NOVEL ANATOMY OF CRYPTOCLIDID PLESIOSAURS WITH COMMENTS ON AXIAL LOCOMOTION.

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# Table of Contents

**Acknowledgements** ........................................................................................................................................... ii

**Table of contents** .................................................................................................................................................. iii-iv

**List of Figures, Tables, and Graphs** ...................................................................................................................... v

**Abstract** ................................................................................................................................................................. vi

**Chapter 1- Introduction to plesiosaurs** ...................................................................................................................... 1-14

  - Introduction ......................................................................................................................................................... 1-5
  - Phylogenetic relationships ................................................................................................................................. 5-10
  - Locomotion in plesiosaurs and other marine tetrapods ............................................................................... 11-14
  - Conclusions ....................................................................................................................................................... 14

**Chapter 2- A new partial skeleton of a cryptocleidoid plesiosaur from the Upper Jurassic Sundance Formation of Wyoming** .................................................................................................................. 14-35

  - Introduction ......................................................................................................................................................... 14-16
  - Geological setting ............................................................................................................................................... 16-18
  - Materials ............................................................................................................................................................ 19
  - Systematic paleontology .................................................................................................................................. 19-20
  - Description ......................................................................................................................................................... 20-30
  - Discussion ......................................................................................................................................................... 30-34
  - Conclusions ....................................................................................................................................................... 34

**Chapter 3- Osteological evidence for a tail-fin in cryptocleidoid plesiosaurs and the role of the tail in plesiosaur locomotion** ................................................................................................................. 35-59

  - Introduction ......................................................................................................................................................... 35-37
  - Materials and Description ............................................................................................................................... 38-41
  - Discussion ......................................................................................................................................................... 41-59
    - Form of tail fin ................................................................................................................................................ 41-47
    - Function of tail fin ........................................................................................................................................ 47-57
Table of Figures

Figure 1.1: Plesiosaur limb girdles………………………………………………………………………………3
Figure 1.2: Plesiosaur morphotypes………………………………………………………………………………4
Figure 1.3: Phylogeny of diapsids………………………………………………………………………………6
Figure 1.4: Phylogeny of Sauropterygia………………………………………………………………………………7
Figure 1.5: Phylogeny of Plesiosauria………………………………………………………………………………10

Figure 2.1: Map of new localities………………………………………………………………………………18
Figure 2.2: Cervical vertebrae of USNM 536963………………………………………………………………21
Figure 2.3: Axial column of USNM 536965……………………………………………………………………23
Figure 2.4: Caudal vertebrae of USNM 536965………………………………………………………………25
Figure 2.5: Caudal vertebrae of USNM 536965 with chevrons………………………………………………27
Figure 2.6: Ribs and gastralia of USNM 536965………………………………………………………………28
Figure 2.7: Pelvic girdle of USNM 536965……………………………………………………………………29
Figure 2.8: Ilium of USNM 536965………………………………………………………………………………31

Figure 3.1: Caudal region of Seeleysaurus guilemiimperatoris………………………………………………37
Figure 3.2: Sacral and caudal vertebrae of R 8575………………………………………………………………39
Figure 3.3: Posterior caudal vertebrae of R 2864………………………………………………………………42
Figure 3.4: Caudal vertebrae of ichthyosaurs……………………………………………………………………45
Figure 3.5: Caudal region of Rhacheosaurus (Geosaurus) gracilis………………………………………………46
Figure 3.6: Reconstruction of the tail fin in Cryptoclidus…………………………………………………………48
Figure 3.7: Partial vertebral column of Delphinus delphis…………………………………………………………50
Figure 3.8: The two-joint system in cetaceans……………………………………………………………………51
Figure 3.9: Peduncle in bottlenose dolphin……………………………………………………………………55

Graph 3.1 Changes in VLI through the caudal series of R 8575………………………………………………53

Table 2.1: Measurements of centra preserved in USNM 536965………………………………………………60
Table 3.1: Measurements of centra preserved in R 8575…………………………………………………………61-62
ABSTRACT

Novel anatomy of cryptoclidid plesiosaurs with comments on axial locomotion.

By Benjamin C. Wilhelm

Cryptoclidid plesiosaurs are best known from the Oxford Clay of England, but have also been found in the western US and Cuba. Two new specimens from the Upper Jurassic Sundance Formation of Wyoming, tentatively referred to the taxon *Pantosaurus striatus*, provide significant new information on the osteology of these lesser known plesiosaurs. In addition, examination of two exceptionally well-preserved caudal regions from *Cryptoclidus eurymerus* and *Muraenosaurus leedsi* has revealed previously undescribed features indicating the presence of a tail fin in these taxa. Comparisons of these features to fossil and extant animals with tail fins allow the shape of the tail fin in plesiosaurs to be constrained. These comparisons also reveal shared similarities in patterns of flexibility of the tail in plesiosaurs, scombroid fishes, and lamnid sharks. These data strongly suggest that the tail was involved, along with the limbs, in active thrust production during plesiosaur locomotion.
Chapter 1- Introduction to plesiosaurs

Introduction

Plesiosaurs, members of the clade Plesiosauria, are marine reptiles that lived during the Mesozoic Era. They were among the first fossils described when the study of vertebrate paleontology was in its infancy (Taylor, 1997). The first plesiosaur remains were identified by De la Beche and Conybeare (1821), who were at the time working on material from another group of marine reptiles, the ichthyosaurs. These workers recognized the uniqueness of this new material and called it Plesiosaurus, meaning “near-lizard.” Conybeare (1822) was the first to reconstruct a plesiosaur, and many of his hypotheses about the morphology of this bizarre new creature were confirmed by the discovery of the first complete plesiosaur skeleton in 1823 (Conybeare, 1824). Since this time, the discovery of numerous other specimens from all continents has demonstrated that plesiosaurs are a morphologically diverse clade with a wide temporal range; from the late Triassic (200 million years ago) to the end of the Cretaceous (65 million years ago) (Carroll, 1988).

Plesiosaurs are characterized by features of the skull and postcranium that distinguish them from all other reptiles. No skull material is presented in this thesis, so modifications of the skull will not be discussed. For a thorough discussion of this topic, see O'Keefe (2001a). The modifications to the postcranium, including the limbs and limb girdles, are relevant to the material discussed in chapters 2 and 3.

All four limbs in plesiosaurs are modified into long, tapering flippers. These flippers are formed by hyperphalangy, a duplication of the distal limb elements that lengthens the limb (Carroll, 1988). These limbs have a hydrofoil cross-section, allowing
them to generate lift (Robinson, 1975). The relative size between the fore- and hindlimbs varies between different clades (O'Keefe and Carrano, 2005), as does the overall profile of the flipper (O'Keefe, 2001b).

The limb girdles of plesiosaurs are also greatly modified (Fig. 1.1). Both the pectoral and pelvic girdles are expanded along the ventral surface of the trunk. The scapulae are expanded ventrally, and meet along the midline in some taxa (O'Keefe, 2001a). This is unlike the condition seen in nothosaurs (Storrs, 1993), early ancestors of plesiosaurs, that have smaller scapulae that do not meet along the midline. The coracoids are also greatly expanded ventrally, forming a large plate of bone. The clavicles and interclavicle are greatly reduced. The condition of the pelvic girdle is similar, with ventral expansions of the ischia, and to a greater degree, the pubes. The ilium is greatly reduced and is only loosely attached to the vertebral column, as life in the water reduces the need for weight-bearing support (Sato, 2002). The presence of large, plate-like limb girdles presumably created greater area for attachment of muscles to move the limbs (Robinson, 1975).

