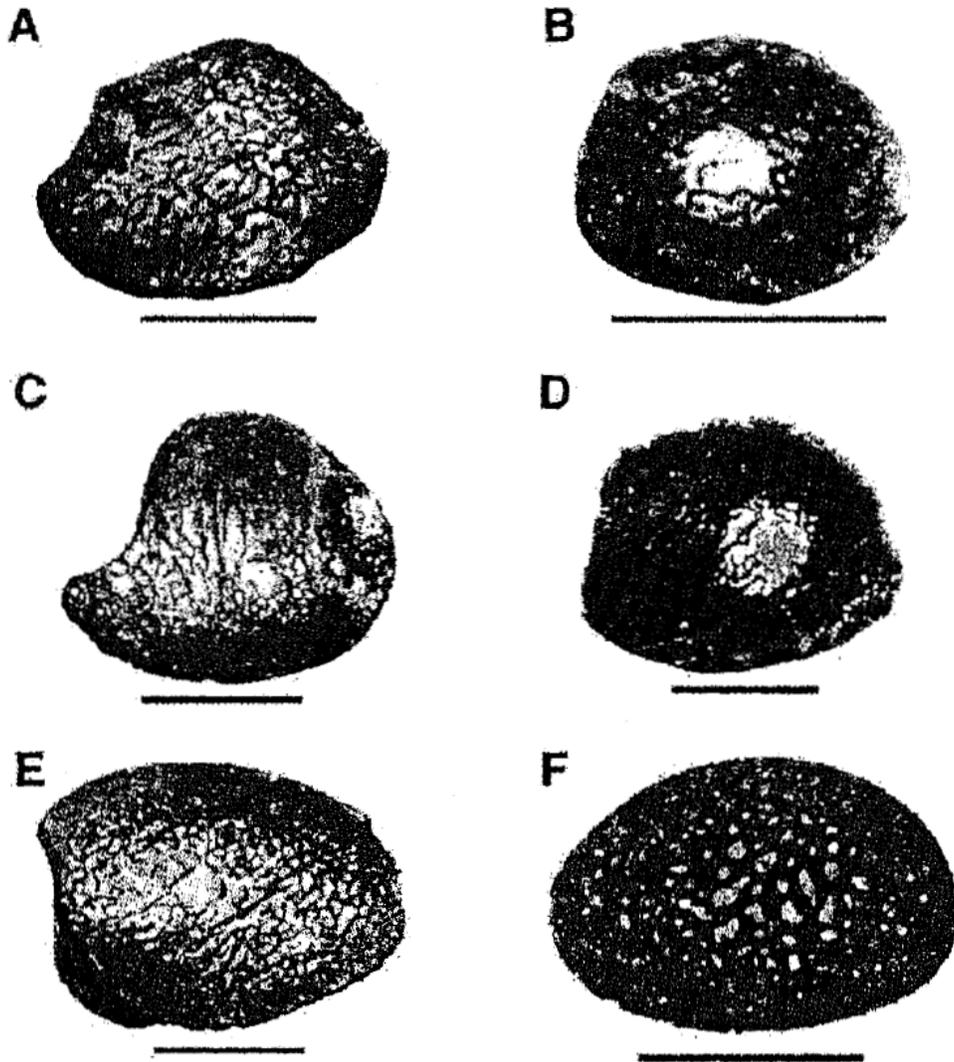
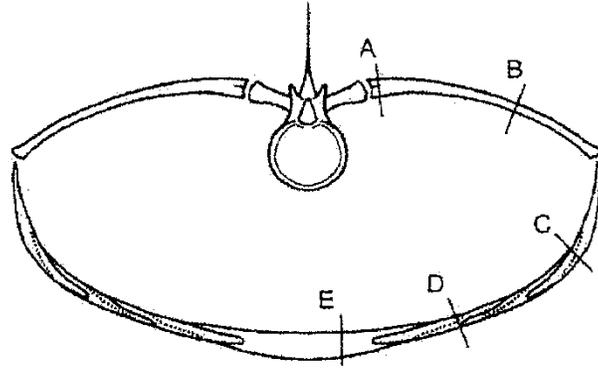


FIGURE 3. Schematic transverse section of *Tatenectes* (top). Labeled cross-sections through ribs and gastralia of USNM 536974 (A-E) correspond with respective labeled hatch marks on transverse section. Crosssection F from *Pantosaurus* USNM 563965, presented for comparison with normal histology.

