Osteology and relationships of a plesiosaur (Sauropterygia) from the Thermopolis Shale (lower Cretaceous) of Montana
by Patrick Scott Druckenmiller

A thesis submitted in partial fulfillment of the requirements for the degree Of Master of Science in Biological Sciences
Montana State University

Abstract:
A recently discovered plesiosaur, MOR 751, from the upper Thermopolis Shale (upper Albian) from south-central Montana is described. The specimen occurs in marine sediments deposited during an early transgression of the Western Interior Seaway and provides new information regarding plesiosaur diversity and distribution during Albian time. Detailed examination of the well preserved skull, neck and anterior paddle suggests that MOR 751 may represent a new taxon. A phylogenetic analysis using skull and neck characters is performed in order to establish the relationships of MOR 751 to other well known Jurassic and Cretaceous plesiosauroid and pliosauroid taxa. The results of this cladistic analysis suggest that MOR 751 is the sister taxon to a clade comprising upper Cretaceous polycotylids plus traditional plesiosauroid taxa, not Jurassic pliosaurids. The traditional concept of the Pliosauroidea is thus paraphyletic. MOR 751 is plesiomorphic with respect to polycotylids in that it possesses a relatively robust and moderately elongated rostrum, a pineal foramen, caniniform teeth, a shorter mandibular symphysis, and an increased number of cervical vertebrae.

OSTEOLOGY AND RELATIONSHIPS OF A PLESIOSAUR (SAUROPTERYGIA) FROM THE THERMOPOLIS SHALE (LOWER CRETACEOUS) OF MONTANA

by

Patrick Scott Druckenmiller

A thesis submitted in partial fulfillment
of the requirements for the degree
of
Master of Science
in
Biological Sciences

MONTANA STATE UNIVERSITY-BOZEMAN
Bozeman, Montana

November 1998

APPROVAL

of a thesis submitted by

Patrick Scott Druckenmiller

This thesis has been read by each member of the thesis committee and has been found to be satisfactory regarding content, English usage, format, bibliographic style, and consistency, and is ready for submission to the College of Graduate Studies.

John R. Horner — John R Horner (Signature) — 11/23/98 Date

Approved for the Department of Biology

Ernest Vyse — E R Vyse (Signature) — 11/23/98 Date

Approved for the College of Graduate Studies

Joseph J. Fedock, PhD — Joseph J. Fedock (Signature) — 12/15/98 Date

STATEMENT OF PERMISSION TO USE

In presenting this thesis in partial fulfillment of the requirements for a master's degree at Montana State University-Bozeman, I agree that the Library shall make it available to borrowers under rules of the Library.

If I have indicated my intention to copyright the thesis by including a copyright notice page, copying is allowable only for scholarly purposes, consistent with "fair use" as prescribed in the U.S. Copyright Law. Requests for permission for extended quotation from or reproduction of this thesis in whole or in parts may by granted only by the copyright holder.

Signature ______________________

Date 11.23.98

The earth was not unlike the ocean, when its restless waters are heaving heavily, after the agitation and fury of the tempest have begun to lessen. There was the same waving and regular surface, the same absence of foreign objects, and the same boundless extent to the view. Indeed, so very striking was the resemblance between the water and the land, that, however much the geologist might sneer at so simple a theory, it would have been difficult for a poet not to have felt, that the formation of one had been produced by the subsiding dominion of the other.

From:
The Prairie
James Fenimore Cooper
1827

ACKNOWLEDGEMENTS

Funding was provided by Gail and Roland Johnson, Barbara Lee, Jack Horner and Jean and Stan Druckenmiller. Department of Biology Chairmen Robert Moore and Ernie Vyse were very helpful in securing Graduate Teaching Assistantships for me as well. Thanks to the Desavier, Tilstra, Newton and Bequette families for granting me access to their land. The project would not have been possible without the discovery of the specimen by Doug Tingwall and Buck Damone who collected the skeleton with Ken Olson.

Celeste Horner offered computer advice and Glen Daleo kindly provided CT scan images of the specimen. I spent valuable field time with Karen Porter, and Bill Cobban kindly identified ammonite specimens. Betsy Nicholls reviewed drafts and provided invaluable help and support in my education of marine reptiles.

To the many other people who offered guidance and support, I would like to thank The Museum of the Rockies paleontology staff and students, and the Camp Makela staff and field school participants. I would like to acknowledge the patience and advice of my committee members Matt Lavin, Calvin Kaya as well as Jack Horner who provided me with an opportunity to study non-dinosaurs at the museum. Finally, a special thanks to my parents for supporting me and my interests over the years.

TABLE OF CONTENTS

Page

TABLE OF CONTENTS--Continued

LIST OF TABLES

LIST OF FIGURES

LIST OF FIGURES--Continued

ABSTRACT

A recently discovered plesiosaur, MOR 751, from the upper Thermopolis Shale (upper Albian) from south-central Montana is described. The specimen occurs in marine sediments deposited during an early transgression of the Western Interior Seaway and provides new information regarding plesiosaur diversity and distribution during Albian time. Detailed examination of the well preserved skull, neck and anterior paddle suggests that MOR 751 may represent a new taxon. A phylogenetic analysis using skull and neck characters is performed in order to establish the relationships of MOR 751 to other well known Jurassic and Cretaceous plesiosauroid and pliosauroid taxa. The results of this cladistic analysis suggest that MOR 751 is the sister taxon to a clade comprising upper Cretaceous polycotylids plus traditional plesiosauroid taxa, not Jurassic pliosaurids. The traditional concept of the Pliosauroidea is thus paraphyletic. MOR 751 is plesiomorphic with respect to polycotylids in that it possesses a relatively robust and moderately elongated rostrum, a pineal foramen, caniniform teeth, a shorter mandibular symphysis, and an increased number of cervical vertebrae.

INTRODUCTION

Introduction

One of the most successful groups of extinct Mesozoic marine reptiles were the plesiosaurs (Diapsida: Sauropterygia). These large, predatory reptiles first appeared in the uppermost Triassic, rapidly achieved world-wide distribution and became extinct by the end of the Cretaceous (Maastrichtian) (Welles, 1962; Storrs, 1997). The plesiosaur body plan represents a novel morphology secondarily adapted for life in an aquatic environment (Storrs, 1993). The group is characterized by limb-dominated (paraxial) propulsion through the use of two pairs of large, hyperphalangic limbs (Taylor, 1981; Massare, 1988; Nicholls and Russell, 1991). This locomotor adaptation was unique among contemporary aquatic diapsid reptiles which relied on lateral undulation of the tail (e.g., ichthyosaurs), or body (e.g., mosasaurs and marine crocodilians).

The monophyly of the Plesiosauria has been confirmed by numerous cladistic analyses (Sues, 1987; Tschanz, 1989; Storrs, 1991). Within the Plesiosauria, two superfamilies have been traditionally recognized; the Plesiosauroidea and the Pliosauroidea (Welles, 1943) (Figure 1). The plesiosauroids are characterized by cranial features such as a small skull relative in size to the torso, a short mandibular symphysis bearing the first pair of dentary alveoli only, and teeth with slim crowns. Postcranial features also include relatively short ischia, short propodials with the humerus longer than the femur and a tendency to increase the number of cervical vertebrae, giving rise to the popular name for the group, the "long-necked plesiosaurs".

ORDER: Plesiosauria

Superfamily: PLESIOSAUROIDEA

Family: Plesiosauridae
Plesiosaurus dolichodeirus

Family: Cryptoclididae
Cryptoclidus eurymerus

Family: Elasmosauridae
Muraenosaurus leedsi
Libonectes morgani

Superfamily: PLIOSAUROIDEA

Family: Pliosauridae
Rhomaleosaurus megacephalus
Liopleurodon ferox
Peloneustes philarchus
Pliosaurus brachyspondylus
Leptocleidus capensis

Family: Brachaucheniidae
Brachauchenius lucasi

Family: Polycotylidae
Trinacromerum bentonianum
Dolichorhynchops osborni

Figure 1. Traditional classification of selected plesiosaurs, modified from Brown (1981) and Carpenter (1997).

In contrast, the pliosauroids are characterized by relatively large skulls, a long mandibular symphysis bearing several pairs of dentary alveoli, and broad crowned teeth. The postcrania typically have relatively long ischia, long and narrow propodials with the femur longer than the humerus and a trend to decrease the number of cervical vertebrae, hence the name for the group, the "short-necked plesiosaurs".

Traditionally, workers approached the classification of a new plesiosaur taxon by lumping it into either superfamily based on a quick analysis of overall morphology. Attempts to further refine relationships have been limited only to comparisons with other forms within that superfamily (Welles, 1943; Brown, 1981; Tarlo, 1960; Hampe 1992) This approach was based on the underlying assumption that both the pliosauroids and plesiosauroids represent monophyletic clades within the Plesiosauria.

Huge gaps in the spacial and temporal distribution of the Plesiosauria, however, limit our understanding relationships. As Storrs (1997) states, "The evolutionary and systematic relationships of the Plesiosauria are almost entirely unknown". The stratigraphic distribution of the group is known to span at least 145 million years, yet the vast majority of material to interpret their evolutionary history by, comes from relatively small windows of time in the Upper and Lower Jurassic of Europe and Upper Cretaceous of North America (Tarlo, 1960; Welles, 1962). Material from the Triassic, Middle Jurassic and Lower Cretaceous is either sparse, fragmentary or non-existent.

As a consequence of this scattered stratigraphic distribution, our understanding of character evolution is limited. Were similar character states acquired independently in two or more separate lineages? For example, the plesiosaur body plan is remarkably consistent in the proportions of the torso, limbs and caudal region but vary widely in neck length and skull size. Are neck length and skull size apomorphies of their respective clades or do they represent homoplasies, developed as a result of similar selective pressures in different clades?

Williston (1907, pg. 485) was the first to suggest the possibility of convergence. In reference to the shortened neck of some genera he stated his assumption that "... the shortened neck... has been acquired in more than one phylum [subfamily of today]". Important questions are therefore raised. Are the Upper Jurassic short-necked pliosaurids ancestral to Upper Cretaceous polycotylids or did short necks and large skulls evolve at least twice? Similarly, could the long neck and small skull of Cretaceous elasmosaurs have evolved independent of Jurassic long-necked taxa?

New preparation techniques, a reexamination of described forms and a reassessment of important characters have recently led several workers to question the long-held assumption of a monophyletic Pliosauroidea and/or Plesiosauroidea. In a discussion of cryptoclidid characters, Brown et al. (1994, pg. 950) states that an ongoing review of Lower Jurassic genera "is almost certain to overthrow the present superfamily and family divisions of the Plesiosauria".

Other workers have discussed the possibility that important characters of the skull and atlas-axis complex shared by some of the pliosauroids and plesiosauroids may suggest a closer relationship between the two groups than previously believed. Based on a comparative study of two Upper Cretaceous taxa, the polycotylid *Dolichorhynchops osborni* and the elasmosaurid *Libonectes morgani*, Carpenter (1997) hypothesized both families are sister groups that share a common plesiosauroid ancestor. In direct contrast, Bakker (1993) considers Upper Cretaceous polycotylids and elasmosaurids as descendants of a short-necked pliosaur clade that survived the Jurassic-Cretaceous boundary extinction.

While these hypotheses have yet to be fully tested in a extensive cladistic analysis an important point is raised. Comparisons of new taxa should be made with members of both superfamilies in order to limit the possible influences of convergence. The current study describes and compares a well preserved plesiosaur from the upper Thermopolis Shale of the Western Interior Basin to well known representatives of each plesiosaur family.

The Specimen

In the spring of 1993 a well preserved partial plesiosaur skeleton was discovered by Doug Tingwall and Buck Damone of Lewistown, Montana and was collected on September 27, 1993 with the assistance of Museum of the Rockies Associate Ken Olson, also of Lewistown. The specimen, designated MOR (Museum of the Rockies) 751, was found in the upper part of the Thermopolis Shale (Albian) in Carbon County, Montana, T 5 S, R 24 E, Section 28, on a small parcel of land owned by the U. S. Bureau of Land Management near the town of Edgar (Figure 2).

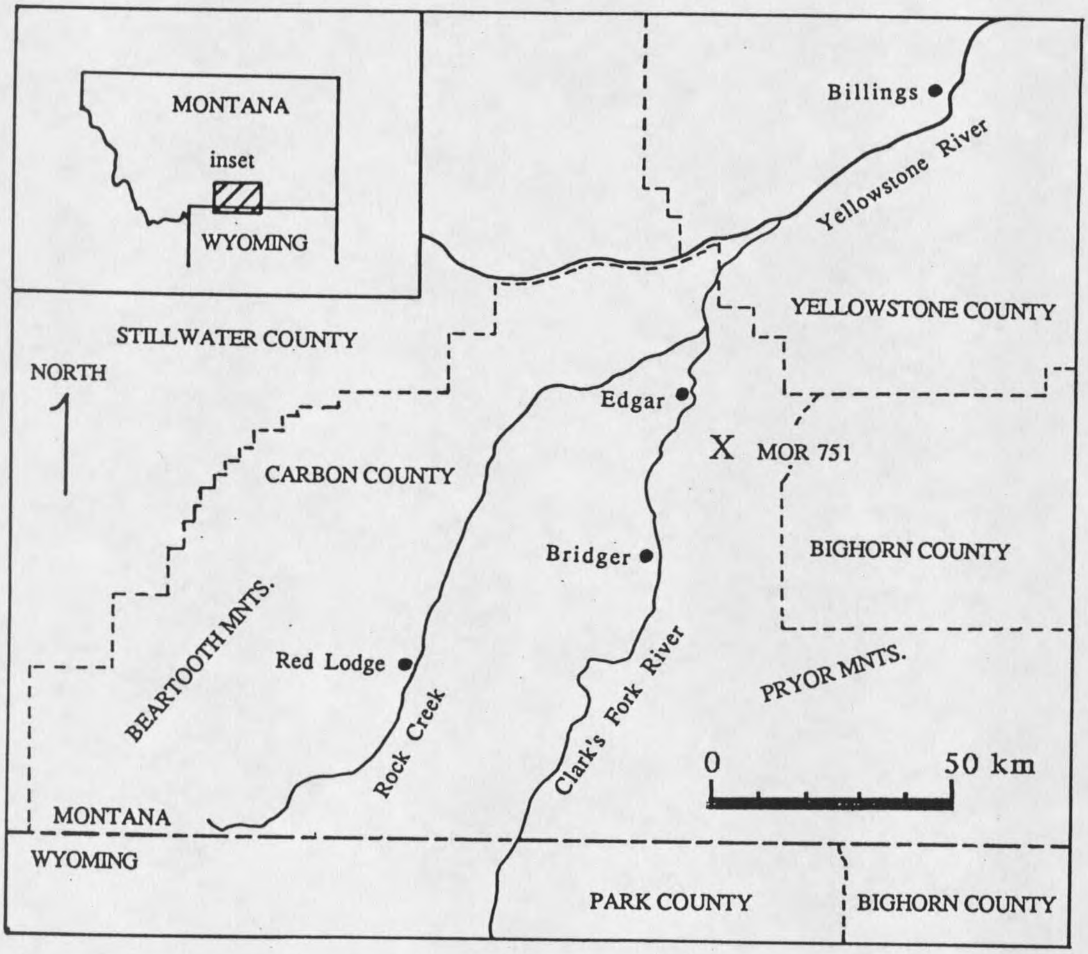

Figure 2. Locality map of MOR 751 in south-central Montana.