Although all plesiosaurs share the aforementioned modifications to the limbs and limb girdles, there is a great deal of morphological diversity within the clade. Traditionally, plesiosaurs have been divided into two general morphotypes (Fig. 1.2) based on the relative size of the skull, the number and dimensions of cervical vertebrae, relative size of the fore- and hind limbs, and relative size of the scapulae and ischia (Brown, 1981). Taxa with smaller skulls, long necks, and larger forelimbs are considered “plesiosauromorphs.” Taxa with larger skulls, shorter necks, and larger hindlimbs are considered “pliosauromorphs.” Primitive taxa often have necks of
Figure 1.1- The limb girdles of Cryptoclidus, showing the ventrally elaborated elements of the limb girdles. Relevant abbreviations; i. cl., interclavicle; sc., scapula; cor., coracoids; p., pubis; il., ilium; isc., ischium. Reproduced from Andrews (1910).
Figure 1.2- Examples of a plesiosaurotomorph (*Cryptoclidus*) (a.) and a pliosaurotomorph (*Liopleurodon*) (b.). These morphotypes are classified based on the morphology of the skull, neck, and girdles. Reproduced from O'Keefe (2002)
intermediate lengths and do not fall into either of these distinct categories. As a result, these terms are better applied to more derived taxa, where the different morphotypes may represent different trophic specializations (O’Keefe 2002; O’Keefe and Carrano, 2005). The phylogenetic implications of these morphotypes are discussed in the following section. Taxa discussed in chapters 2 and 3 of this thesis are considered to be plesiosauromorphs, although the length of their necks are not as extreme as in more derived taxa such as *Elasmosaurus* and *Hydrotherosaurus*.

**Phylogenetic relationships**

Plesiosaurs are modified diapsids, where the lower temporal fenestra is not present due to the loss of the lower temporal arch (Rieppel, 2000). Their exact position among diapsids is labile, although Müller (2003) found them, along with all other sauropterygians, to be the sister taxa to all other Lepidosauria, a clade that includes turtles, snakes, lizards, and rhynchocephalians (Fig. 1.3).

Sauropterygians are members of the clade Sauropterygia, of which Plesiosauria is the crown clade (Fig. 1.4) (Rieppel, 2000). All sauropterygians are adapted to varying degrees to the marine lifestyle. The most basal sauropterygians are the placodonts, a group characterized by adaptations to the benthic environment (Diedrich, 2010). Other sauropterygians within the clade Eosauropterygia show a general trend from a more generalized “lizard-like” morphology to the highly modified morphology of plesiosaurs (Rieppel, 2000). Pachypleurosauria and nothosaurs both have long, presumably flexible tails, with limbs that are not greatly modified into flippers. In pistosauria, features of both
Figure 1.3- Phylogeny of diapsids, showing plesiosaurs (in Eosauropterygia) along with placodonts as the sister taxa to modern lepidosaurs. From Müller (2003).
Figure 1.4- Phylogeny of the Sauropterygia, showing Plesiosauria as the crown clade.

Reproduced from Rieppel (2000).
the skull and post-cranium are intermediate between nothosaurs and plesiosaurs, leading to their placement as outgroup to Plesiosauria (Rieppel, 2000; O'Keefe 2006).

Study of the relationships within Plesiosauria has been influenced by the differences between the two plesiosaur morphotypes, as defined in the previous section. These morphotypes were thought to represent two monophyletic clades, the Plesiosauroidea and Pliosauroidea (Welles, 1943). All long-necked taxa were considered to be part of the Plesiosauroidea, while taxa with large skulls were placed within the Pliosauroidea. This dichotomy was the prevailing view through most of the history of the study of plesiosaurs and was supported by a number of authors including Owen (1841), Lydekker (1889), Seeley (1892), Andrews (1910, 1913), Welles (1943, 1952), Tarlo (1960), Persson (1963) and Brown (1981). Before the first cladistic analyses of this group, only Williston (1907) suggested these two morphotypes may not form monophyletic clades.

Cladistic analyses of the relationships within Plesiosauria have retained the clades Plesiosauroidea and Pliosauroidea, but membership within these clades is variable. The first cladistic analyses of Plesiosauria by O'Keefe (2001a, 2004) found the pliosauromorph clade Polycotylidae to be within the Plesiosauroidea, indicating that the pliosauromorph condition arose in multiple clades. The cladistic analysis of Druckenmiller and Russell (2008) once again retained the traditional dichotomy, finding Polycotylidae to fall within the Pliosauroidea. They also recovered the clade Leptocleididae within the Pliosauroidea, a grouping not found by O'Keefe (2001a, 2004). This clade was also recovered by Smith and Dyke (2008) in their analysis of pliosauromorph relationships. The most recent and largest analysis of the Plesiosauria

8
by Ketchum and Benson (2009) (Fig. 1.5) supports the hypothesis of O'Keefe (2001a, 2004) that the pliosauromorph condition arose independently in the Plesiosauroidea and Pliosauroid. In this phylogeny, Polycotylidae and Leptocleididae were recovered within the Plesiosauroidea.

Polycotylidae and Leptocleididae, along with basal taxa such as Cryptoclidus and Muraenosaurus, form the clade Cryptoclidia (Ketchum and Benson, 2009). The position of these taxa is quite labile, due to the relatively incomplete nature of many of these taxa. The best known taxa include the polycotylids Dolichorhynchops and Trinacromerium (Williston, 1914; O'Keefe, 2004) from North America and the basal cryptoclidids Muraenosaurus and Cryptoclidus (Andrews, 1910; Brown, 1981) from the Oxford Clay of England. Most other taxa are known from a limited number of specimens that do not always include cranial material. Taxa from the Sundance formation are also though to fall within this clade, but to date they have not been included in any global analyses of plesiosaur relationships (O'Keefe and Wahl, 2003; O'Keefe and Street, 2009). Additional material from basal cryptoclidids, such as the new material of the Late Jurassic Sundance Formation taxon Pantosaurus described in chapter 2, is necessary to help clarify the relationships of these plesiosaurs.
Figure 1.5- Time calibrated phylogeny of the Plesiosauria, from Ketchum and Benson (2009). Note the clade Cryptoclidia on the left, with members Polycotylidae and Leptocleididae, along with basal taxa including *Cryptoclidus* and *Muraenosaurus*. 
Locomotion in plesiosaurs and other marine tetrapods

Aquatic locomotion among tetrapods can be considered either axial, utilizing movement of the body axis, or paraxial, utilizing the appendages (Riess and Frey, 1991). Plesiosaurs are hypothesized to have utilized four-limbed underwater flight, a form of paraxial locomotion unique among marine tetrapods (Robinson, 1975). Plesiosaurs differ from other sauropterygians in their adaptations for this type of locomotion, including the modification of all four limbs into hydrofoils.

Most fossil and extant marine tetrapods use some form of axial locomotion to move through the water. In axial locomotion, propulsion is generated by undulations of the body, tail, or both (Riess and Frey, 1991). Ichthyosaurs and mosasaurs, two Mesozoic clades of marine reptiles, both utilized axial locomotion to generate thrust (Carroll, 1988). Crocodiles are very similar to mosasaurs in their form of locomotion, utilizing lateral undulations of their long tail for propulsion (Massare, 1988). Most mammalian marine tetrapods also utilize axial locomotion, although inherited in a slightly different manner than in marine reptiles. Due to the phylogenetically determined dorso-ventral flexibility and lack of lateral flexibility in the mammalian vertebral column, axial locomotion in several marine mammal clades is generated by dorso-ventral undulations of the tail. Both cetaceans and sirenians utilize this manner of propulsion (Fish, 1998).