DISCUSSION

Proportional and histological data indicate that although the gastralia of *Tatenectes* are indeed disproportionately large and hence pachyostotic, the gastralia are not pachyosteosclerotic. The nature of the pachyostosis exhibited by *Tatenectes* also appears to be different from that seen elsewhere. Based on the cross-sections made of the gastralia, the osseous tissue is distributed in a sandwich-like conformation with two rinds of hyperplastic cortical bone surrounding osteoporotic tissue. That band of cancellous bone, although asymmetric, trends generally anteroposteriorly. It is possible that this observed adult morphology persisted throughout ontogeny. On the other hand, if, as Wiffen et al. (1995) suggest, plesiosaurian bone tissues change throughout the life span, it is possible that the asymmetric cancellous bone region arose ontogenetically. The individual described here was a fully mature adult at the time of its death, and it is possible that the bones had experienced a high degree of resorption. The thick cortical layer could therefore have originally completely encircled each gastralium, only to be preferentially reabsorbed along the anteroposterior axis.

Whether the hyperplastic cortical bone was originally deposited in this sandwich-like formation, or the current distribution is a result of ontogeny, the increase in overall size of the gastralia suggests hypotheses about the ecology of *Tatenectes*. When pachyostosis is exhibited by secondarily marine tetrapods, it is most common among taxa that inhabit shallow water (de Ricqlès and de Buffrénil, 2001). Examples of such taxa, which also exhibit pachyostosis in the thoracic region, are primitive archaeocetes and sirenians (de Buffrénil et al., 1990; Damning and de Buffrénil, 1991). Although these mammalian taxa, particularly the herbivorous sirenians, are not ideal marine reptile analogs, their bone histology and known habitats can elucidate both the beneficial and restraining effects of pachyostosis on *Tatenectes*. It is thought that pachyostosis, particularly of the ribs and other thoracic elements, acts as hydrostatic ballast, which increases stability (Cruickshank et al., 1996). Hydrostatic ballast, such as osteosclerosis or swallowing gastroliths for negative buoyancy, and expanded lung volume for positive buoyancy, aids in maintaining the overall trim of the body within the water column without the need to expend energy. Conversely, hydrodynamic ballasts, such as the control surfaces that flippers or paddles provide, allow for the maintenance of equilibrium when an organism is in motion (Damning and de Buffrénil, 1991).

Of course, the increased stability provided by pachyostosis at a low energy expenditure does not come without costs. Pachyostosis, the source of negative buoyancy, is often seen with a corresponding increase in lung volume for positive buoyancy (Taylor, 2000). This means that the volume of the organism is increased twice: in the lungs and in the pachyostotic skeletal elements. The increase in volume increases the effects of inertia and drag (Cruickshank et al., 1996). Therefore, any movements significantly influenced by inertia, such as accelerating or making precise turns at any swimming speed, would be reduced (Taylor, 2000; de Ricqlès and de Buffrénil, 2001). These effects would also become greater with increased speed, thereby reducing the top efficient speed an organism with pachyostosis could achieve (Cruickshank et al., 1996). Therefore, animals exhibiting pachyostosis are usually interpreted as being restricted by their low swimming speeds and lack of agility to living in shallow water environments, in which their increased stability is advantageous (de Ricqlès and de Buffrénil, 2001).

We propose that *Tatenectes laramiensis* would have lived in very shallow marine environments, and may not have been a particularly agile swimmer. The Sundance Sea at the time of deposition was quite shallow, less than 50 m in depth, and was a high-energy environment with large areas above storm wave base (Wahl, 2006). The sediments in which USNM 536974 was

found, a lens of coarse-grained sand within a silt matrix, support this shallow-marine hypothesis. The fossil was also found near the top of the formation, which shows other signs (ripple marks and cross-bedding) of shallow water sediment deposition. Surrounding invertebrate fossils, including numerous burrows, belemnites, and oyster shoals, offer the final evidence of *Tatenectes* lived in a shallow marine environment.

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