MOR 751 consists of a well preserved and complete skull, the entire series of 26 cervical vertebrae and most cervical ribs, three pectoral vertebrae, five anterior dorsal vertebrae and a paddle. The paddle, interpreted as the left forelimb, is nearly complete but lacks the proximal half of the propodial and part of the postaxial portion of the epipodial row. With the exception of a few, small associated fragments, the pectoral girdle is lacking.

In addition to the paddle, the proximal end of a plesiosaur propodial was found eroded out in the outwash slope below the excavation site. The fragment is clearly part of MOR 751 and is interpreted as the proximal portion of the left humerus.

The plesiosaur was preserved lying at an angle on its right, ventral surface, resulting in a slight oblique distortion of the skull. The neck curves to the left and twists so that the distal-most vertebrae are lying almost entirely on their right side. The skull and 25 cervical vertebrae were found in articulation. Nine other vertebrae, found as outwash, formed a continuation of the vertebral column, with the exception of three dorsal vertebrae which could not be confidently rearticulated to the series in original order. The paddle was found within a meter of the left posterior end of the vertebral column. It was presumably articulated with the rest of the skeleton before becoming isolated by erosion.

The specimen was preserved in a black, fissile mudstone matrix. A very hard, well indurated mudstone was found within the braincase and between most vertebrae. Internal pore spaces were permineralized with gypsum in addition to a tightly adhering gypsum layer which covered most exterior bone surfaces and lined larger fractures.

Preparation

Prior to mechanical preparation, the skull and articulated atlas, axis and vertebra three was sent to the San Diego Children's Hospital and scanned on a General Electric 9800 Computerized Tomography (CT) scanner. A series of 1 mm digital slices, with .5 mm of overlap between slices was created and saved on 8 mm digital tape. The images were processed on CEMAX medical software yielding a three dimensional computer image that could be manipulated to view internal and external structures of the skull.

Manual preparation began by removing the loose mudstone matrix from external surfaces down to the gypsum layer covering the bone. The gypsum was mechanically removed with a dental pick. Finally, an air abrasive unit using crushed corundum was employed to clean bone surfaces and remove the hard mudstone matrix within the braincase. Polyvinyl acetate and cyanoacrylate glue were used as a bone hardener and adhesive, respectively.

During the course of preparation and study, much of the skull was disassembled into units in order to more easily see otherwise inaccessible portions of the skull, as well as facilitate preparation of the braincase. The main units include the anterior and posterior halves of the rostrum, the skull roof, braincase and posterior palate, the right and left suspensorium, the left cheek, the anterior dentary, and the left and right posterior dentaries. These units are easily reassembled and rest together in a plaster cradle.

Ontogeny

A determination of the ontogenetic state of MOR 751 is hampered by a lack of conspecific or congeneric material to compare with. However, changes in bone morphology correlated with different ontogenetic states have been identified in other plesiosaur genera for which a more complete growth series is known. In his review of upper Jurassic plesiosauroids, Brown (1981) defined three age classes based on the degree of fusion between the neural arches and cervical ribs with the centrum. In 'juveniles', fusion between the neural arches and centra has not occurred, while in 'adults', fusion is complete. In 'old adults' the neural arches and centra are fused, and additional characters of advanced ossification are seen.

The degree of separation between the capitulum and tuberosity (in the humerus) and trochanter (in the femur) can also be used to estimate growth stage. Brown (1981, pg. 334) states:

> "In 'juvenile' individuals the capitulum and tuberosity (or trochanter) are covered by a single sheet of cartilage, but as ossification proceeds the isthmus between them becomes reduced in width, and they may eventually become separated completely by a strip of periosteal bone in 'old adults'".

An examination of cervical vertebrae and ribs as well as the proximal propodial fragment of MOR 751 indicate a growth stage at, or nearly approaching the 'adult' state. The sutures between the neural arches and cervical ribs with the centrum remain visible, however ossification between these elements appears to have progressed in all but the anterior cervical ribs. On the proximal humerus only a narrow isthmus connects the capitulum to the tuberosity, indicating an 'adult' state.

Significance

MOR 751 is significant in several regards. First, the specimen is very well preserved and only moderately distorted allowing a detailed examination and description of the skull roof, braincase, palate as well as atlas and axis complex to be made. Based on a comparative analysis, MOR 751 differs significantly in its skeletal morphology from other described plesiosaurs and may represent a new taxon.

Secondly, the stratigraphic position of MOR 751 is of interest and importance. The vast majority of North American plesiosaur remains are known from Upper Cretaceous strata deposited in the Western Interior Basin. The occurrence of MOR 751 in Albian rocks places it as one of the oldest known plesiosaurs from the Cretaceous of North America. As such, it helps bridge the gap in knowledge of plesiosaur diversity and morphology between North American and European Jurassic taxa.

Finally, throughout most of the Late Cretaceous, the Western Interior Seaway was home to a diverse assemblage of marine reptiles whose temporal and spatial distributions are well documented. The Thermopolis Shale represents deposits from the initial marine transgressions of that seaway into North America. The occurrence of MOR 751 in the Thermopolis may help elucidate paleobiogeographic patterns that were becoming established within the seaway at that time.

Purpose

In this study two primary questions are posed. First, is MOR 751 a previously described taxon or is it new? Secondly, what is its closest sister group? In order to address these questions, the following four objectives are proposed.

1. To provide an osteological description of the skull, vertebrae and paddle of MOR 751.
2. To use this new morphologic data to assemble a suite of characters useful in phylogenetic studies.
3. To perform a phylogenetic analysis using a cladistic methodology of MOR 751 and selected short and long-necked Jurassic and Cretaceous plesiosaurs.
4. To compare this phylogeny to traditional and recently proposed hypotheses of plesiosaur relationships.

It is hoped that this work will contribute to recent work on plesiosaur distribution, morphology and phylogeny that is being undertaken by several workers (Storrs, 1997; Carpenter, 1997; Brown, 1994; Taylor and Cruickshank, 1993).

STUDY AREA AND STRATIGRAPHY

Study Area

The study area is located in the northern Bighorn Basin, a Laramide structural basin which was part of the larger Western Interior Basin during the Cretaceous (Thomas, 1965). The study area is located along a north-south axis parallel to the east side of the Clark's Fork River between the towns of Edgar and Bridger, Montana were good exposures of the Thermopolis are found (Figure 2). West to northwest dipping outcrops of the Thermopolis Shale are exposed beneath the overlying erosionally-resistant ridges of Mowry Shale.

Stratigraphic sections were measured at the type locality (T 5 S, R 24 E, Sec. 28), Black Butte (T 4 S, R 24 E, Sec. 20) approximately 10 kilometers north of the type locality and at Bridger Ridge (T 8 S, R 24 E, Sec. 14) approximately 37 kilometers south of the type locality. A complete section measured through the upper Thermopolis at Black Butte is presented in Figure 3.

Stratigraphy

MOR 751 occurs in the upper Thermopolis Shale, upper Albian marine deposits of the Cretaceous Western Interior Seaway. In the

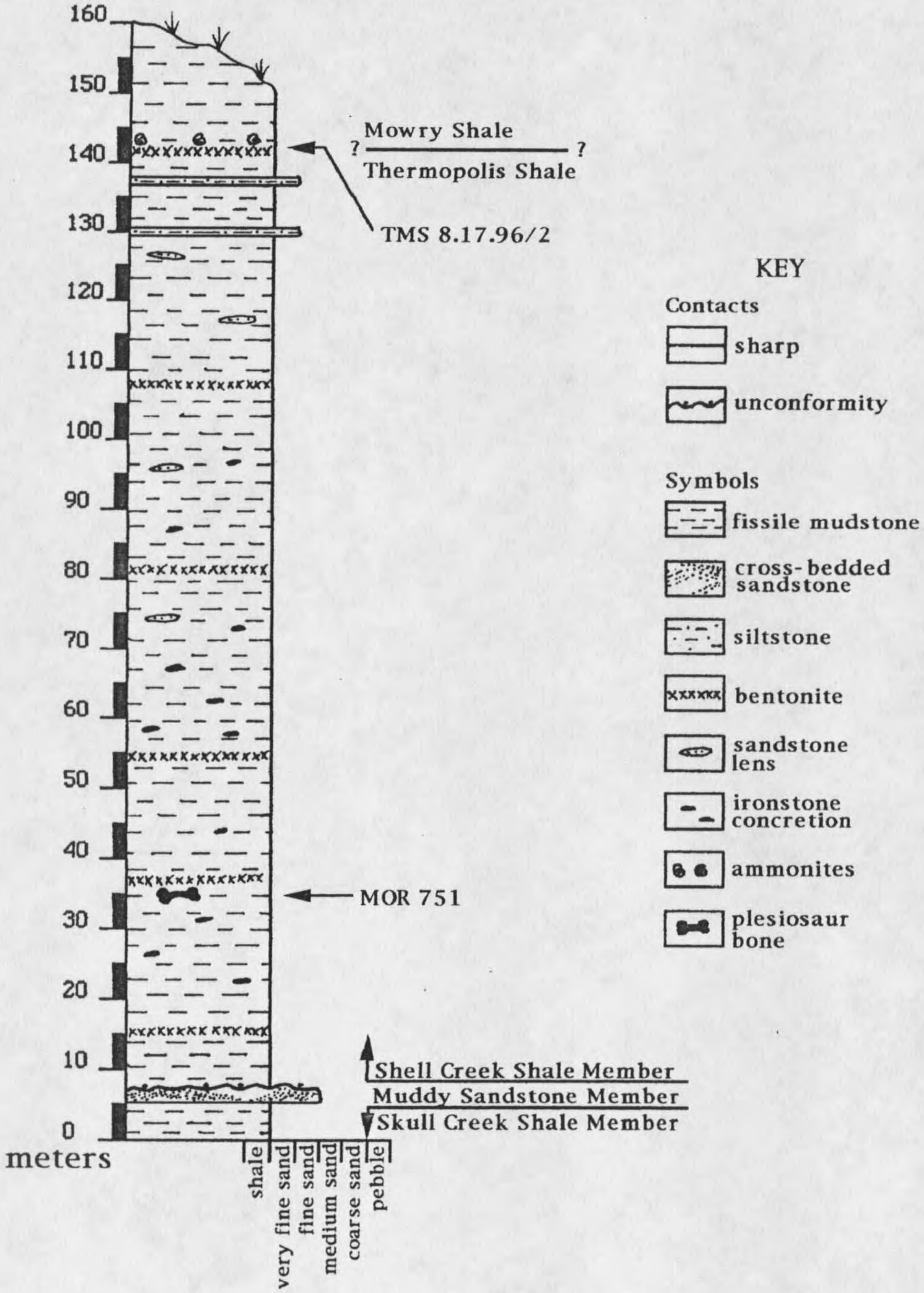

Figure 3. Measured section through the upper Thermopolis Shale (Shell Creek Member equivalent) at the Black Butte locality (T 4 S, R 24 E, Sec. 20), Carbon County, Montana.

study area the Thermopolis Shale is underlain by a sandy, near shore marine sequence locally known as the Dakota Sand, a Fall River Formation equivalent (K. Porter, pers. comm.). The Dakota Sand is unconformably bounded at its base by terrestrial deposits of the Kootenai (Cloverly) Formation. The Thermopolis is conformably overlain by marine shales and siltstones of the Mowry Shale.

The Thermopolis Shale can be divided into three units; a lower shale unit, the Skull Creek Member equivalent, a middle sandy unit the Muddy Sandstone Member equivalent, and an upper shale unit, the Shell Creek Member equivalent. This paper uses the term "Thermopolis Shale" to refer to all three units, in contrast to some studies restricting the term to only the lower shale (Eicher, 1960).

The Skull Creek Member is composed primarily of siltstones and black, fissile mudstones that are erosionally non-resistant and form valleys in the study area. Deposition of the Skull Creek Member equivalent records the initial transgression of a northern, boreal arm of the seaway into the Western Interior Basin (Vuke, 1984). The uppermost shales of this unit were deposited as the northern and southern arms of the seaway joined and spread the entire length of the North American continent for the first and only time in the Early Cretaceous (Eicher, 1960).

The Muddy Sandstone Member (Newcastle Sandstone equivalent) (Dyman, 1995), is a laterally persistent unit composed of sandstone, siltstone and shale. In the study area the Muddy Sandstone Member forms a distinctive, erosionally-resistant marker horizon within the Thermopolis, varying from 0-3 meters in thickness. Deposition of the Muddy Sandstone occurred in a variety of very shallow water marine environments following separation of the northern and southern arms of the sea during the Albian regression (Vuke, 1984).

An unconformity identifies the Muddy Sandstone contact with the overlying Shell Creek Member equivalent in the field area. The contact is distinguished by a conspicuous change in lithology, including a laterally extensive chert pebble conglomerate. This distinctive horizon also contains abundant small vertebrate remains including teeth and bones of sharks, teleost fish, turtles and marine reptiles. The unconformity is interpreted as a lowstand surface of erosion, sequence boundary 2 (SB2) (Porter et al., 1993 and Dolson et al., 1991). SB2 corresponds to a basin-wide, eustatically-controlled sea-level lowstand dated at 98.5 Ma (Mega annum or million years) or older (Obradovich, 1993).

The Shell Creek Member of the Thermopolis Shale is a black, fissile mudstone with abundant bentonite layers. The bentonites are especially prevalent in the lower section of this unit and may reach a meter or more in thickness. The black mudstones of the Shell Creek equivalent are overlain by the overlying siliceous mudstones of the Mowry Shale. Deposition of the Shell Creek occurred during the second major Albian transgression, however the northern and southern arms of the seaway did not reunite during this time (Vuke, 1984).

MOR 751 occurs in the Shell Creek Member equivalent, approximately 30 meters above the top of the Muddy Sandstone Member equivalent and corresponding unconformity, SB2. Ammonites (field number TMS 8.17.96/2), identified as

Neogastroplites haasi (W. Cobban, pers. comm.) were collected at the Bridger Ridge locality approximately 120 meters above the top of the Muddy Sandstone Member equivalent and approximately 90 meters above the MOR 751 horizon. *Neogastroplites haasi* represents the oldest of five zones of *Neogastroplites* and the few localities known have been found in the uppermost part of the Thermopolis Shale (Kauffman et al., 1993). Recently established radiometric dates using 40Ar/39Ar laser fusion approach of bentonites within the range of *N. haasi* have been determined at 98.54 +/- 0.70 Ma and 98.74 +/- 0.59 Ma (Obradovich, 1993). Thus, the approximate stratigraphic occurrence of MOR 751 is constrained by the age of the underlying unconformity, SB2 and overlying ammonite zone at 98.5 Ma - 99.0 Ma.

OSTEOLOGY

Skull Description

Dorsal Elements

The paired premaxillae form much of the anterior half of the preorbital region of the skull (Figures 4-9; Table 1). They meet along the dorsal longitudinal midline at a straight suture. There are six to seven alveoli on the left premaxilla and at least six on the right premaxilla which bear large, procumbent, slightly recurved, caniniform teeth. A lateral bulge on the premaxilla is present in the vicinity of alveolus three and four. On the left side of the skull the premaxilla-maxilla suture is digitate and runs posteromedially from the tooth row margin just posterior to alveolus six. Slender dorsal processes of the premaxillae extend caudad along the skull midline and unlike *Plesiopleurodon wellesi*, do not form the dorsal margin of the external nares. They separate the frontals and taper to their endpoint just anterior to the frontal-parietal suture. The anterior portion of the premaxilla is pitted and several nutrient foramina parallel the external dorsal tooth row on both the premaxilla and maxilla.