Not surprisingly, considering its occurrences among other marine reptiles, plesiosaur ancestors also utilized axial locomotion. In nothosaurs, the trunk was rigid due to the form of the vertebrae and gastralia, but the long tail suggests that these animals used axial locomotion (Carroll, 1988). Nothosaurs also exhibit some
modifications to the forelimb, including hyperphalangy, reduced flexibility within the limb, and flattening of limb elements, suggesting these limbs were used to some extent during locomotion (Storrs, 1993). However, the limbs are not as modified as those in plesiosaurs and are not thought to have been used in underwater flight (Carroll and Gaskill, 1985).

While axial locomotion is more common, there are some extant marine tetrapods that utilize paraxial locomotion. Sea lions, penguins, and sea turtles all use a form of underwater flight as their primary mode of locomotion (Robinson, 1975). In sea lions and penguins, only the forelimbs are modified into hydrofoils (Robinson, 1975; Godfrey, 1984). Sea turtles are the only other tetrapod besides plesiosaurs in which all four limbs are modified into hydrofoils; however in turtles the hindlimbs seem to be used only as rudders (Walker, 1971). The form of the flight stroke in these animals is different, as sea lions do not generate thrust with the recovery portion of the flight stroke, while penguins and sea turtles do (Robinson, 1975; Godfrey, 1984). Among fossil marine tetrapods, paraxial locomotion is also seen in placodonts, although they presumably did not use underwater flight as the limbs are not modified into hydrofoils. Placodonts have rigid trunks with limbs partially modified for underwater locomotion. The tail does not appear to be the primary propulsive structure despite its length (Carroll, 1988). Placodont locomotion probably utilized motions of both the limbs and tail, resulting in relatively inefficient swimming (Massare, 1997).

It is the highly modified limbs of plesiosaurs that provide the strongest evidence for paraxial locomotion in Plesiosauria. According to Robinson (1975), all plesiosaur limbs share a number of features that suggest they were used for underwater flight,
including; hyperphalangy, flattening of elements on the horizontal plane, tapering of phalanges at the distal end of the limb, and lack of flexibility within the limb. These features are much more developed than in nothosaurs, indicating a more advanced form of aquatic locomotion (Storrs, 1993). Instances of soft tissue preservation suggest that there was a region of soft tissue on the trailing edge of the flipper (Dames, 1895; von Huene, 1923) that would have given the limb a hydrofoil cross section, similar to the wings of an airplane (Robinson, 1975). However, unlike the wings of an airplane that are fixed and can only generate upward lift, the hydrofoils of plesiosaurs can be rotated to direct lift forward. Both the forelimbs and the hindlimbs share these features, unlike in nothosaurs where only the front limbs are modified for aquatic locomotion (Storrs, 1993). Plesiosaurs develop much larger sizes than nothosaurs, so this four-limbed method of locomotion may have been necessary to overcome the drag created by this increase in size (Storrs, 1993).

While the contribution of the limbs to locomotion has been addressed by a number of authors, the role of the neck and tail during locomotion has received considerably less attention. The neck of plesiosaurs is often elongate, and creates drag anterior to the center of mass (Massare, 1997). The neck had some flexibility, with the ability to move both dorso-ventrally and laterally (Zarnick, 1925). The drag caused by these movements would likely cause the animal to veer off course (Alexander, 1989). Robinson (1997) hypothesized that this may have been compensated for by slower swimming speeds. The tail has been suggested to be involved in ruddering, aided by a vertical tail fin (Robinson, 1975). The evidence for such a structure and the role of the
tail during plesiosaur locomotion is discussed in chapter 3.

**Conclusions**

Plesiosaurs were a diverse and widespread group, both temporally and geographically. They survived from the late Triassic to the end of the Cretaceous and their remains have been found on all continents. They are basal diapsid reptiles within the clade Sauropterygia, characterized by a number of adaptations for underwater flight. This manner of locomotion is relatively common among fossil and modern marine tetrapods, but the active use of all four limbs is unique. This thesis aims to fill two gaps in our knowledge of plesiosaurs. The second chapter describes new material of the poorly known Sundance Formation plesiosaur *Pantosaurus striatus* in the hopes that new information on basal cryptoclidids will clarify relationships within the clade. The third chapter addresses the anatomy of the tail in cryptoclidids and the role of the tail during plesiosaur locomotion.

**Chapter 2- A new partial skeleton of a cryptocleidoid plesiosaur from the Upper Jurassic Sundance Formation of Wyoming.**

**Introduction**

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

The new material described herein is provisionally referred to the genus *Pantosaurus* on the basis of the posteriorly directed neural spines seen in both specimens; however this referral is equivocal for the partial skeleton (see discussion). The first material of *Pantosaurus*, the anterior axial column and forelimb of a juvenile, was described by Marsh (1891) and named “*Parasaurus*” *striatus*. This name was preoccupied (Marsh, 1893), necessitating the change to *Pantosaurus*. Marsh formally described and figured the holotype in 1895. Mehl (1912) figured a forelimb from the Sundance Formation, which he referred to “*Muraenosaurus reedii*”, a taxon determined to be a junior synonym of *Pantosaurus striatus* by O'Keefe and Wahl (2003a). Mehl also mentioned holotype material from the posterior axial column including dorsal and caudal vertebrae, but this material now appears to be lost (O'Keefe, pers. observ., 2003).

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

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


Geological Setting

The Sundance Seaway was a shallow epicontinental seaway that covered much of Wyoming and parts of Montana, South Dakota, and Colorado in the late Jurassic (Kvale et al., 2001). Marine sediments deposited by this seaway in southeastern
Wyoming were named the “Shirley Stage” by Knight (1900), and later the Sundance Formation by Reeside (1919). In the Laramie Basin, Imlay (1947) divided the Sundance Formation into seven members. In the Bighorn Basin, where the specimens described here were recovered, Kvale et al. (2001) divided the Sundance into Lower and Upper Members. This more general division is the one in current use given the lateral heterogeneity of the Sundance Formation and the fact that Imlay’s (1947) detailed stratigraphy is highly localized.

Both specimens reported here were found near the top of the Upper Member of the Sundance Formation, in the equivalent of the ‘Redwater Shale Member’ of Imlay (1947). This set of beds represents the last transgressive-regressive cycle of the Sundance Seaway (Brenner and Peterson, 1994). Molluscan biostratigraphy places this member in the Oxfordian (Kvale et al., 2001). It is highly fossiliferous, with numerous invertebrate remains and occasional, usually isolated, vertebrate remains. Articulated ichthyosaur remains are locally common, while articulated plesiosaur remains are relatively rare (O’Keefe and Street, 2009). Both specimens described here were found in articulation and were discovered in outcrops near the towns of Greybull and Shell, Wyoming (Fig. 2.1).
Figure 2.1- Map of north-central Wyoming showing Sundance Formation outcrops and localities. Open stars indicate localities of USNM 536963 (1) and USNM 536965 (2). Closed stars indicate localities of University of Wyoming specimens.
Materials

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

Both specimens are crushed to some degree, but are not deformed like much of the Oxford Clay plesiosaur material. Vertebral centra are generally well-preserved; neural arches and spines are present but crushed laterally in many cases, while sacral ribs and transverse processes are largely undeformed. The right pubis is shattered but complete and has been reassembled, while the left pubis is fragmentary. Both ischia are well-preserved, as are both ilia.

Systematic Paleontology

SAUROPTERYGIA Owen, 1860
PLESIOSAURIA de Blainville, 1835
PLESIOSAUROIDEA Welles, 1943
CRYPTOCLEIDOIDEA O'Keefe, 2001a

PANTOSAURUS STRIATUS Marsh, 1891
(Figs. 2.2–2.8)
**Parasaurus striatus** Marsh, 1891:338 (original description)

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

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

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

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

**Stratigraphic Occurrence**—Upper Member of the Sundance Formation (“Redwater Shale” informal member), Upper Jurassic (Oxfordian); Natrona and Carbon Counties, Wyoming.

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

**Description**

**USNM 536963**—USNM 536963 preserves three posterior cervical vertebrae in articulation, and fragments of a fourth (Fig. 2.2). The centra are waisted and wider than
Figure 2.2- USNM 536963, in right lateral view, showing dorsal excursion on rib facet for a tubercle of the cervical rib and posteriorly directed neural spine.
they are tall and long. The vertebral length indexes (Brown, 1981; O’Keefe and Hiller, 2006) for the 3 complete vertebrae, from anterior to posterior, are 84.9, 88.4, and 79.7. Comparisons of their dimensions to those of other Oxfordian plesiosaurs are not diagnostic, as the dimensions of posterior cervical centra tend to be similar in plesiosauroid plesiosaurs (O’Keefe and Hiller, 2006). The rib facets are single headed, blade-like, and carried on a pedestal, with a dorsal excursion for a tubercle of the cervical rib. These facets resemble those of *Muraenosaurus leedsi*, which has a similar dorsal excursion. The neural spine preserved is posteriorly angled, as in the holotype of *Pantosaurus*, but unlike the upwardly-directed spines of other Oxfordian cryptocleidoids.

The antero-ventral and postero-ventral edges of the centra do not bear the short anterior-posterior striations seen in the anterior cervical vertebrae of the *Pantosaurus* holotype and *Muraenosaurus*. Their presence in the posterior cervical vertebrae of these taxa is unknown; the condition in *Muraenosaurus* is not mentioned by Andrews (1910).

**USNM 536965**—USNM 536965 preserves four dorsal, three sacral, and eight caudal vertebrae (Fig. 2.3; Table 1). The centra are waisted and wider than tall, and taller than long. The articular faces are amphicoelus and bear a notochordal pit slightly dorsal to center. The articular faces of the caudal vertebrae have more rounded edges than those in the sacrum. When the centra are articulated in life position, there is a slight downward bend of the tail beginning at the fourth caudal. As with the cervical vertebrae of the *Pantosaurus* holotype and USNM 536963, the dorsal, sacral, and caudal neural spines are posteriorly directed. These spines shorten in the anterior caudals, but then begin to lengthen again after the fifth caudal. Anterior zygapophyses
Figure 2.3- Axial column of USNM 536965 in left lateral and dorsal views. The lateral view is in articulation while the dorsal view is aligned to show the ribs without overlap.
are well-developed and extend beyond the anterior face of the centra, while the posterior zygapophyses are reduced.

The preserved dorsal vertebrae bear short ribs that are completely fused to the transverse processes. These ribs angle dorsally, becoming more horizontal in successively posterior vertebrae. They are widest at the point of attachment, dorso-ventrally flattened, and swept-back posteriorly. The sacral vertebrae bear stout sacral ribs that lie at a 90° angle to the neural spine. They are constricted at their midpoint and then widen again at the distal end. Each bears a facet for cartilaginous articulation with the ilia. The second sacral ribs extend dorsal to the more posterior ribs, which are notched to allow them to articulate. The ribs of the anterior caudal vertebrae are angled slightly downward behind the sacral ribs, and then begin to angle upward again. These ribs are not as wide as those of the sacral vertebrae and are angled more posteriorly. In ventral view (Fig. 2.4), the articular faces of the last preserved caudal vertebra are not parallel, but and are at a slight angle to each other. This centrum is well preserved and free of compression, so this feature is likely real. If the subsequent vertebrae had similar angles between the articular faces, there would have been a permanent bend of the tail to the left.

Pedestals for chevrons begin on the ventral surface of the second caudal, and distinct facets begin on the fourth caudal. The sizes of the facets are quite variable, but articulated chevrons are similar in size despite disparity in the size of their facets. Twenty-two chevrons are preserved, more than can articulate with the vertebrae present. Following Andrews (1910) in placing chevrons with one articular facet anterior to those with two, it appears that the chevrons are quite short anteriorly, and then
Figure 2.4- Last four preserved caudal vertebrae of USNM 536965 in ventral view, showing the angle between the articular faces on the last preserved centra and variable sizes of the chevron facets.
become longer as the chevrons begin articulating between adjacent centra, and then rapidly shorten again. This is unlike the chevrons seen in most plesiosaurs, which start long and then become shorter posteriorly. The chevrons of USNM 536965 are also unusual in the degree to which they curve inward below the tail (Fig. 2.5). Moving posteriorly down the column, the chevrons begin to curve inward until they point ventrally from the centra, almost parallel to the sagittal plane.

A number of ribs and gastralia that belong to segments anterior to the vertebrae present are preserved (Fig. 2.6). The ribs and gastralia are similar in thickness and do not show any signs of pachyostosis in cross-section, unlike the Sundance taxon *Tatenectes* (Street and O’Keefe, in press). Two bifid gastralia are present. Similar pathologies have been observed in other Oxford Clay skeletons (Wilhelm, pers. observ., 2008).

USNM 536965 preserves a nearly complete pelvic girdle (Figs. 2.7, 2.8). The fragmentary left pubis is not figured, as its position cannot be determined due to poor preservation and asymmetries in the pelvic girdle. When articulated, the pubes and ischia are at an angle of 25° above horizontal. The pelvic girdle is wider than it is long, with a width to length ratio of 1.28. This ratio is more similar to that of *Cryptoclidus* (1.35) than it is to *Muraenosaurus* (1.08) (Andrews, 1910). The width of the pubis is increased by a prominent antero-lateral horn, more similar to those of *Cryptoclidus*, but not lacking in the pubis of *Muraenosaurus* (Andrews, 1910). The acetabular margin of the pubis is more concave than in *Cryptoclidus* and *Muraenosaurus*. The lateral-posterior edge of the ischium is more concave than it is in *Muraenosaurus* or *Cryptoclidus*. In life position, the symphyseal margin of the right pubis crosses the
Figure 2.5- Fifth (top row) and seventh (bottom row) caudal vertebrae of USNM 536965 in posterior and left lateral views showing the inward curving chevrons.
Figure 2.6- Ribs (left), pathological gastralia (top middle and right), and normal gastralia (right) of USNM 536965.
Figure 2.7- Dorsal view of the pubis and ischia of USNM 536965 in life position. Angle of elements from horizontal is 25°. The partial left pubis is not figured as its exact position is uncertain. Antero-lateral horn indicated by a.l.h., postero-lateral horn indicated by p.l.h.
sagittal plane. There is no deformation of the pubis, so this asymmetry is probably real. The posterior portion of the ischium also has a posterolateral horn, more prominent than that seen in Cryptoclidus, and not present in Muraenosaurus. The neck of the left ischium is bent slightly ventrally, while the right ischium it is much flatter. Both ischia are free of compression, so this asymmetry appears to be pathological.

The ilia of USNM 536965 (Fig. 2.8) differ markedly from those of Muraenosaurus and Cryptoclidus, and from all other plesiosaurs. Both Muraenosaurus and Cryptoclidus have ilia that are straight along their posterior edges and concave on their anterior edges (Andrews, 1910); the iliac blades are also flared and wider than the shafts. In contrast, the ilia of USNM 536965 are widest at the acetabular end and approximately the same width at the midpoint of the shaft and the iliac blade. The posterior edges are also much more curved those of Muraenosaurus. The left and right ilia differ significantly, with the blade of the left ilium being twisted clockwise. Like the ischia, the ilia are free of deformation, so this feature appears to be pathological.