The maxilla is the major lateral element of the rostrum. Dorsally, it contacts the premaxilla along a straight suture up to the

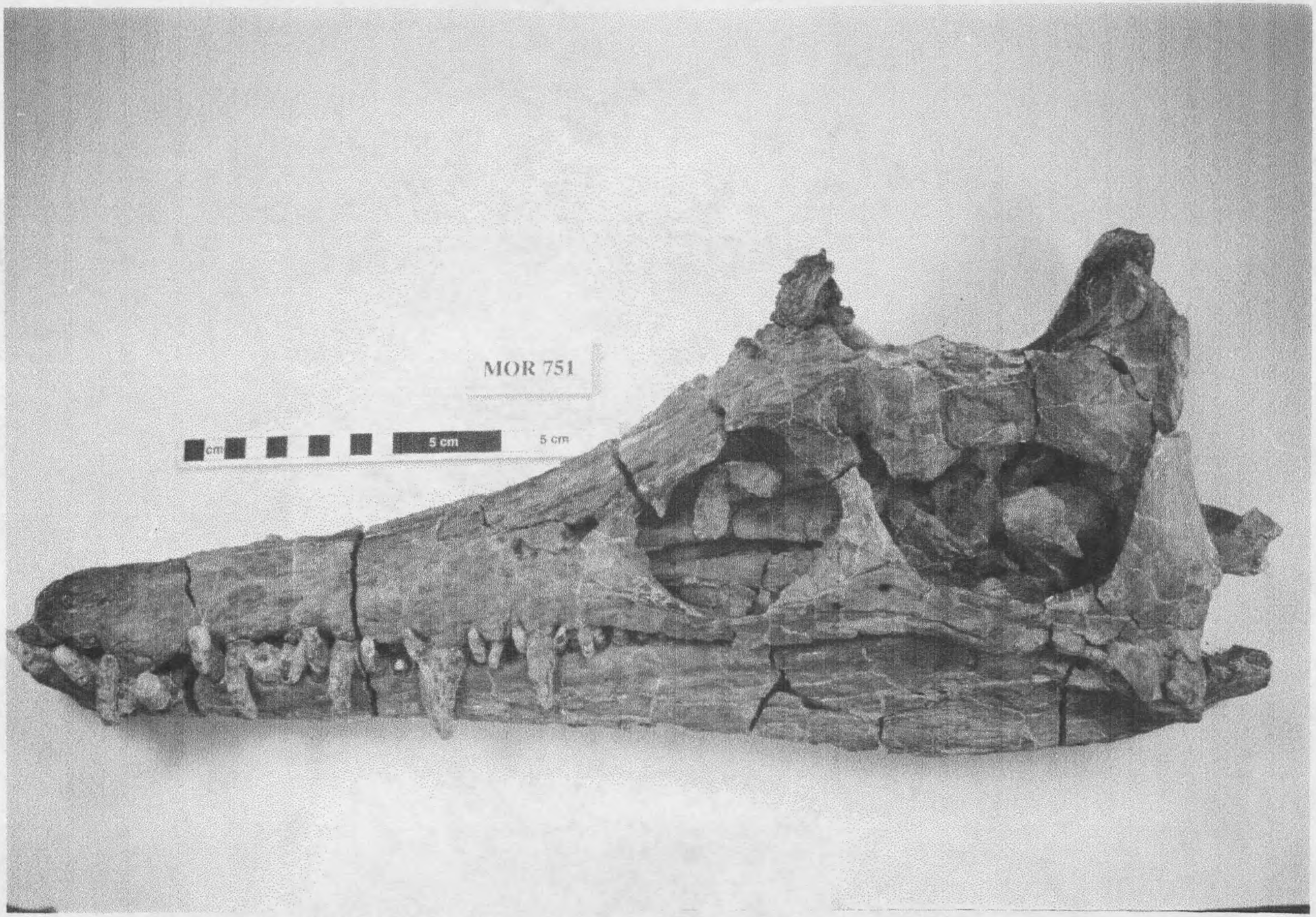

Figure 4. Skull of MOR 751, in left lateral view.

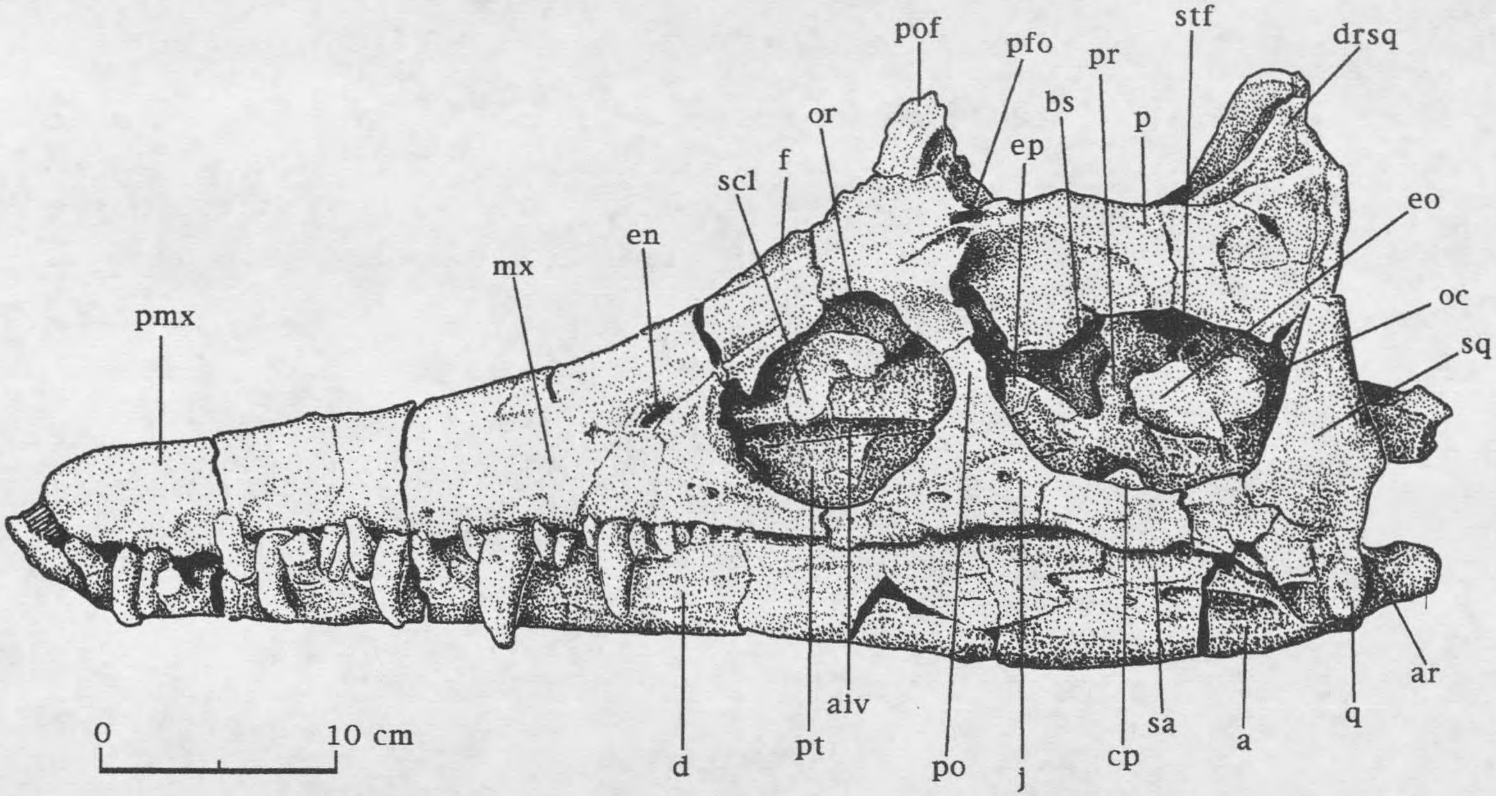

Figure 5. Interpretation of skull of MOR 751, in left lateral aspect. Abbreviations: a, angular; aiv, anterior interpterygoid vacuity; ar, articular; bs, basisphenoid; cp, coronoid process; d, dentary; drsq, dorsal ramus of squamosal; en, external nares; eo, exoccipital-opisthotic; ep, epipterygoid; f, frontal; j, jugal; mx, maxilla; oc, occipital condyle; or, orbit; p, parietal; pfo, pineal foramen; pmx, premaxilla; po, postorbital; pof, postfrontal; pr, prootic; pt, pterygoid; q, quadrate; sa, surangular; scl, sclerotic ring; sq, squamosal; stf, supratemporal fenestra.

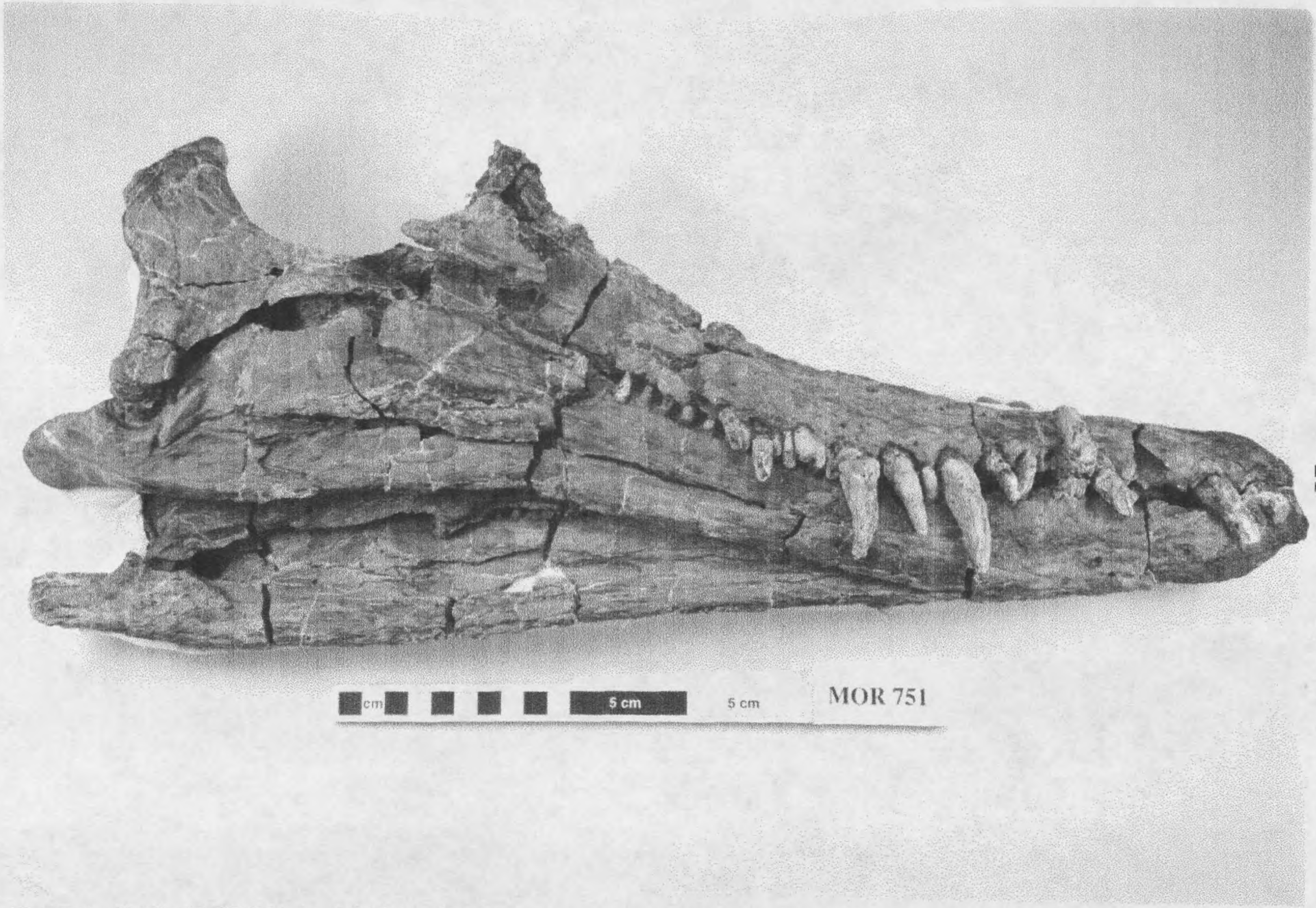

Figure 6. Skull of MOR 751, in right lateral aspect

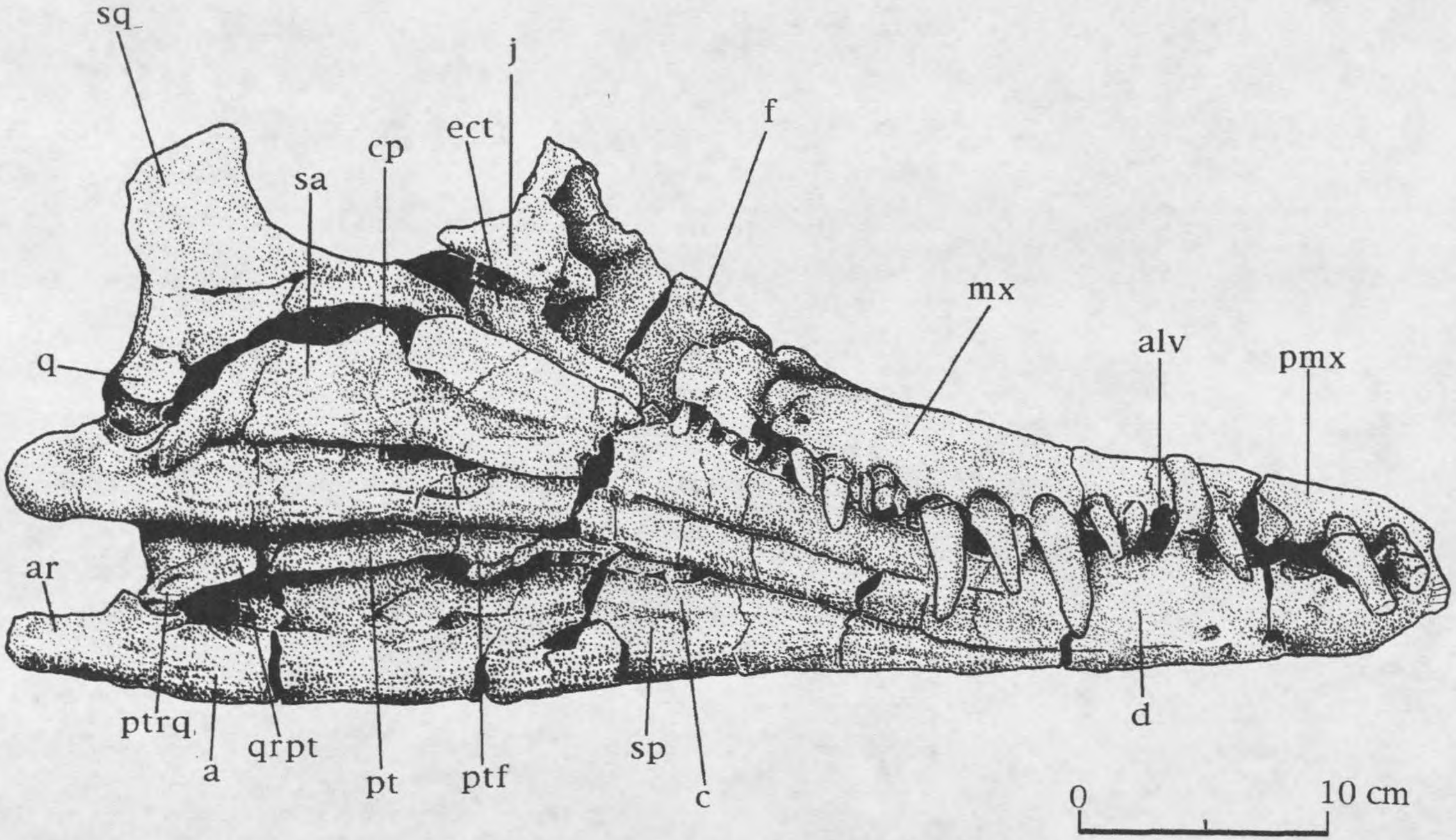

Figure 7. Interpretation of skull of MOR 751, in right lateral aspect. Abbreviations: a, angular; alv, alveolus ar, articular; c, coronoid; cp, coronoid process; d, dentary; ect, ectopterygoid; f, frontal; j, jugal; mx, maxilla; pmx, premaxilla; pt, pterygoid; ptf, pterygoid flange; ptrq, pterygoid ramus of quadrate; q, quadrate; qrpt, quadrate ramus of pterygoid; sa, surangular; sp, splenial; sq, squamosal.