**Discussion**

Taxonomic assignment of the fossils reported here is difficult due to the lack of overlap of this material with the Pantosaurus holotype, and the fact that the holotype is a juvenile. The specimens were compared to four cryptocleidoid taxa; Muraenosaurus and Cryptoclidus from the Oxford Clay, and Pantosaurus and Tatenectes from the Sundance Formation. The plesiosaurs of the Jagua Formation of Cuba were examined from the literature. They are of doubtful relevance because they are represented mainly by cranial and disarticulated postcranial material. Pliosaurs, such as Peloneustes from the Oxford Clay (Andrews, 1913) and Megalneusaurus from the Sundance Formation.
Figure 2.8- Left and right ilia of USNM 536965. Views are: top row, lateral; second row, anterior; third row, medial; bottom row, posterior.
(Knight, 1898), were excluded from study because USNM 536963 lacks the double headed cervical ribs and USNM 536965 lacks the large pelvis typical of pliosaurs.

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

Referral of USNM 536965 is more difficult, as material from the posterior axial column of *Tatenectes* and *Pantosaurus* is limited (although unreported *Tatenectes* material does exist (Street and O'Keefe, 2009). This specimen can be excluded from *Tatenectes*, as it lacks the pachyostotic gastralia diagnostic of the genus (Street and O'Keefe, In press). While similar in some ways to *Cryptoclidus* and *Muraenosaurus*, the pelvic girdle of USNM 536965 is distinct in its autapomorphic ilium. This ilium is unique in that the iliac blade is approximately the same width as the midpoint of the shaft. In *Cryptoclidus* and *Muraenosaurus*, the iliac blade is flared and wider than the shaft.
Despite the lack of overlapping material, some evidence suggests that USNM 536965 may be referable to *Pantosaurus*. The dorsal, sacral, and caudal neural spines of USNM 536965 are posteriorly directed, as are the cervical neural spines of *Pantosaurus striatus*. Posteriorly directed neural spines are uncommon in Oxfordian plesiosaurs, being seen only in the anterior cervicals of ‗*Picrocleidus* beloclis* (Andrews, 1913; pl. VII, fig. 5) and the posterior caudals of *Cryptoclidus*. In *Cryptoclidus*, this feature appears to be associated with dermal structures in the distal portion of the tail (Wilhelm, pers. observ., 2009). The posteriorly directed neural spines in ‗*Picrocleidus*‘ are problematic, as this genus was synonymized with *Muraenosaurus* (Brown, 1981), which lacks posteriorly directed anterior cervical neural spines. This suggests that *Picrocleidus* may not be synonymous with *Muraenosaurus*. Because posteriorly directed neural spines are rare, we tentatively refer USNM 536965 to *Pantosaurus*. It remains possible, however, that this specimen represents a third, currently unknown cryptocleidoid taxon from the Sundance Formation.

The morphology of the caudal region of USNM 536965 indicates that it may have played a role in locomotion. The articular faces of the caudal vertebrae are more rounded than those of the sacral vertebrae immediately antecedent, indicating greater flexibility in the proximal tail. This flexibility would have allowed for the tail to be moved laterally, possibly acting as a rudder. If the tail was used in such a manner, it might explain some of the pathologies seen in the partial skeleton. The left ilium and ischium are rotated compared to their counterparts on the right side, and the tail appears to be bent to the left. If this individual had a missing or damaged flipper on its right side, it is possible that the tail was bent to the left side to provide drag to counteract the bilateral...
imbalance of propulsion. A dermal tail fin could be used to create increased drag and would make the tail a more effective rudder. The presence of a dermal tail fin in plesiosaurs has been suggested before (Dames, 1895; Tarlo, 1957; Smith, 2007), but no osteological evidence has been described for its presence in cryptocleidoid plesiosaurs. The imbalance of forces acting on the two sides, and habitual asymmetric behaviors resulting from this, could eventually lead to the distortion seen in the left girdle elements and in the axial column. Distortion due to habitual asymmetric swimming behaviors is seen in captive bottlenose dolphins, who tend to swim in a primarily counterclockwise direction around their tanks. This behavior results in a permanent leftward turn of the dorsal fin (Ridgway, 1990).

Conclusions

USNM 536963 and USNM 536965 are significant new specimens given the paucity of cryptocleidoid plesiosaur material from the Sundance Formation. USNM 536963 is referable to *Pantosaurus* due to the posteriorly directed neural spines and cervical rib articulation morphology. USNM 536965 is also referred to *Pantosaurus* for the former reason, although this referral is tentative because posteriorly directed neural spines sometimes appear in other Oxfordian plesiosaurs. This specimen is excluded from all other Oxfordian plesiosaur genera on the basis of its autapomorphic ilium. The caudal vertebrae and pelvic girdle of USNM 536965 are also notable as they suggest the tail may have been used as a rudder. The role of the tail during plesiosaur locomotion warrants further examination.
Chapter 3- Osteological evidence for a tail-fin in cryptcleidoid plesiosaurs and the role of the tail in plesiosaur locomotion.

Introduction

Tail fins and flukes are common in extant and marine vertebrates, where they aid in the generation of thrust during axial locomotion. Among fossil marine reptiles, ichthyosaurs (Merriam, 1908; Buchholtz, 2001; McGowan, 1992), thalattosuchians (Fraas, 1902; Andrews, 1913), and mosasaurs (Lindgren et al., 2008) all display osteological evidence for the presence of a convergently evolved tail fin. Extant marine taxa, such as sharks (McGowan, 1992), also have tail fins. Sirenians and cetaceans (Fish and Hui, 1991; Fish, 1998) have tail flukes, a similar structure which lies along a horizontal plane, rather than a vertical plane. While these fins and flukes are found in a wide variety of forms, they are all similar in their function: producing thrust generated by oscillations of the tail. Plesiosaurs are hypothesized to utilize appendicular underwater flight (Robinson, 1975), rather than axial locomotion, so a tail fin would not be necessary for thrust production, and plesiosaurs are generally reconstructed without one. Despite this, its presence has been suggested in plesiosaurs for almost a century and a half.

Owen (1865) was the first to hypothesize plesiosaurs had a vertical tail fin, due to the lateral compression seen in the last ten caudal vertebrae of Archaeonectrus rostratus. The only soft tissue evidence for a tail fin was reported by Dames (1895), in his description of the holotype of Seeleysaurus guilemiimperatoris. This specimen preserves a dark outline in the caudal region (Fig. 3.1) that seems to show a dermal tail
fin on the dorsal side of the tail (Dames, 1895: Pl. I). Although providing no other osteological evidence, a number of other authors (Zarnick, 1925; Tarlo, 1957: Newman and Tarlo, 1967) used this reference as evidence when reconstructing a tail fin in a number of different plesiosaur groups. These tail fins were reconstructed as having a larger ventral lobe, or with the dorsal and ventral lobes being equal, despite the fact that the cited evidence (Dames, 1895) clearly indicates a large lobe on the dorsal side and almost no lobe on the ventral side. Smith (2007) presented the second piece of osteological evidence for a tail fin in plesiosaurs, in *Rhomaleosaurus zetlandicus*. He noted that the 21st caudal vertebrae was much shorter than the preceding or following vertebrae, corresponding with a “subtle kink” in the tail (Smith, 2007:p255). He also noted lateral compression in the distal caudal vertebrae, like that seen by Owen (1865). Neither feature gives much information about the shape of the tail fin, so it was reconstructed following Dames (1895) and Newman and Tarlo (1967), again with the larger lobe on the ventral side of the tail.

The presence of a tail fin in cryptocleidoids has not been discussed, but is possible due to the presence of this feature in distantly related clades. The hypothesis that cryptocleidoid plesiosaurs had a tail fin will be tested by examining the caudal anatomy of two exceptionally well-preserved specimens of *Cryptoclidus oxoniensis* and *Muraenosaurus leedsi* from the Oxford Clay of England. Comparisons to fossil and extant taxa with tail fins will demonstrate the presence of a tail fin and will allow further constraints to be placed on the form and function of this feature in plesiosaurs.
Figure 3.1- Caudal region of the holotype of *Seeleysaurus guilemiimperatoris* showing dark outline of soft tissue preservation. Reproduced from Dames (1895).
Materials and Description

A complete caudal series from Cryptoclidus oxoniensis and a partial series from Muraenosaurus leedsi were examined from the collections of the Natural History Museum (London). Both specimens are undeformed and easily articulated, allowing detailed study of their caudal anatomy.

Cryptoclidus oxoniensis: The specimen of Cryptoclidus oxoniensis described here, R 8575 (Fig. 3.2) comprises 4 sacral vertebrae (S1-4), 26 caudal vertebrae (Ca1-26), and a terminal “pygostyle” formed by 5-6 fused vertebrae. Dimensions of the vertebrae are recorded in Table 3.1. The centra are not deformed and all but one neural spine is present, as are the majority of caudal ribs. The articular faces of the vertebrae are well-ossified, indicating an adult individual (Brown, 1981), and largely complete, allowing their position in life to be determined. The edges of the articular faces are also more rounded in the tail than they are in the sacrum, although this varies along the column. Articulation of the vertebrae shows that there is a downward turn of the tail beginning at the end of the sacrum and leveling out around Ca23.

Viewed dorsally (Figure 3.2), the caudal ribs widen through the first 7 caudal vertebrae, and then narrow again until around Ca14. Anterior to Ca14, the point where the first narrowing occurs, the anterior and posterior zygapophyses are well developed and articulate closely with each other. These zygapophyses quickly become reduced and disappear completely at Ca14.

Slightly posterior to the loss of zygapophyses there is another distinct change in morphology of the neural spines. Moving from the sacrum down the tail, the spines gradually get shorter until Ca17. This spine is taller than the preceding neural spines,
Figure 3.2- Sacral and caudal vertebrae of R 8575 in dorsal (top) and lateral (bottom) views. Arrow indicates position of Ca 17.
and directed further posteriorly. The distal end of the neural spine is also longer in the anterior-posterior direction and much wider medio-laterally. In all the following neural spines, the distal end is proportionately larger than in anterior caudal neural spines. They also bear a larger region for articulation with cartilage. The posterior angle of the neural spine continues until Ca22, where the angle changes to point nearly straight up from the centrum, and then reverses in the last four neural spines to become anteriorly directed. Due to this change in direction, the neural spines of Ca21-23 all articulate closely together, creating a large, continuous area for articulation with cartilage.

The ribs and centra of the last few caudal vertebrae rapidly narrow, resulting in lateral compression. This compressed region is extended by the “pygostyle” structure, which has no caudal ribs. While it does not support the same structures as in birds, the convergences between the two structures led to similar description when first observed by Kear et al. (2006) in *Umoonasaurus*, an early Cretaceous leptocleidid (Ketchum and Benson, 2010). This pygostyle is approximately 7.5 cm in length and is composed of 5-6 vertebral centra that are fused together. It is difficult to determine the exact number due to the fusion. The lack of any apparent gap between the vertebrae indicates that this fusion is not the result of preservation. This pygostyle is longer than the one described by Kear et al. (2006), although they both comprise approximately the same number of vertebrae, indicating further reduction of the tail in more derived plesiosaurs. Such shortening of the tail may reduce drag behind the center of mass, making underwater locomotion more efficient (Nicholls and Godfrey, 1994).

A few chevrons are also preserved with the specimen. Most are disarticulated, but the last 3 are fused to the vertebrae. In all three cases, the chevron fuses to the
anterior of the two vertebrae it articulates between (Andrews, 1910). The chevrons are longer in the anterior portion of the tail and rapidly shorten around Ca14, remaining short into the pygostyle.

**Muraenosaurus leedsi**- R2864 is a juvenile specimen of *Muraenosaurus leedsi*, portions of which are distorted. Caudal vertebrae from this specimen are figured by Andrews (1910: text-fig. 59) in his description of the genus *Muraenosaurus*. The specimen comprises 15 caudal vertebrae (Fig. 3.3) from the posterior end of the tail, and are undeformed and largely complete, with complete centra and a majority of neural spines and caudal ribs. Most of the neural spines and caudal ribs have been glued to the centra, as ossification between these elements was not complete due to the juvenile status of the individual.

This specimen shares several similarities with the caudal region of *Cryptoclidus oxoniensis*. Both tails have a rapid narrowing in their posterior portion, created by a decrease in size of both the centra and caudal ribs. The neural spines lack zygapophyses, as do those in the posterior portion of the caudal region of *Cryptoclidus*. The neural spines also change direction from posteriorly to anteriorly directed, resulting in a similar region for articulation with cartilage along the ends of these three neural spines. The distal ends of all neural spines preserved are also wide like those in the posterior portion of the *Cryptoclidus* tail.

**Discussion**

**Form of the tail fin in cryptocleidoids**- There are a number of features of the posterior caudal region of * Cryptoclidus* that indicate it had a tail fin including; a
Figure 3.3- Posterior caudal vertebrae of R 2864 in dorsal (top) and lateral (bottom) views.
disproportionally large neural spine at Ca17, neural spines with wide distal ends, a change in direction of neural spines at Ca 22, and a lateral compression of the tail in the most distal vertebrae. The presence of some of the same features in the juvenile *Muraenosaurus* specimen is significant, as it indicates these features are true osteological correlates of a tail fin and not pathological or the result of deformation. Comparisons of these features to fossil and extant animals with tail fins of a variety of forms indicate a number of similarities that allow the size and shape of the tail fin in cryptocleidoids to be constrained.

The dramatic change in neural spine morphology at Ca17 of *Cryptoclidus* indicates that this is the start of the tail fin. This neural spine is taller and has a distal end both wider and longer than those preceding and following it. This large area at the end of the neural spine could have supported a section of cartilage, forming the leading edge of the tail fin. Past this point, all neural spines have large areas for articulation with cartilage that may have added rigidity and height to the tail fin. Large, osseous neural spines form nearly the entire upper lobe of the tail fin in mosasaurs (Lindgren et al., 2008). Large neural spines in the tail fin are also seen in Triassic ichthyosaurs (Merriam, 1908). However, in more derived ichthyosaurs the height of the neural spines decreases just before the beginning of the tail fin, indicating ossified neural spines are not necessary for support within the tail fin (Merriam, 1908).

The change in direction of the neural spines around Ca22 in *Cryptoclidus* results in three neural spines in close articulation, creating a large area for articulation with cartilage. The same feature is seen in the juvenile specimen of *Muraenosaurus*. A similar converging of neural spines occurs in the tails of Triassic ichthyosaurs, many of
which were examined by Merriam (1908). In *Mixosaurus* (Fig. 3.4a) and *Cymbospondylus* (Fig. 3.4b), there is a change in neural spine direction from posteriorly-directed to anteriorly-directed just anterior to the downward bend of the tail. In *Delphinosaurus*, the change in neural spine direction occurs just after the downward bend. In thalattosuchians, a similar change of direction occurs after the bend of the tail (Fraas, 1902; Andrews, 1913). Soft tissue impressions indicate this change in direction occurs just below the tallest portion of the tail fin, with the fin rapidly dropping off past this point (Fig. 3.5). The large cartilage structure articulating with the neural spines would have provided support to this tall portion of the tail fin.