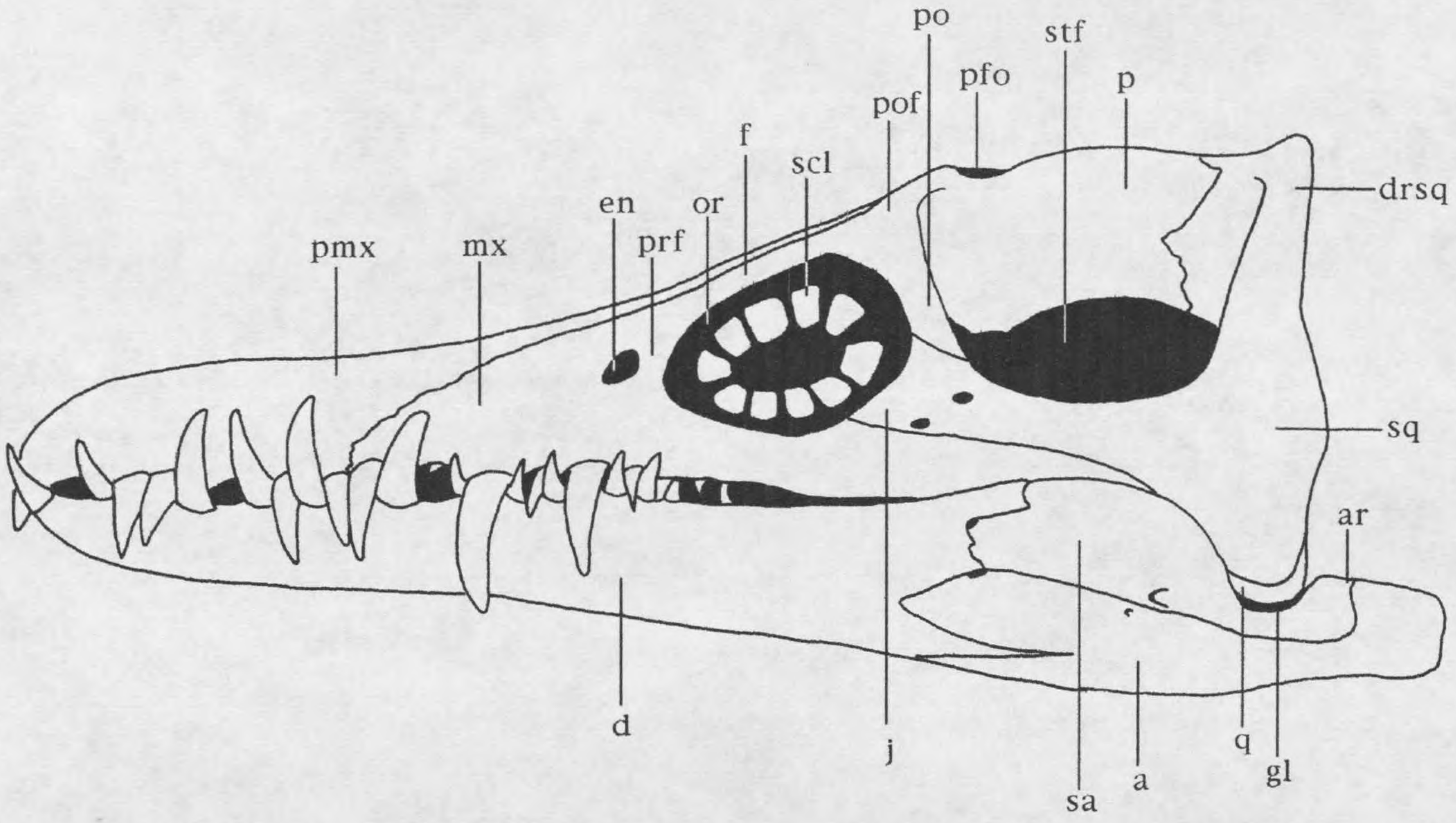

Figure 8. Reconstruction of skull of MOR 751, in left lateral aspect. Abbreviations: a, angular; ar, articular; d, dentary; drsq, dorsal ramus of squamosal; en, external nares; f, frontal; gl, glenoid fossa; j, jugal; mx, maxilla; or, orbit; p, parietal; pfo, pineal foramen; pmx, premaxilla; po, postorbital; pof, postfrontal; prf, prefrontal; q, quadrate; sa, surangular; scl, sclerotic ring; sq, squamosal; stf, supratemporal fenestra.

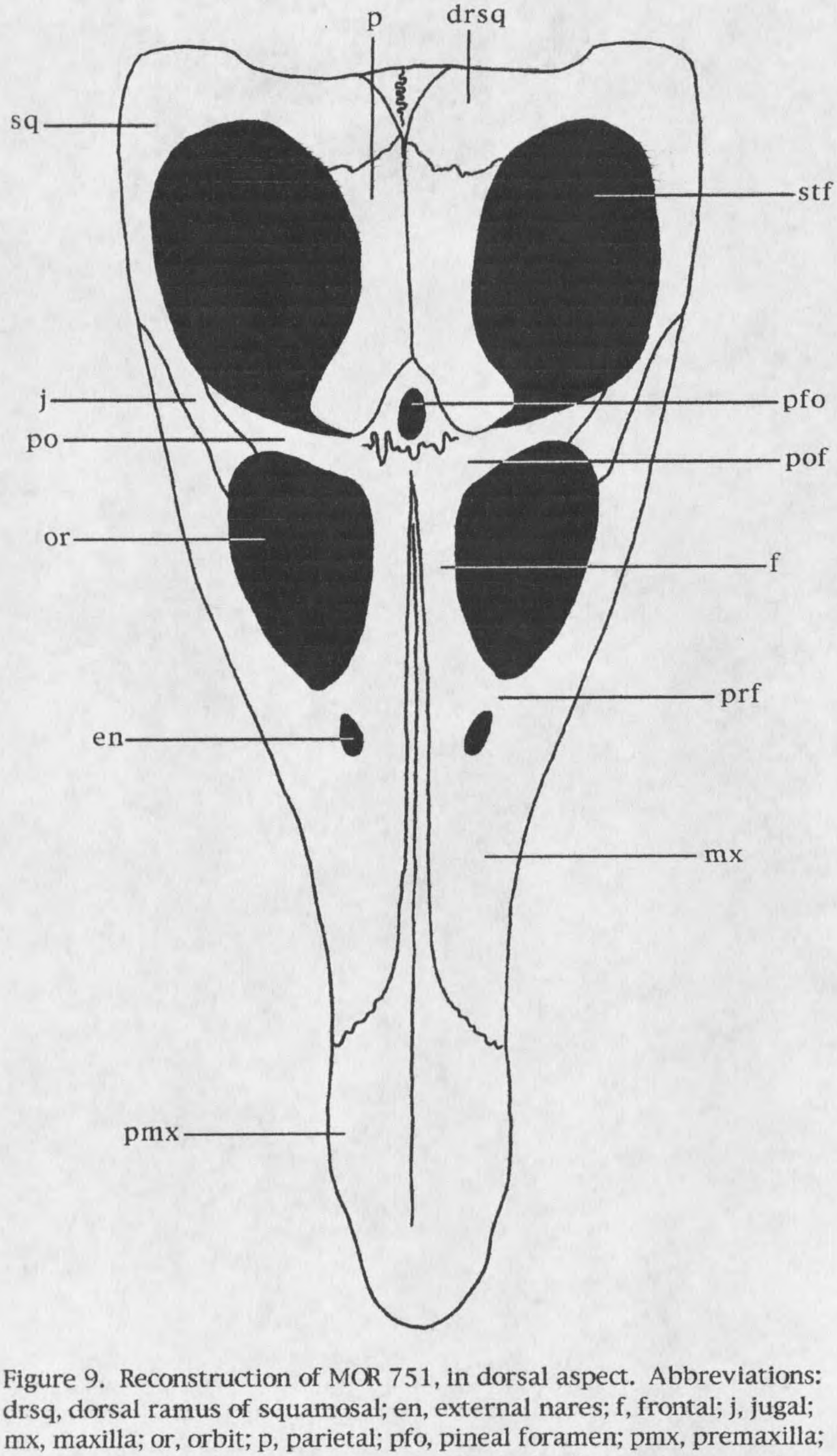

Figure 9. Reconstruction of MOR 751, in dorsal aspect. Abbreviations: drsq, dorsal ramus of squamosal; en, external nares; f, frontal; j, jugal; mx, maxilla; or, orbit; p, parietal; pfo, pineal foramen; pmx, premaxilla; po, postorbital; pof, postfrontal; sq, squamosal; stf, supratemporal fenestra.

Table 1. Selected skull dimensions of MOR 751.

Measurement	Dimensions (in mm)
Skull length (rostrum to quadrate)	475
Rostrum length (rostrum to anterior orbit margin)	255
Supratemporal fenestra length (on dorsal midline)	115
Subtemporal fenestra length	105
Orbit length	87
Estimated skull width	?150
Pineal foramen length	10
Left maxillary tooth row length	245
Left premaxillary tooth row length	115
Maximum maxillary tooth crown height	49
Anterior interpterygoid vacuity length	68
Posterior interpterygoid vacuity length	61
Braincase length (sella turcica to occipital condyle)	84
Braincase width (between prootics)	?23
Right paraoccipital process length	45
Average sclerotic plate height	12
Average sclerotic plate width	12
Mandibular symphysis length (ventral surface)	145
Mandible length	520
Retroarticular process length (posterior to glenoid)	40
Coronoid process height	75
Dentary tooth row length	360
Left glenoid fossa width	30
Hyoid length	47

region of the external nares. The right naris is crushed nearly shut , while the left is largely undistorted. Here the maxilla can be seen to form at least the anterolateral corner of the naris. The region between the external nares and the orbits is poorly preserved. The presence of a prefrontal is uncertain. Likewise, it is not possible to detect the lachrymal, whose presence in plesiosaurs is problematical and may be lacking in sauropterygians altogether (Storrs, 1991). The maxilla appears to form the poorly preserved ventral rim of the orbit and continues caudad into a long, slender posterior ramus which extends to the midpoint of the ventral surface of the temporal bar. The left maxilla has 26 alveoli which diminish in size caudad. A total right maxillary tooth count is not possible due to crushing.

The frontals are separated along the dorsal midline by the dorsal processes of the premaxilla. The anterior extent of the frontal is uncertain due to poor preservation in the region of the external nares. It is also unclear whether the frontals form the dorsal rim of the orbit or if this border is shared by the prefrontals. The frontal-parietal contact is marked by a deeply digitate suture which is positioned in line with the posterior margin of the orbits. Thin, blade-like processes of the frontals extend and meet ventrally, forming a bony septum between the orbits. The lateral walls of the olfactory sulcus, present as a medial groove or foramen, is housed in these ventral processes (Carpenter, 1997).

The bones of the cheek region are poorly preserved. Both postorbital bars are present but the right side has been distorted and crushed medially and dorsally while the left side is largely intact but partially obscured by a hard, dense matrix. The postorbital separates the orbit anteriorly from the supratemporal fenestra posteriorly. The position and shape of the postorbital-postfrontal suture cannot be discerned. Along its ventral surface the postorbital contacts the jugal near the base of the postorbital bar along an oblique, straight suture running anterodorsally to posteroventrally. A thin flange runs along the medial surface of the postorbital bar forming a partial internal wall between the orbit and the supratemporal fenestra.

The exact size and shape of the postfrontal is uncertain. Its inferred position lies at the dorsolateral corner of the orbits, bounded by the postorbital laterally and ventrally, the supratemporal fenestra posteriorly, the parietal medially and the frontal anteriorly. A low crest runs roughly parallel to the longitudinal midline of the skull in this region. Similar crests have been described on the postfrontal in *Pliosaurus brachyspondylus* (Taylor and Cruickshank, 1993) and in *Rhomaleosaurus zetlandicus* (Taylor, 1992a).

The jugal lies at the intersection of the postorbital bar with the lateral temporal bar. The left jugal is well preserved and intact, while the right is incomplete and partially displaced. The jugal forms the posterolateral margin of the orbit and the anterolateral margin of the supratemporal fenestra. The maxilla bounds the jugal ventrally. Posteriorly, the contact with the squamosal is unclear although the jugal appears to form at least the anterior half of the rim of the lower temporal bar. Both jugals are perforated by two conspicuous foramina at the base of the postorbital bar.

The parietals are large bones forming most of the dorsomedial walls of the supratemporal fenestra. A conspicuous pineal foramen is situated just posterior to the frontal-parietal suture in a position in line with the anterior margin of the supratemporal fenestra. In CT images the pineal foramen can be seen to perforate the parietal, sloping ventrally and posteriorly from its dorsal opening. Dorsally, the parietals meet along the midline to form a distinct sagittal crest that then slopes steeply ventrolaterally to form the medial walls of the supratemporal fenestra. The parietals form the roof of the braincase and, along the ventral midpoint, contact the supraoccipital.

A thickened flange on the anteroventral corner of the parietal probably allowed for a ligamentous contact with the epipterygoid although this contact is now lost due to crushing.

The parietal-squamosal suture extends from a point along the apex of the posterior third of the sagittal crest and runs ventrolaterally along the medial wall of the supratemporal fenestra. This contact is defined as a narrow zone of thickened, ankylosed bone on both the dorsolateral and ventromedial surfaces of the parietal. It can also be seen as a distinct change in bone fiber orientation between the posterior margin of the parietal and the anterior edge of the dorsal ramus of the squamosal similar to that described by Taylor (1992) for *Rhomaleosaurus zetlandicus*. The squamosals overlap the parietals dorsally along this contact. This overlapping contact is also apparent in CT images.

The suspensorium of MOR 751, composed of the squamosal and quadrate, forms a rigid brace between the skull roof and the glenoid fossa. Notably, the suspensorium is oriented along the vertical axis, not inclined anteriorly as in *Trinacromerum bentonianum* and *Plesiopleurodon wellesi* (Carpenter, 1996).

The squamosals form the posterior and part of the lateral walls of the supratemporal fenestra. The dorsal ramus of the squamosal meets its opposite at a digitate suture along the dorsal midline. Together, the posterior portion of the parietals and the dorsal ramus of the squamosal form a shelf which overhangs the back of the skull and extends posteriorly beyond the occipital condyle, nearly as far as the point of articulation between the axis and vertebra three.

The anterior ramus of the squamosal forms part of the posterior portion of the lateral temporal bar. An arm of the squamosal extends anteriorly to contact the jugal although the location of this contact is uncertain due poor preservation in that region.

The quadrate ramus of the squamosal is split into ventromedial and ventrolateral flanges by a dorsally projecting prong of the quadrate. This contact forms an inverted 'V' shape typical in plesiosaurs. The ventrolateral flange extends to a point just dorsal to the lateral condyle of the quadrate. The ventromedial flange is shorter than the ventrolateral flange and curves anteriorly to contact the pterygoid ramus of the quadrate. It is unclear if the quadrate ramus of the pterygoid contacts the squamosal in this region. A horizontally oriented sulcus for reception of the paraoccipital process contacts the squamosal at this point.

The quadrate constitutes the remainder of the suspensorium. Both quadrates have been slightly compressed laterally but remain well sutured to the quadrate ramus of the squamosal. The medial condyle of the right quadrate has been laterally displaced and has fused into the lateral portion of the glenoid fossa. The left quadrate is entirely free of the glenoid fossa and the lateral and medial condyle can be seen in plan view of the articular surface. However, fracturing and distortion in the region between the two condyles makes their relative size and orientation difficult to discern. The pterygoid ramus of the quadrate meets the quadrate ramus of the pterygoid along a squamous contact, with the quadrate lying medial to the pterygoid. Taken together at the point of this contact, both rami form a narrow triangular cross section.

Within the left orbit, four or five elements of the dorsal portion of the sclerotic ring are present. They have been crushed in towards the midline of the orbit and now rest along the left lateral surface of the ventral process of the frontal. At least three palpebrals are fused end-to-end along their lateral margin with an adjacent element.

Braincase

The exoccipital-opisthotic forms part of the posterolateral wall of the braincase. They are fused together as a single unit, as in other plesiosaurs, although this suture is not visible. The right exoccipital-opisthotic is well preserved and largely uncrushed. It has been displaced from the basioccipital ventrally along a clearly defined, pitted suture but remains fused to the prootic anteriorly and the supraoccipital dorsally. The left remains sutured to the basioccipital but is laterally compressed, leaving the paraoccipital process flattened along its lateral surface. It has been displaced from its contacts with both the prootic and supraoccipital.

Three foramina pierce the right exoccipital-opisthotic near the base of the paraoccipital process for passage of cranial nerves and blood vessels. Two closely associated foramina, placed posteriorly on the exoccipital-opisthotic are interpreted as exits for cranial nerve XII (hypoglossal). A single large foramen, anterior to those for XII, may represent exits for IX (glossopharyngeal nerve), X (vagus nerve) and XI (accessory nerve) as well as the jugular vein. Visible within the left exoccipital-opisthotic is the ventral portion of the posterior vertical semicircular canal as well as the posterior portion of the horizontal semicircular canal. The paraoccipital process extends posterolaterally from the lateral surface of the exoccipital-opisthotic to a distal facet for reception with the squamosal.

The supraoccipital forms the dorsal margin of the foramen magnum. A ventral facet for reception of both the exoccipital-opisthotic and prootic is visible on the left supraoccipital. This facet is perforated by the dorsal continuation of both the anterior and posterior vertical semicircular canals. Dorsally, the supraoccipital contacts the ventral surface of the parietals but the nature of this contact is uncertain due to crushing and distortion.

The fenestra ovalis forms a distinct opening in the lateral wall of the braincase. Roughly circular in outline, its margin is composed almost equally in thirds by the prootic anteriorly, exoccipital-opisthotic posteriorly and basioccipital-basisphenoid ventrally. Although preservation was detailed enough to preserve both hyoids, no evidence for an osseous stapes was observed.

The structure of the prootic is best observed on the left side where it has been displaced medially from both the exoccipital-opisthotic and supraoccipital. The facet for the supraoccipital faces dorsoposteriorly and is pierced by an opening for the anterior vertical semicircular canal. The contact with the exoccipital-opisthotic is obscured from view, however the distinct horizontal semicircular canal visible on the anterior facet of the exoccipital-opisthotic presumably continued into the prootic. The utriculus is represented by a recess on the dorsomedial surface of the prootic. The anteroventral portion of the prootic is a pillar of bone which forms the anterior margin of the fenestra ovalis. A small foramen at the base of this pillar may represent the exit for cranial nerve VII (facial).

The basioccipital forms the posterior portion of the basicranium and is well preserved and largely undistorted. The occipital condyle is slightly heart shaped in posterior view and lacks a nototchordal pit. A shallow constriction rings the occipital condyle, setting it off from the rest of the basioccipital. The exoccipital-opisthotic does not participate in the occipital condyle.

Prominent basipterygoid processes are borne solely on the basioccipital and are not shared with the basisphenoid. The roughened articular facet for reception of the pterygoid is angled and faces both anterolaterally and ventrolaterally. The ventral surface of the basioccipital is completely underlain by, and fused with the pterygoids forming a distinct shelf of bone which also projects 1 cm caudally, ventral to the occipital condyle. The basioccipital bears large, roughened exoccipital-opisthotic facets which lie immediately lateral to the posterior floor of the braincase. A longitudinally oriented, elliptical fossa is present on the floor of the braincase near the anterior end of the basioccipital.

The basisphenoid forms the anterior floor of the braincase. It is very well preserved and only slightly distorted on the left lateral side where the left epipterygoid has partially folded over the sella turcica. There does not appear to be fusion along the basioccipital-basisphenoid contact, along which the basisphenoid has been slightly displaced ventrally. The prootic attaches to the dorsolateral surface of the basisphenoid just posterior to the upper cylindrical processes.

The braincase structure on the dorsal surface of the basisphenoid can be clearly seen (Figure 10). In plan view the floor of the braincase is formed of two steps. The lower, anterior most step is formed by the floor of the sella turcica which housed the pituitary. It is bounded laterally by the wing-like projections of the lower cylindrical processes. A pair of conspicuous foramina, for passage of the internal carotids, perforate the sella turcica along its posteroventral surface. The second step, the dorsum sellae, lies posterior to, and partially overhangs the sella turcica. The upper cylindrical processes extend anterolaterally from this surface. Each upper cylindrical process is pierced at its base by a foramen for cranial nerve VI that runs from its posterodorsal to anteroventral surface. A single foramen pierces the floor of the dorsum sellae near the longitudinal midline.

The parasphenoid is fused to the ventral surface of the basisphenoid where it forms a narrow, median keel that both divides the posterior interpterygoid vacuity and forms its anterior most margin. At its anterior end, the parasphenoid forms a wedge of bone that participates in the floor of the palate and separates the posterior interpterygoid vacuity from the anterior interpterygoid vacuity. Here, an elongate, dish-shaped excavation lies on the dorsal surface of the parasphenoid, immediately lateral to which the pterygoids contact the parasphenoid along a digitate suture. At its posterior end the parasphenoid abuts the posterior margin of the posterior

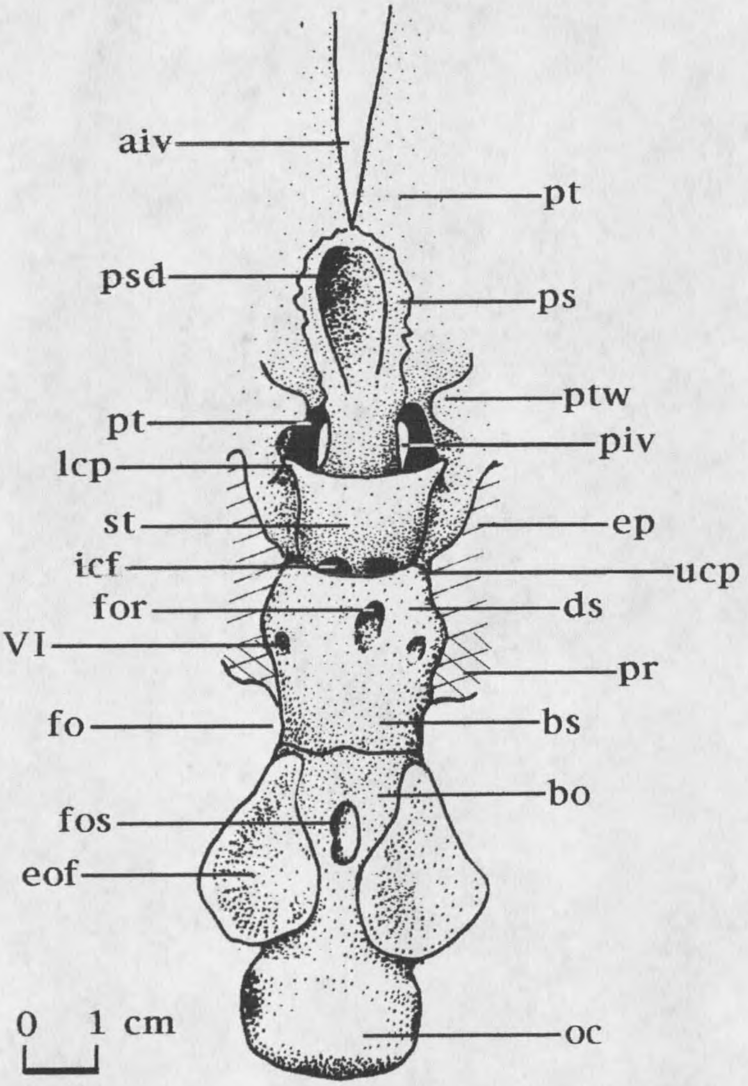

Figure 10. Interpretation of ventral surface of braincase of MOR 751, in dorsal aspect. Abbreviations: aiv, anterior interpterygoid vacuity; bo, basioccipital; bs, basisphenoid; ds, dorsum sellae; eof, exoccipital-opisthotic facet; ep, epipterygoid; fo, fenestra ovalis; for, foramen; fos, fossa; icf, internal carotid foramen; lcp, lower cylindrical process; oc, occipital condyle; piv, posterior interpterygoid vacuity; pr, prootic; ps, parashenoid; psd, parashhenoid dish; pt, pterygoid; ptw, pterygoid wing; st, sella turcica; ucp, upper cylindrical process; VI, abducens foramen.

interpterygoid vacuity which is also the anterior edge of the fused suture between the left and right pterygoids.

Palate

Preservation in the palatal region is variable. The anterior half of the rostrum has been separated into two equal sized pieces, both of which have been freed from the lower jaws allowing a clear view of the ventral surface of the palate. The posterior half of the rostrum, anterior to the orbits, remain firmly fused to the lower jaws with the exception of a small portion of the right lower jaw which has been removed to view the palate in the region just anterior to the orbits. The rest of the palate, posterior to the anterior rim of the orbit has been freed from matrix. The left lateral dorsal skull elements have been removed affording both dorsal and ventral views of the palate. The palate is largely undistorted and well preserved along the longitudinal midline, however the lateral margins of the palate have been subject to considerable crushing and distortion, especially in the region of the palatines making some relationships to the skull roof uncertain.

The vomers are fused together along the midline in the anterior half of the skull. Together they are roughly triangular in cross-section where the rostrum has broken near alveolus eight. Dorsal to the vomer the anterior rostrum houses the large maxillary dental alveoli which are clearly visible in longitudinal CT images. A narrow, longitudinal ridge of bone extends along the ventral surface of the palate from near its anterior tip, between the premaxillae, to the region of alveolus six or seven where the palate flattens between the maxillae. At this point the vomers clearly separate the maxillae but anteriorly the extent to which the vomers contact or split the premaxillae is uncertain. Dental alveoli are present within grooves which parallel the ridge on each side. A vomeronasal fenestra is not present in the anterior half of the rostrum. As the vomeronasal fenestra typically occurs at the anterior end of the vomer (Carpenter, 1997) it is presumed to be absent in MOR 751. Posteriorly, contacts with the palatines and pterygoids are not visible. Internal nares could not be identified with certainty on the palate, anterior to the orbits, where it was exposed.

The palatines are thin sheets of bone that form much of the lateral portion of the palate, anterior to the supratemporal fenestra. Laterally, the palatines contact the maxilla, although the nature of this contact is uncertain due to extensive crushing and distortion on both sides. The presence of a suborbital fenestra is equivocal. The palatines butt against the pterygoids medially along a straight contact. This contact terminates posteriorly at what appears to be a small palatal fenestra, approximately 1 cm wide by 2 cm long, which does not appear to be a preservation artifact. The fenestra has suffered some modification from postmortem distortion but the anterior and lateral margins appear formed in the palatine. The medial and posterior margins of the fenestra are unclear but may have been shared by the pterygoids and/or ectopterygoids. The posterolateral corner of the palatines contact the ectopterygoids.

The ectopterygoids form the anterior margin of the subtemporal fenestra which, together with the lateral ramus of the pterygoid, create a brace to transfer stress between the palate and the lateral wall of the skull roof. The ectopterygoid is best preserved on the left side where some distortion has occurred but its relationships to the surrounding bones can still be discerned. The anteromedial surface of the ectopterygoid contacts the palatine. Laterally, the ectopterygoid fuses to the medial wall of the jugal with its contact beginning along the anteromedial corner of the supratemporal fenestra and sweeping anteroventrally, just ventral to the medial flange of the postorbital bar. The ectopterygoid contacts and lies ventral to the lateral ramus of the pterygoid where they unite to form a distinct pterygoid flange which bears a boss on its ventral surface.

The pterygoids are well preserved. Similar to other plesiosaurs, the pterygoid can be divided into anterior, lateral, posterior and quadrate rami. The anterior ramus of the pterygoid forms the medial surface of the anterior palate in the region ventral to the orbits and external nares. Its lateral margins contact the palatines but its anterior margin is not visible. The anterior ramus is split along most of its midline by a conspicuous, well formed anterior interpterygoid vacuity, 8 mm wide and 8 cm in length. The extreme posterior corner of the anterior interpterygoid vacuity is formed by the anterior tip of the parasphenoid.

The lateral ramus of the pterygoid overlaps the ectopterygoid laterally and participates in the pterygoid flange of the palate. The parasphenoid contacts the lateral ramus of the pterygoid medially. A small wing of bone, just anterior to the basal articulation, projects medially from the lateral ramus and partly extends over the fenestra that communicates between the dorsal surface of the palate and the posterior interpterygoid vacuity.

The posterior ramus of the pterygoid forms the medial edge of the subtemporal fenestra. The anteromedial portion of the posterior ramus contacts the anterolateral corner of the basisphenoid forming the basal articulation. Ventral to the basal articulation, the pterygoids are split by the anterior end of the posterior interpterygoid vacuity. The pterygoid resumes contact with the basicranium at the basipterygoid articulation. Here, the left and right pterygoids expand medially and meet their opposite along the midline, forming a shelf of bone that forms the posterior margin of the posterior interpterygoid vacuity. The pterygoids also appear to expand dorsally, infilling the area ventral and medial to the basipterygoid processes, a condition apparently unique to MOR 751. This slightly differs from, and may be a modification of, the pterygoid structure described by Carpenter (1997) for the Cretaceous elasmosaur *Libonectes* and the polycotylid *Dolichorhynchops* where the pterygoids form simple flat plates ventral to the basicranium.