The lateral compression seen in the distal-most vertebrae in both *Cryptoclidus* and *Muraenosaurus* is caused by a reduction in width of both the centra and caudal ribs. Compression of the centra lead Owen (1865) and Smith (2007) to conclude that lateral compression at the end of the tail indicates the presence of a tail fin. Lateral compression of centra within the tail fin is seen in ichthyosaurs, mosasuars, and thalattosuchians (Merriam, 1908; Everhart, 2005; Andrews, 1913). Cetaceans also have compressed centra within the fluke, although these are dorso-ventrally rather than laterally compressed, as the fluke is horizontal. In *Cryptoclidus*, the last 4-5 centra are compressed versus the ten reported by Owen (1865) and at least eight by Smith (2007). This suggests that the tail fin in *Cryptoclidus* may have been shorter than in these other taxa, although this difference may be negligible with the addition of the pygostyle. The lateral compression in the end of the tail fin has another implication. The soft tissues at the leading edge and highest point of the tail fin would likely cause this region to be thicker than the more posterior portions of the fin. This streamlines the fin (Felts, 1966)
Figure 3.4- Caudal vertebrae of the ichthyosaurs a) *Mixosaurus cornalianus* and b) *Cymbospondylus petrinus* showing a change in neural spine direction. Reproduced from Merriam (1908).
Figure 3.5- Caudal region of *Rhacheosaurus* (*Geosaurus*) *gracilis* showing a change in neural spine direction and the outline of a tail fin based on soft tissue evidence.

Reproduced from Andrews (1913).
and gives it a hydrofoil shaped cross-section (Robinson, 1975). The significance of this feature will be discussed further in the following section.

Other features in the caudal region of Cryptoclidus can help us constrain the shape of the tail fin. The chevrons in the posterior region of the tail are small and lack areas for the articulation with cartilage like those on the neural spines. This indicates that the tail fin was restricted to the dorsal side of the tail. This agrees well with soft tissue impressions in the holotype of Seeleysaurus guileliimperatoris (Dames, 1895) that depict a tail fin with the larger lobe on the top.

With data from Cryptoclidus and other animals with tail fins, the size and shape of the tail fin can be reconstructed (Fig. 3.6). The leading edge of the fin begins at Ca17 and this edge can be continued until it is above Ca22, which represents the highest point of the fin. The trailing edge of the fin is reconstructed similar to thalattosuchians, due to the similarities between the caudal regions. This reconstruction is conservative in its estimation of the size of the tail fin; increasing the angle of the leading edge of the fin leads to an increase in the overall size of the fin, and the form of Ca17 suggests the angle could be greater than is reconstructed.

**Function of the tail fin**—Just as comparisons to fossil and extant animals allow constraints to be placed on the size and shape of the tail fin in plesiosaurs, they can also provide information on the function of this structure during locomotion. There are features of the caudal region in Cryptoclidus that represent points of muscle attachments, joints within the tail, and other regions of flexibility. The presence of similar features in other marine taxa implies similar function and can be used to help understand how the tail was used in plesiosaurs.
Figure 3.6- Reconstruction of the tail fin in *Cryptoclidus*. 
The edges of caudal centra in *Cryptoclidus* are more rounded than the centra in the sacrum. This indicates that there is greater flexibility within the tail. Neural spines would greatly limit dorso-ventral movements of the tail, but lateral movements would be possible. This flexibility would be increased in the posterior portion of the tail, as the zygapophyses are lost around Ca14, just anterior to the start of the tail fin. It is in the context of this lateral flexibility that the lateral widening mid-tail can be interpreted (Fig 3.2). The long caudal ribs would have provided longer lever arms for muscles acting in this region, allowing powerful movement along the horizontal plane. In cetaceans, there is an increase in the depth of the mid-tail caused by an increase in the length of the chevrons (Fig 3.7). These chevrons are a point of attachment for tendons of m. hypaxialis lumborum, the primary muscle involved in ventral flexion of the tail (Pabst, 1990). The mechanical advantage created by the chevrons in this region has been noted by a number of authors (Slijper, 1961; Smith et al., 1976; Pabst, 1990). The primary direction of motion in the cetacean tail is along the sagittal plane, hence the difference in lever arm orientation versus plesiosaurs.

Cetacean locomotion is aided by a two-joint system (Fig 3.8) that allows the fluke to be moved independently from the anterior tail. The first joint occurs behind the lumbar region, which is stiff due to the presence of dorsal and ventral ligaments. These ligaments terminate in the anterior tail, giving flexibility to this region (McGowan, 1992). The second region of flexibility is created by large intervertebral spacing and convex articular surfaces (Rommel, 1990; McGowan, 1992). Both of these joints increase the flexibility of the tail along the sagittal plane. Similar two-joint systems, with flexibility caused by different adaptations to the axial skeleton, have been identified in scombroid
Figure 3.7- Partial vertebral column of *Delphinus delphis* showing an increase in chevron length mid tail. From (Van Beneden and Gervais, 1880).
Figure 3.8- The two-joint system in cetaceans, with a joint just behind the dorsal fin and one at the start of the tail fluke. From McGowan (1992).
fishes (such as the swordfish, *Xiphias gladius*) (Fierstine and Walters, 1968) and lamnid sharks (Reif and Weishampel, 1986). In these animals, flexibility is increased along the horizontal plane.

Like cetaceans, scombroid fishes, and lamnid sharks, plesiosaurs also appear to have a two joint system. These joints are created by changes in the length of the centra, the form of the articular surfaces, a reduction in caudal rib length, and a loss of zygapophyses. The first joint occurs at the base of the tail. The first few caudal centra have rounded edges and short caudal ribs. These short caudal ribs allow greater lateral excursions of the tail, as movement will be less limited by occlusion of the caudal ribs. The flexibility in this region is also increased by a change in the relative length of the centra. VLI, or vertebral length index, is a measure of the relative length of the centra (Brown, 1981; O'Keefe and Hiller, 2006). VLI is calculated as: \[ VLI = 100 \left( \frac{l_v}{(H+W)^{0.5}} \right) \]. Using the measurements from Table 3.1, VLI was calculated and graphed along the caudal series (Graph 3.1). This demonstrates that VLI decreases dramatically after the sacrum. These short centra, along with the shortened caudal ribs and rounded edges of the centra, create a region of enhanced flexibility analogous to the first joint in other animals with a two joint system. Anterior to the second joint, there is another decrease in VLI near Ca7. This does not seem to represent a joint, as the caudal ribs in this region are long and their occlusion would greatly limit lateral flexibility. Lateral flexibility in this region is also limited by interlocking zygapophyses. Posterior to this, near Ca14, is where the second joint in the tail occurs. VLI decreases rapidly (Table 3.1) in this area, due to a relative shortening of the centra. Flexibility is also increased by the loss of
Graph 3.1- Changes in VLI through the caudal series in R 8575.
zygapophyses at Ca14. The increased flexibility created by both these features contributes to this second joint within the tail.

The presence of a two joint system in cetaceans, scombroid fishes, lamnid sharks and plesiosaurs allows for separate movements of the tail and fluke. The purpose of this two-joint system seems to be to allow the tail fluke to “maintain an acute angle of attack relative to the water flow” regardless of the position of the tail (McGowan, 1992:p. 564). This allows the lift-based forces generated by the hydrofoil cross section of the tail fin to be directed forward while the tail oscillates.