The quadrate ramus of the pterygoid constitutes the posterior portion of the posterior ramus of the pterygoid and unites with the pterygoid ramus of the quadrate along a squamous contact, the pterygoid overlapping the quadrate medially.

In lateral view the epipterygoid is a triangular shaped blade of bone. It projects dorsally from the basal articulation, lies lateral to the sella turcica and contacts the prootic along its posterolateral corner. The dorsal tip of the epipterygoid is somewhat thickened and roughly textured, presumably for a ligamentous attachment to the parietal dorsally. Cranial nerve V (trigeminal nerve) passed from the braincase through a lateral opening, bounded anteriorly by the epipterygoid and posteriorly by the prootic.

Mandible

Both mandibular rami are preserved in MOR 751 and are largely complete. Each ramus remains fused to its opposite at the mandibular symphysis but have been displaced from each other posteriorly. The right mandible has been displaced vertically from life position and has come to lie along the right lateral surface of the skull roof, pressed over the ventral portion of the orbit and supratemporal fenestra. The left ramus remains nearly in life position but has been tightly pressed against the left side of the palate.

During the course of preparation most of the jaws have been removed from the skull for study. A 17 cm portion of both rami remains fused to the skull roof and each other, between dentary alveoli 7-22 on the left side and 7-23 on the right side. In addition, a small portion of the middle right mandible remains fused to the skull just ventral to the postorbital bar.

The mandibular rami unite along the midline anteriorly and form a stout mandibular symphysis which extends posteriorly to, and includes the sixth dentary alveolus, in contrast to eight symphyseal teeth seen in *Plesiopleurodon wellesi.* Ventrally, the splenials can be observed to participate in the symphysis up to alveolus four. It is not known if the coronoids extend into the symphysis.

The dentary is the major anterior element of each ramus. Beginning at a point just anterior to the coronoid eminence the dentary interdigitates with the surangular dorsally and the angular ventrally. Medially, the dentary is covered by anterior extensions of the coronoid, splenial and angular with the exception of its dorsal margin, which is exposed at the base of the tooth row. The external surface of the dentary is roughened and pitted at its anterior end.

There are 29-30 dentary alveoli in the left dentary and 31 in the right. The anterior six to seven alveoli bear robust, caniniform teeth which decrease in size caudad. The anterior two teeth are strongly procumbent, being inclined at nearly a 45 degree angle from the vertical, with successive teeth becoming progressively vertical posteriorly. A groove for the secondary dental alveoli is bounded laterally by each tooth row and medially by a small ridge. Each ridge becomes well developed anteriorly and unites with its opposite in the region of the mandibular symphysis into a large, single median ridge. A weekly developed diastema is present between alveolus three and four.

The coronoid is a slender, laterally compressed bone which runs along the dorsomedial surface of the dentary for most of its length. The posterior margin of the coronoid originates immediately anterior to the coronoid eminence, contacting the surangular laterally and the splenial ventrally. It is uncertain if the coronoid extends into the mandibular symphysis.

The splenials are poorly preserved. Each splenial is a narrow blade of bone that lies along the ventromedial surface of the mandibular ramus. Anteriorly, each splenial unites with its opposite along the ventral margin of the rami at the mandibular symphysis and together, participate in the symphysis until pinching out between the dentaries below alveolus three. The splenial appears to butt against or slightly overlap the coronoid along its dorsal margin and considerably overlaps the angular along its ventral margin. The splenial also forms the medial wall of the meckelian canal, although the canal has been lost due to crushing, with the splenial coming to lie against the medial wall of the dentary. The posterior termination of the splenial is uncertain due to poor preservation in that region.

The prearticular is interpreted as a thin splint of bone that lies in a trough formed in the angular. Its anterior margin cannot be discerned. The posterior margin of the prearticular extends toward the anteromedial corner of the medial condyle of the articular. Here if forms part of the medial wall of a deep cleft in the angular. On the left ramus a shallow trough appears to mark the former position of the prearticular, the dorsal margin of which closely follows a longitudinal, dorsomedial crest formed by the contact between the surangular and angular. The left prearticular is otherwise lost, with the possible exception of a lip of bone that lies ventromedial to the medial condyle of the articular.

The surangular is the major dorsal element of the post-dentary portion of the mandible. At its anterior end it is a thin wedge of bone, hidden between the coronoid medially and the dentary laterally. The surangular is overlapped by the dentary at its anterolateral corner along a broadly digitate suture. Several foramina perforate the surangular adjacent to this contact. The surangular forms the apex of a very pronounced coronoid eminence. Posterior to the coronoid eminence the dorsal margin of the surangular descends posteroventrally as a thin, laterally compressed blade of bone to the anterolateral corner of the glenoid fossa. A conspicuous, broad and shallow fossa, interpreted as the posterior margin of the adductor fossa, is bounded laterally by this dorsal blade. Posteriorly the adductor fossa is bounded by the anterior edge of the lateral condyle of the glenoid fossa and medially by a dorsomedial crest. In cross section through the adductor fossa the dorsomedial crest is seen to represent the contact between the surangular and the angular. This contact slopes ventrolaterally and can be traced to the lateral surface of the mandible. The articular appears to be firmly fused to the surangular along their contact and no vestiges of a suture can be discerned.

The angular forms much of the ventral surface of the ramus. At its anterior end the angular is a narrow wedge of bone lying between the dentary and splenial. In ventral view it can be seen to taper out between the dentary and splenial at alveolus nine. At a point roughly ventral to the coronoid eminence, the angular loses contact with the dentary and the surangular forms its dorsolateral border. A trough for reception of the probable posterior termination of the splenial and for the prearticular forms its dorsomedial border.

Caudad, the angular forms the ventral and ventrolateral portion of the retroarticular process.

A deep, longitudinal cleft is formed in the angular immediately anterior to the anteromedial margin of the glenoid fossa. The lateral wall of the cleft is formed entirely in the angular where the angular sends a dorsal flange to participate with the surangular in the dorsomedial crest. The posterior margin of the cleft is partly, if not entirely, formed in the articular while the medial wall is possibly formed by the prearticular. A large foramen pierces the posterior corner of the cleft and appears to extend into the articular. The cleft may represent the posterior vestige of the meckelian canal (Taylor, 1992).

The articular is fused along its entire margin with the angular and surangular. Both the glenoid fossa and the dorsomedial portion of the retroarticular process are formed in the articular. The glenoid fossa is of the typical bicondylar arrangement seen in plesiosaurs for reception of the quadrate. The posterior margin of the glenoid is deeply indented by a notch that leads ventrally into a large foramen just posterior to the glenoid fossa and into the articular, creating distinct medial and lateral condylar margins. The anterior margins of the glenoid forms the posterior end of the adductor fossa laterally and the angular cleft medially. The retroarticular process is concave dorsally and roughened posteriorly for insertion of the *M. depressor mandibulae* (Taylor, 1992).

The remains of at least one hyoid and possibly a poorly preserved fragment of a second are present in MOR 751. A rod of bone 48 mm long and averaging 4 mm wide was found pressed against, and parallel to, the ventral keel of the parasphenoid where it divides the posterior interpterygoid vacuity. This corresponds well to the expected position of the hyoid as the medial surface of the right lower jaw was displaced and preserved against the ventral surface of the palate. The remains of a second possible hyoid element was found in close proximity to the first. It was not in contact with other bones but was found in the shale matrix between the posterior margins of the left and right mandibular rami. It was poorly preserved and heavily modified by gypsum permineralization.

Dentition

Nearly all of the teeth have been preserved in MOR 751. A few teeth were found loose of the skull and jaws, but the vast majority remain in sockets in their original life position. Unfortunately, actual tooth preservation is poor. A considerable amount of gypsum permineralization has covered and infiltrated the teeth, in many instances creating a honeycombed array of dentine, enamel and gypsum, rendering preparation nearly impossible. Only occasional glimpses of the enameled surface of the tooth are possible.

A fairly reliable tooth count can be made however. A full compliment of 31-32 alveoli are preserved in the upper left tooth row, six to seven of which are contained in the premaxilla and 26 in the maxilla. The right premaxilla also bears at least six alveoli but only 15 alveoli can be counted in the right maxilla due to damage and loss at its posterior end. There are 29-30 alveoli (probably 30) in the left dentary and 31 in the right. Several smaller, secondary alveoli are visible in a groove or trough, lingual to the primary alveoli.

CT imaging clearly reveals the size and position of replacement teeth within the rostrum. The bulk of the maxilla, anterior to the orbits, house the large, caniniform replacement teeth (Figure 11). A conspicuous example can be seen in the tooth emerging from position seven in the upper left tooth row. Externally only .5 cm of the crown is visible erupting from the alveolus. Internally however, CT images reveal the 4 cm remainder of a large crown and root. The base of the root begins dorsally, nearly at the maxilla-premaxilla suture and can be traced anteroventrally past a bulbous root with a radiotransparent pulp cavity. The enameled crown is apparent as the conical, radiotranslucent ventral end. Several other teeth are visible in the rostrum anterior and posterior to number seven.

When the upper and lower jaws are occluded, the dorsal and ventral tooth rows deeply interdigitate against one another. This is particularly conspicuous in the mid and anterior regions of the snout where large, curved, caniniform teeth are present. The largest of these have crowns that project up to 5 cm beyond the alveolar margin and are 1.5 cm in diameter at the base of the crown, although the base diameter measurement may be slightly exaggerated due to gypsum permineralization. The largest teeth occur in the upper and lower tooth rows between positions 3-8. The two anterior most teeth in the premaxilla and dentary are inclined anteriorly at nearly 45 degree angles from the vertical. Further caudad, the teeth gradually

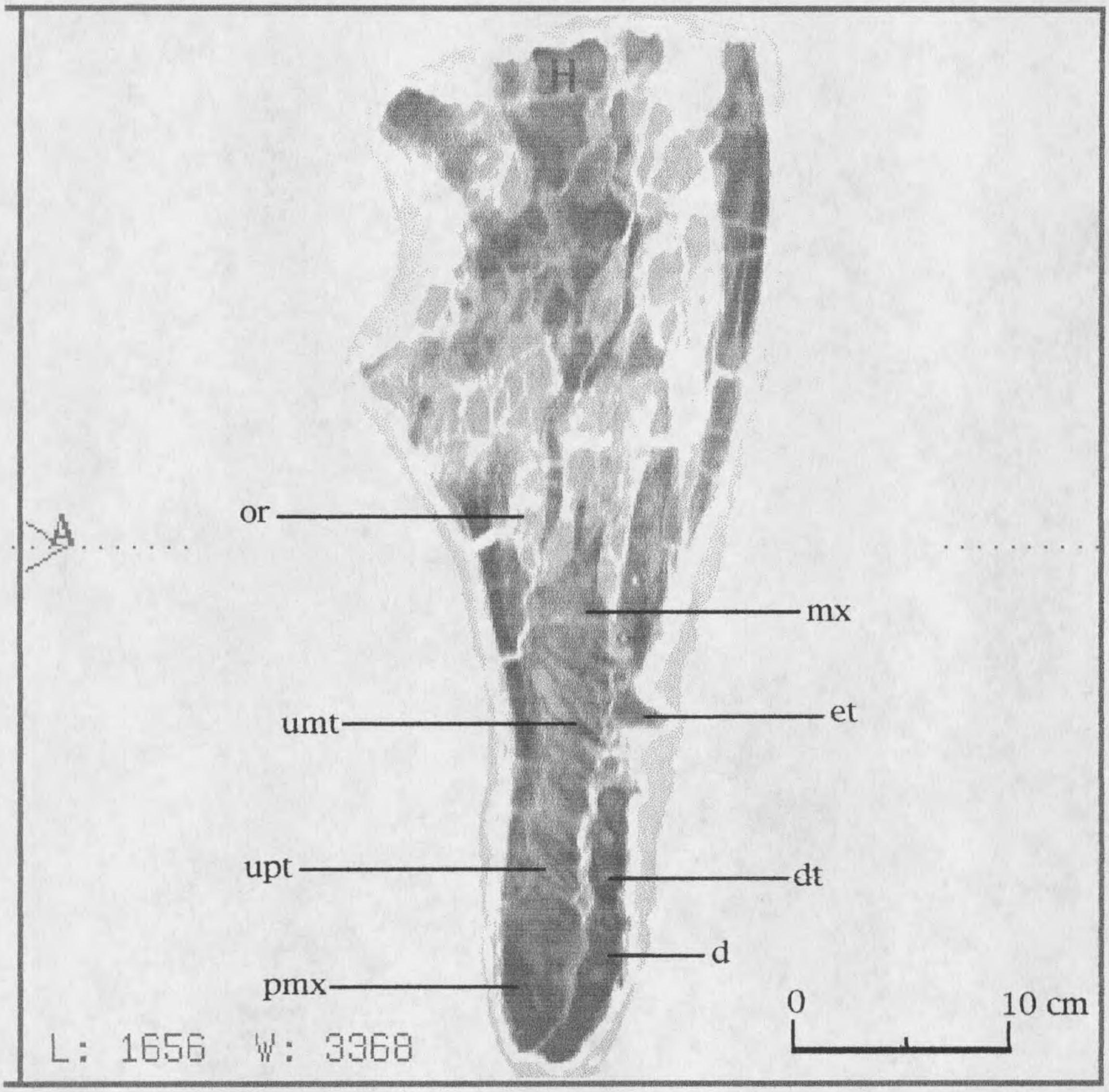

Figure 11. CT image of skull of MOR 751, in lateral view. Anterior is at bottom of page. Abbreviations: d, dentary; dt, dentary tooth; et, erupted tooth; mx, maxilla; or, orbit; pmx, premaxilla; umt, unerupted maxillary tooth; upt, unerupted premaxillary tooth.

become progressively less procumbent and are nearly vertical by upper tooth row positions 8-10. The remainder of teeth in the posterior half of the ramus are considerably smaller, averaging 1-1.5 cm in height. The tooth row terminates beneath the posteroventral corner of the orbits.

The enameled crowns of the teeth, although poorly preserved, all appear to be nearly circular in cross section. The anterior teeth are curved while the small, posterior teeth, appear to be simple, straight cones. Numerous wavy, longitudinal and in some cases, bifurcating striations are present on the outer enameled surface. Striations are present on all sides of the teeth but it is not possible to discern whether they are more numerous on the lingual or labial surfaces. No evidence of wear facets was observed.

Postcranial Skeleton

Atlas and Axis

The atlas and axis elements form a single unit that functions to bridge the skull to the vertebral column. The elements are fused together with the exception of the atlas intercentrum and atlas neural arches which can be removed from adjacent elements. Suture lines between other elements are still discernible (Figure 12).