The plesiosaur tail shares another similarity to cetaceans, scombroid fishes, and lamnid sharks in the presence of a peduncle. In cetaceans, the peduncle is a rapid lateral narrowing of the tail occurring just before the fluke (Fig. 3.9). This narrowing is created by lateral compression of the vertebrae, just before the vertebrae become dorso-ventrally compressed in the fluke (Rommel, 1990). In scombroid fishes and lamnid sharks, there is a dorso-ventral compression of the tail anterior to the fluke. These changes in width or depth streamline the tail in the direction of oscillation, reducing the effort necessary to move the tail during propulsion (Lighthill, 1967; 1970). A narrower peduncle is associated with more rapid movements of the tail in fast swimming animals such as dolphins (Fish and Hui, 1991). In Cryptoclidus, anterior to the start of the tail fin, there is a reduction of neural spine and chevron length, resulting in a decrease in the depth of the tail. This streamlines the tail, aiding in lateral movement. This peduncle is not as dramatic as the changes in width or depth seen in other animals with a peduncle, indicating that movement of the tail was not as rapid in plesiosaurs.
Figure 3.9- Body outline of the Bottlenose dolphin, *Tursiops truncates*, showing the form of the peduncle (p). Redrawn from Fish and Hui (1991).
The similarities between plesiosours, cetaceans, scombroid fishes, and lamnid sharks indicates that plesiosours were capable of producing thrust through lateral oscillations of the tail. The direction of this thrust could be directed through the center of mass regardless of the position of the tail, as the two-joint system allows the tail fin to be moved independently. The lateral movements of the tail necessary for generating this propulsion would have been aided by robust and long caudal ribs, which may have attached to muscles such as the caudifemoralis and isciocaudalis (Robinson, 1977). These muscles would have great mechanical advantage due to the long level arms created by the long caudal ribs.

In addition to producing thrust through oscillations of the tail, the tail fin may have also generated downward forces due to its form. In sharks, where the upper lobe of the fluke is supported by skeletal elements, greater flexibility in the lower lobe is thought to create upward thrust (Alexander, 1965). In plesiosours, where the upper portion of the fin is more flexible, a downward force is expected to be produced. This may possibly be used to overcome buoyancy, or to counteract lift generated by the limbs. Work on the tail fin in sharks has shown that the forces generated by the heterocercal tail are more complex than originally thought and may vary between shark species based on the exact shape and flexibility within the fin (Wilga and Lauder, 2002). Determining the non-thrust forces generated by the plesiosaur tail fin may be difficult without knowing more about its flexibility.

Along with production of thrust, lateral movements of the tail could also be for ruddering. When positioned laterally, the tail would create drag at the end of the animal, behind the center of mass. The tail could be used in this manner to counteract the
ruddering caused by movements of the neck, or used along with these movements to
generate rapid turns. This ruddering ability has implications for the movement of the
limbs during locomotion. Sea turtles are the only other animal besides plesiosaurs in
which all four fins are developed into hydrofoils. However, only the front pair generates
propulsion while the rear pair is used in ruddering (Walker, 1971). Four winged flight in
plesiosaurs may be possible by partially transferring responsibility for ruddering from the
rear limbs to the tail, allowing for a simplified flight stroke. No matter what the exact role
of the tail fin during locomotion is, its presence in juveniles and adults indicates that it is
functionally relevant at all life-stages.

**Other implications of a tail fin in plesiosaurs** - The caudal anatomy of
*Cryptoclidus* also has other implications for plesiosaur anatomy. The agreement
between the hypothesized form of the tail fin and that thought to be preserved in the
holotype of *Seeleysaurus guilelmiimperatoris* suggests that this soft tissue impression is
real. Soft tissue evidence can be faked during preparation (McGowan, 1992) and the
legitimacy of the impression in *Seeleysaurus* can no longer be directly determined, as
the specimen has been reported by Grossman (2006) as being covered in paint. The
validity of this soft tissue preservation bears relevance beyond the caudal region, as this
specimen preserves impressions along the posterior portion of the right forelimb
suggesting a flexible trailing edge (Robinson, 1975). Similar impressions have been
noted, but in a limited number of specimens (Huene, 1923). Evidence of this flexible
trailing edge is important, as a limb of this form has a hydrofoil shape, a feature crucial
to underwater flight (Robinson, 1975).
The flexibility at the base of the tail in plesiosaurs has not been described before and is important to the “archer's bow” theory. Robinson (1977) proposed that the pectoral and pelvic girdles, along with the gastralia, are held in tension by muscles and ligaments attached to the vertebral column. Such a system was hypothesized to add rigidity to the trunk. This would lead to a rigid base of the tail, quite different from the situation observed in Cryptoclidus. It appears the girdles and gastralia were not held in tension, although the trunk was likely still rigid due to the expanded girdles.

**Future Work** - Evidence for a tail fin in plesiosaurs has now been found in Seeleysaurus, Rhomaleosaurus, Cryptoclidus and Muraenosaurus. The presence of a tail fin in both Cryptoclidus and Muraenosaurus, indicates that this may be a feature of all cryptocleidoids. This may help explain the pathologies of the caudal region observed in another cryptocleidoid, Pantosaurus striatus (see chapter 2). The presence of a pygostyle in Umoonasaurus may also indicate this taxon had a tail fin as well. Examination of other caudal regions in different clades is necessary to verify whether this feature is found in all plesiosaurs; restricted to more basal plesiosaurs; or derived independently in different clades. The presence of this feature in elasmosaurs is of particular interest, as it could further inform about the role of this structure. Elasmosaurs are characterized by a long neck, so if the tail fin is used to counteract ruddering effects from movements of the neck it would be expected to be large in these groups. However, if it is used for active thrust production it might be reduced if they were slow swimmers (O'Keefe, 2001b).

The hydrodynamics of the caudal region in plesiosaurs is another area of potential research. Using a scale model of a plesiosaur in a flow tank (Vogel, 1981) the
flow of water over the caudal region can be observed to observe features such as turbulence. The magnitude of forces generated by lateral movements of the tail and neck could also be quantified. Hydrodynamic properties of this region may support either ruddering or thrust generation as the primary function of the tail.

**Conclusion**

Evidence from two exceptionally well preserved caudal skeletons of the cryptocleidoid plesiosaurs *Cryptoclidus eurymerus* and *Muraenosaurus leedsii* demonstrates that these taxa most likely had a tail fin. Features of the distal tail including an increase in the height of the neural spines, long and wide distal ends for articulation with cartilage, a change in neural spine direction, and lateral compression all allow some inference of shape in the plesiosaur fin. In addition, similarities observed between cetaceans, scombroid fishes, and lamnid sharks indicate regions of enhanced flexibility that allow the tail fin to be moved independently of the tail. These data strongly suggest that the tail was involved, along with the limbs, in active thrust production during plesiosaur locomotion.
### Table 2.1. Measurements (in mm.) of centra preserved in USNM 536965. Roman numerals are the order of vertebrae from anterior to posterior. Arabic numbers are field numbers.

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TABLE 3.1. Measurements (in mm.) of centra preserved in R 8575. VLI calculated as in Brown (1981) and O'Keefe and Hiller (2006). The first two sacral vertebrae are not included, as they are stuck together by matrix.

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References


Grossman, F. 2006. Taxonomy, phylogeny and palaeoecology of the plesiosauroids (Sauropterygia, Reptilia) from the Posidonia shale (Toarcian, Lower Jurassic) of Holzmaden, south west Germany. Unpublished PhD dissertation, der Geowissenschaftlichen Fakultät der Eberhard-Karls-Universität Tübingen,