The atlantal cup is a deeply concave, round to heart shaped socket for articulation with the occipital condyle. The atlas

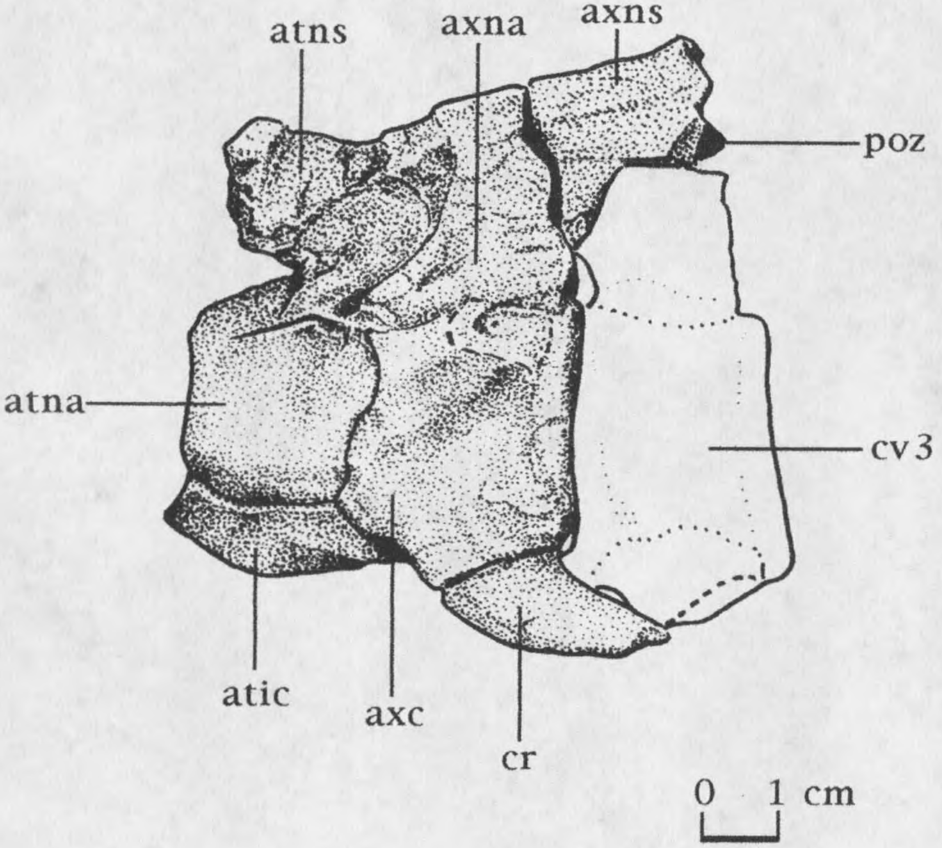

Figure 12. Atlas and axis of MOR 751, in left lateral aspect. Abbreviations: atic, atlas intercentrum; atna, atlas neural arch; atns, atlas neural spine; axc, axis centrum; axna, axis neural arch; axns, axis neural spine; cr, cervical rib; cv3, cervical vertebra 3; poz, postzygopophysis.

intercentrum forms the majority of the ventral half of the cup, the left and right atlas neural arches form its anterodorsal margin and the atlas centrum forms its posterior border. The atlas centrum does not participate in the anterior rim of the atlantal cup. The atlas intercentrum bears five articular surfaces. Its concave anterior face for contact with the basioccipital is truncated dorsally by a single, large, horizontal facet for articulation with the atlas centrum and laterally by two small, dorsolaterally facing facets for the left and right atlas neural arches. A single facet is shared by both the axis centrum and intercentrum caudad. The ventral surface of the atlas intercentrum is convex ventrally and bears a broad median keel.

probably atlas centrum

The atlas neural arch bears a large medial facet for union with the atlas centrum, in addition to anterior and ventral facets for the basioccipital and atlas intercentrum, respectively. A very small facet contacts the axis neural arch posterodorsally. Both arches bear broken bases for the neural spines. The neural spine has been displaced and crushed in on the neural canal but appears to be largely fused with the axis neural spine. The anterior surface of the atlas centrum is concave and houses a distinct notochordal pit at its center. Dorsally, it forms most of the floor of the atlas neural canal and posteriorly, it is bounded by the large axis centrum. In lateral view, only a small elliptically shaped portion of the atlas centrum is visible between the atlas neural arch and the axis centrum.

The axis morphology is more typical of other cervical vertebrae. The axis centrum forms the bulk of the axis complex. The anterior face of the axis centrum is fused to the atlas centrum and little else can be seen. The posterior articular facet is concave and lacks a notochordal pit. A short, posteriorly projecting cervical rib articulates to the ventrolateral margin of the centrum. The axis intercentrum is a small, dorsoventrally flattened element that is firmly fused to the ventral surface of the axis centrum. A well defined ventral keel is formed on its ventral surface. Nutritive foramina are not present on the axis centrum ventrally. The axis neural arch is fused to the axis centrum and to a small extent, anteriorly to the atlas neural arch. The neural spine extends strongly caudad, to a point even with the posterior margin of vertebra three. The posterior portion of the axis neural spine arches entirely over the neural spine of vertebra three and terminates in a pair of postzygopophyses.

In order to achieve an accurate count of cervical, pectoral and dorsal vertebrae, the contact between the neural arches and the centrum must be visible. Although the neural arches are firmly fused to the centrum in MOR 751, a clear suture between the two remains discernible (Figure 13). Based on this observation, the entire cervical series of 26 articulated vertebrae are defined as those vertebrae of the neck region which bear rib facets exclusively on the centrum (Brown, 1981). Three pectoral vertebrae, which are transitional between the cervical and dorsal vertebrae, share the rib facet on both the centrum and neural arch. The rib facets of the five dorsal vertebrae are borne on the neural arch only. Based on the few proximal rib fragments preserved, as well as rib facets, all ribs are single headed (cercidopleurous).

Beginning with the atlas and axis the vertebrae progressively increase in size, with vertebral width, (defined as maximum centrum

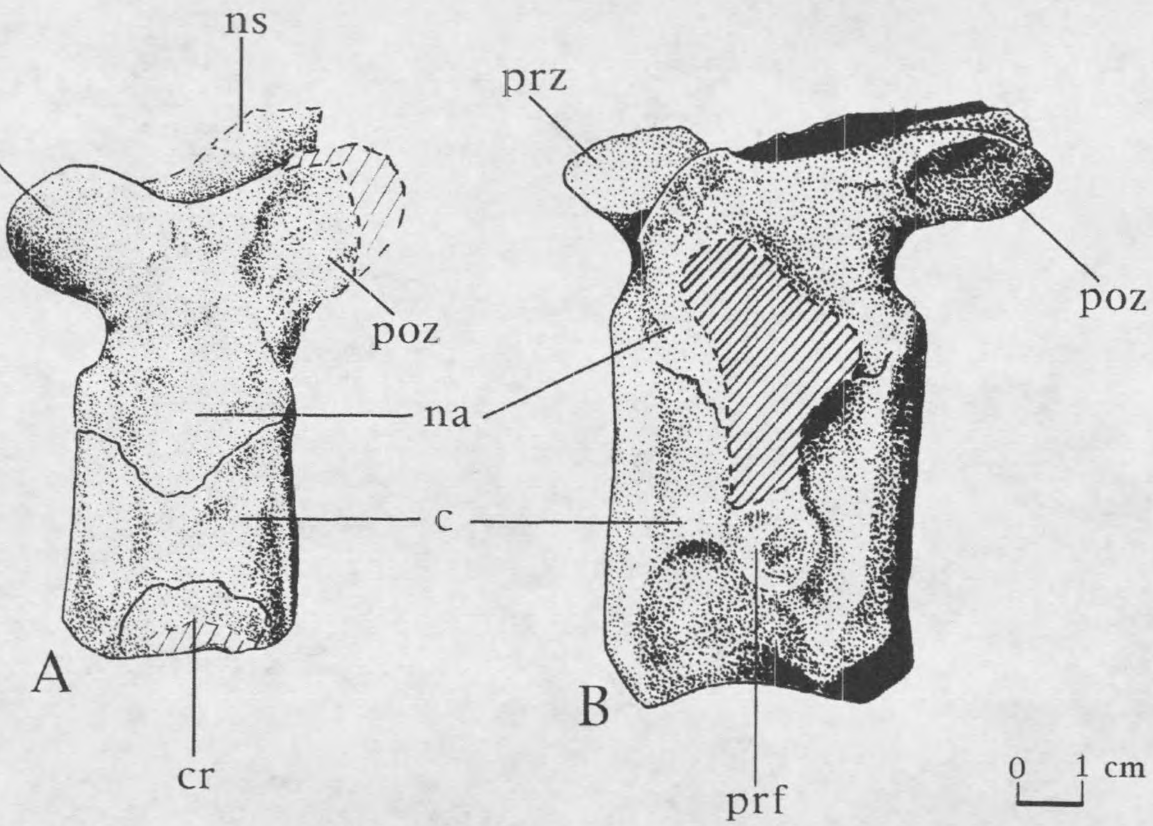

Figure 13. Vertebrae of MOR 751, in left lateral aspect. A. Cervical vertebra 10. B. Pectoral vertebra 28. Abbreviations: cr, cervical rib; na, neural arch; ns, neural spine; poz, postzygopophysis; prf, pectoral rib facet; poz, postzygopophysis.

diameter measured on the posterior articular face), increasing at a faster rate than vertebral length, (measured along the mid ventral surface of the vertebra) (Table 2-3; Figure 14). The articular facet of the cervical vertebrae is nearly circular in outline, while the posterior three uncrushed pectorals become very nearly heart shaped in outline. Typical of all plesiosaurs, the vertebral centra are amphicoelus. The articular facet is proportionately more deeply concave in anterior cervicals than in pectoral vertebrae. With the exception of the anterior face of the axis, a notochordal pit is absent. The zygopophyses of the posterior cervical vertebrae are largest both proportionately and in absolute size. The zygopophyses quickly diminish in size through the pectoral series, and are not preserved on the lone dorsal vertebra. Ventrally a distinct longitudinal keel splits a pair of nutrient foramina. The keel diminishes posteriorly through the pectoral vertebrae and is concomitant with the migration of the ventral nutrient foramina dorsally to the lateral surface of the centrum. Beginning at vertebra 28 and continuing caudad, a single and sometimes closely paired nutritive foramen is present ventrally along the midline.

Appendicular Skeleton

The proximal humerus fragment bears a well developed capitulum and tuberosity. The articular surface of the capitulum is deeply pitted, while the tuberosity is smooth. In life, a narrow cartilaginous isthmus connected the capitulum to the tuberosity. The

Table 2. Vertebral dimensions of MOR 751. Location of measurements: length, along the mid-ventral surface of centrum; width, at maximum diameter on posterior facet of centrum; height, from the ventral margin of posterior facet to base of neural canal.

Vertebra Number	Length	Width	Height
1-2.	50	34	30
3.	30	39	35
4.	29	39	37
5.	28	39	41
6.	32	42	37
7.	33	44	40
8.	33	45	45
9.	32	46	41
10.	36	46	39
11.	36	47	42
12.	39	50	47
13.	41	52	45
14.	41	55	46
15.	42	56	49
16.	35	58	54
17.	41	59	51
18.	40	58	55
19.	45	61	55
20.	45	61	58
21.	47	64	58
22.	44	67	60
23.	45	65	61
24.	47	72	63
25.	48	68	56
26.	47	70	59
27.	46	67	59
28.	47	66	59
29.	50	68	61
30.	49	69	62
31.	52	70	63
32.	50	69	63
?33.	47	66	64
?34.	46	66	65

Table 3. Vertebral column dimensions of MOR 751.

Measurement	Dimensions (in mm)
Cervical series length (articulated)	1020
Pectoral series length (articulated)	145
Dorsal series length (partial)	244
Total vertebra length (as preserved)	1409

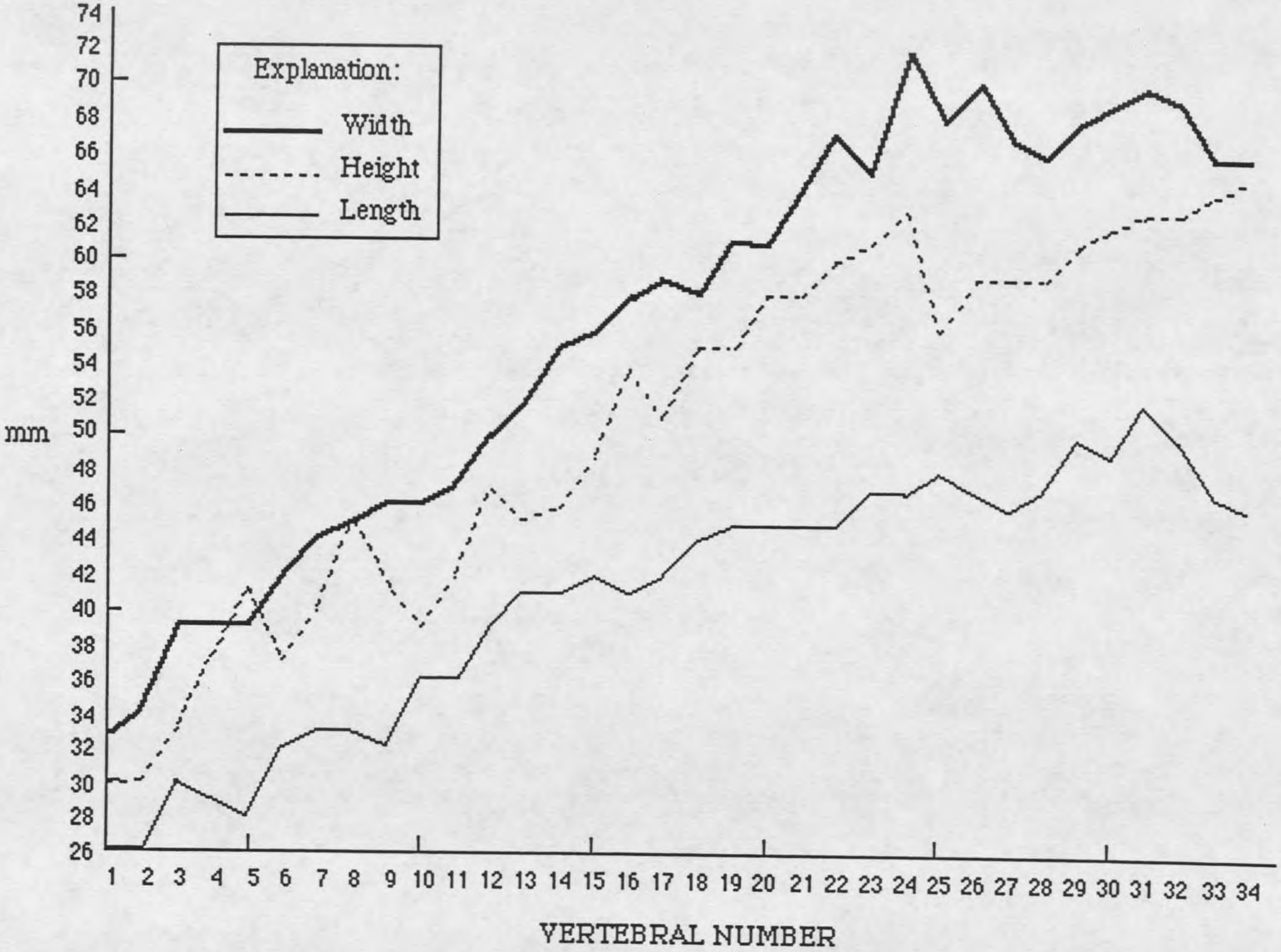

Figure 14. Graph of vertebral measurements of MOR 751.

preaxial margin of the distal half of the humerus is straight while the postaxial surface is concave and expands distally. Rugosities, representing the distal extent of muscle insertions are visible along the preaxial, postaxial and ventral surfaces of the humerus. The expanded distal end of the humerus contacts the radius anteriorly and the ulna and possibly one or more accessory ossicles posteriorly (Figure 15).

Both epipodials are broader than long (Figure 16; Table 4). The radius is larger than the ulna and is pentagonal in outline. It contacts the intermedium posterolaterally and the radiale distally, in addition to the humerus and ulna. Beginning along the anterior margin of the radius, the leading edge of the paddle becomes angled backwards in a smooth arc that continues to the paddles distal end. The ulna is notched along its anterior margin for the epipodial foramen. Distally, the ulna contacts both the intermedium and ulnare. The posterior margin of the ulna however does not continue to the posterior margin of the paddle. Presumably, one or more accessory ossicles filled the void along its posterior margin, although they have been lost due to damage in this region.

The mesopodials consist of a proximal row of three carpals, the radiale, intermedium and ulnare as well as a row of three distal carpals. The fifth metacarpal has shifted proximally into the distal carpal row and contacts the ulnare, as is typical in plesiosaurs later than the lower Jurassic (Brown, 1981). The metacarpal row becomes progressively phalangiform posteriorly. The five digits are closely contacted along their lateral margins and effectively form a single, posteriorly curved blade. The digits are well preserved even to their

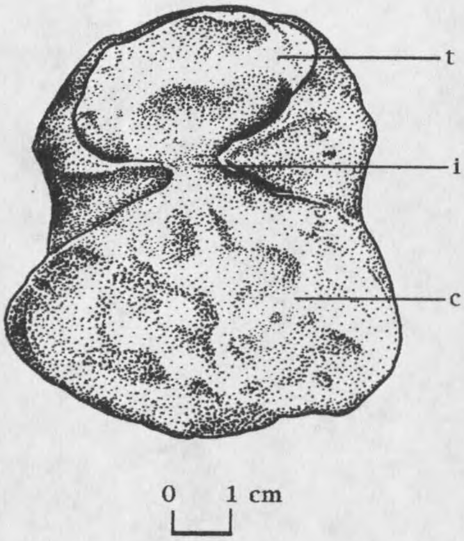

Figure 15. Proximal propodial fragment of MOR 751, in dorsal aspect. Abbreviations: c, capitulum; i, isthmus; t, tuberosity.

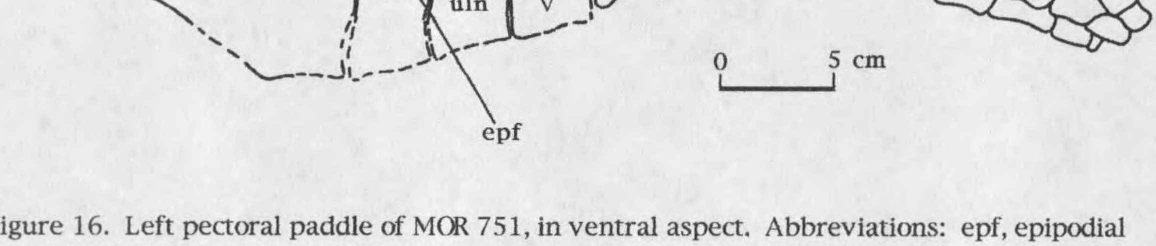

Figure 16. Left pectoral paddle of MOR 751, in ventral aspect. Abbreviations: epf, epipodial foramen; dc1-3, distal carpal 1-3; h, humerus; itm, intermedium; rd, radius; rdl, radiale; ul, ulna; uln, ulnare; I-V, metacarpals I-V.

distal end and display typical plesiosaurian hyperphalangy. The phalangeal count is I-7, II-11, III-10, IV-9 and V-9.

Table 4. Selected paddle dimensions of MOR 751.

Measurement	Dimensions (in mm)
Maximum propodial width (distal margin)	178
Radius width	85
Radius length	48
Ulna width	68
Ulna length	48
Maximum humerus head diameter	73
Minimum humerus head diameter	56
Tuberosity width	49
Tuberosity length	32
Distal paddle length (distal humerus to distal tip)	455
Paddle width (between metacarpals I-V)	151

PHYLOGENETIC ANALYSIS

Introduction

Establishing the relationships of a new taxon to its nearest relatives is a fundamental question in paleontology. Comparative morphologic studies of related forms are employed to reconstruct phylogenies. The outcome of any phylogenetic analysis, therefore, is strongly influenced by two criteria:

1. The selection of specific taxa for comparison.
2. The selection of characters on which to base the comparison.

In this chapter I explain why I chose the taxa and characters I did in light of the limited scope of this study. A brief description of taxa and characters used in this analysis is also provided. Finally, a cladistic analysis is performed to evaluate the possible relationships of MOR 751 to other plesiosaurs.

Selection of Taxa

In this analysis I compare MOR 751 to representatives of each family of plesiosaurs including the Plesiosauridae, Cryptoclididae, Elasmosauridae, Pliosauridae, Brachaucheniidae and Polycotylidae. The taxa chosen represent the most complete and well known members of each family whose cumilative stratigraphic distribution spans most of the Mesozoic (Figure 17). Additionally, many of the taxa have benefited from recent redescriptions resulting from the discovery of new specimens and use of new preparation techniques on previously collected specimens (Taylor, 1992b; Cruickshank, 1994; Brown, 1994; Carpenter, 1996; Storrs, 1997 and others). *Pistosaurus longaevus* from the Triassic of Germany is used for outgroup comparison. A brief review of the taxa used in this analysis follows.

Taxa used in Phylogenetic Analysis

Pistosaurus longaevus Meyer, 1847-1855

P. longaevus is an enigmatic sauropterygian from the middle Triassic (Anisian) Hauptmuschelkalk of Germany. Analyses by Sues (1987) and Storrs (1991) place *Pistosaurus* as either the sister group to, or the most primitive member of, the Plesiosauria. Sander et al., (1997) removes the Pistosauridae (*Pistosaurus* plus *Augustosaurus*) from the stem group of plesiosaurs but confirms the taxon as the sister group to plesiosaurs. *Pistosaurus* shares some primitive characteristics seen in other Triassic sauropterygian such as a long, narrow body, slender humerus and femur and the retention of nasals. However, it also displays a number of characteristics that are synapomorphic for plesiosaurs including an open palate, limb-mediated propulsion for an open marine habitat, ventral nutritive foramina in the vertebral centra, long transverse processes and

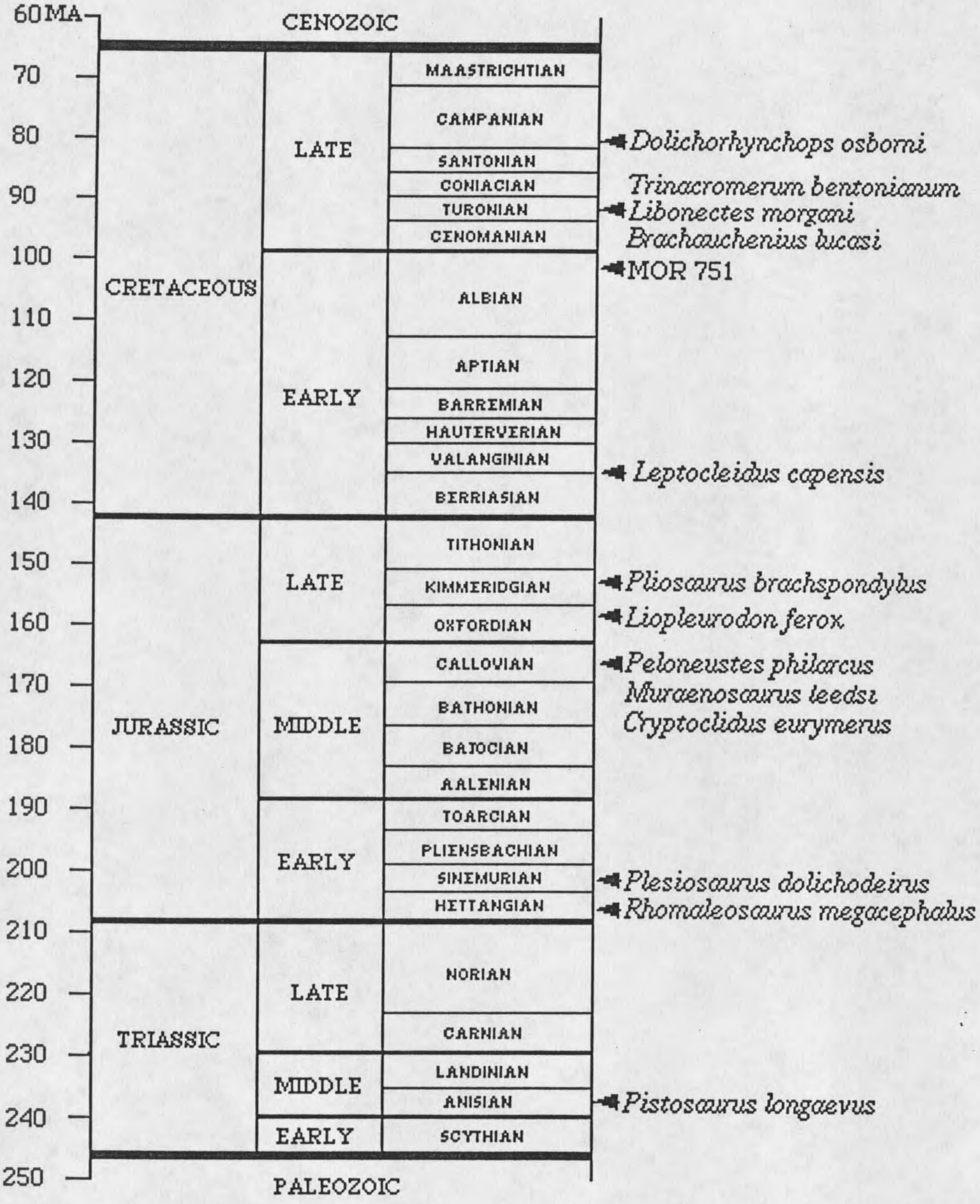

Figure 17. Stratigraphic distribution of selected plesiosaurs.

elongate coracoids. It is used in this analysis for outgroup comparison to selected plesiosaurian taxa.

Plesiosaurus dolichodeirus Conybeare, 1824

P. dolichodeirus is a moderately sized plesiosaur (up to 3.5 meters) from the Jurassic (Sinemurian) of England. Recent work by Storrs (1997), has clarified the taxonomic and morphologic status of this confusing genus. It is considered the sole member of the Plesiosauridae, with the possible exception of *P. guilelmiiperatoris*. It is identified by a small head and elongate neck (up to 40 vertebrae), short mandibular symphysis, moderately sized supratemporal fenestrae and a large pineal foramen. The presence of broad parietals, elongate jugals and a curved humeral shaft suggest a largely plesiomorphic condition, concurrent with its stratigraphic occurrence.

Cryptoclidus eurymerus (Phillips, 1871)

C. eurymerus is known from the Middle Jurassic (Callovian) of the English Oxford Clay and is the best described and understood member of the Cryptoclididae. Recent reviews (Brown, 1994; Brown and Cruickshank, 1994) have helped to elucidate cryptoclidid apomorphies. These include an increase in the number of premaxillary teeth, a regularly-graded upper dentition and enlarged orbit. Additionally, it has a vertically oriented jugal bar resulting from the retention of a deep ventral cheek excavation, reminiscent of the lower temporal fenestra of its diapsid ancestors.

Muraenosaurus leedsii Seeley, 1874

M. leedsii is a Jurassic elasmosaurid from the Oxford Clay of England. The work by Andrews (1910) still serves as the best description of this species. *M. leedsii* exhibits a less derived elasmosaurid morphology in comparison to the Cretaceous elasmosaurid *Libonectes* in that it has a greater number of dentary teeth (approximately 20), has fewer cervical vertebrae (44) and has an open pterygoid structure ventral to the basicranium.

Libonectes morgani (Welles, 1949)

L. (Elasmosaurus) morgani is a North American elasmosaurid known from the Upper Cretaceous (Turonian) of the Eagle Ford Group, Texas. Originally described as *Elasmosaurus morgani* by Welles (1949), this species was placed in a new genus, *Libonectes*, by Carpenter (1997). This separation was based on differences of the atlas and axis and pectoral girdles seen in the holotype SMUSMP (Southern Methodist University, Shuler Museum of Paleontology) 69120 as compared with the generic type, *Elasmosaurus platyurus*. *Libonectes* displays the typical elasmosaurid morphology of a relatively small skull, short mandibular symphysis, reduction in the number of dentary teeth (15-16) and elongated neck region resulting from an increase in the number of cervical vertebrae (62). *Libonectes* also exhibits a derived pterygoid structure and the presence of vomeronasal fenestrae which Carpenter (1997) hypothesized may indicate a loser link to Cretaceous polycotylids than previously believed.

Liopleurodon ferox Sauvage, 1873

L. ferox, a large pliosaurid plesiosaur, is best known from the Upper Jurassic (Oxfordian) Oxford Clay near Peterborough, England. In the detailed description by Andrews (1913), this large-skulled (skull length approximately 1.25 meters), short-necked (22-23 cervical vertebrae) pliosaurid was referred to the genus *Pliosaurus*. Tarlo (1960), however, recognized several key differences between this taxon and *Pliosaurus* and resurrected the generic name *Liopleurodon*. Specifically, *L. ferox* can be distinguished from other Upper Jurassic pliosaurids by its unique spatulate mandibular symphysis, bearing 5-6 pairs of teeth and averaging 25-28 teeth in each jaw ramus. *L. ferox* also differs from Upper Jurassic elasmosaurids by its palatal structure in which the posterior portions of the pterygoids fold under the basicranium, a condition shared with the Upper Jurassic pliosaurid *Peloneustes* and the North American, Cretaceous form, *Brachauchenius*.

Peloneustes philarchus (Seeley, 1889)

P. philarchus is a well described Upper Jurassic pliosaurid from the Oxford Clay (Callovian) of England (Andrews, 1913). Its shortened neck, with 21-22 cervical vertebrae and its elongate mandibular symphysis, bearing 13-14 teeth and a total of 40 in each ramus, distinguish it from other Upper Jurassic pliosaurids. The palate of *P. philarchus* is similar in structure to that of *Liopleurodon* except that *P. philarchus* apparently lacks an anterior interpterygoid vacuity.

Pliosaurus brachyspondylus (Owen, 1868)

P. brachyspondylus is found in deposits of the Upper Jurassic Kimmeridge Clay (Kimmeridgian) of England. This large pliosaurid, reaching 10 meters in length, is best known from a relatively new specimen, BRSMG (City of Bristol, Museum and Art Gallery) Cc332, discovered in 1980 in Westbury, Wiltshire, England and described by Taylor and Cruickshank (1993). *P. brachyspondylus* primarily differs from the only other known Kimmeridgian pliosaurid *Liopleurodon* by its elongate mandibular symphysis bearing 10-11 symphyseal teeth and 31-32 total dentary teeth in each ramus.

Rhomaleosaurus megacephalus (Stuchbury, 1846)

R. megacephalus is a large, Lower Jurassic (Hettangian) pliosauroid from England. Recent work on the best specimen, LEICS (Leicestershire Museums) G221.1851, including the use of new preparation techniques and CT scan imagery, has helped to better elucidate the morphology of the species (Cruickshank, 1994). *R. megacephalus* has 28 cervical vertebrae, and its palate bears suborbital fenestrae, a well developed pterygoid flange and has a unique pterygoid structure in which their posterior portions just contact their opposite along the midline beneath the basicranium. The spatulate mandibular symphysis bears five large dentary teeth, with a total of 30 in each ramus.

Leptocleidus capensis (Andrews, 1911)

Leptocleidus capensis is known from a single specimen, SAM (South African Museum) K5822, found in the Sunday River Formation of the Zwartkops River Valley, South Africa (Cruickshank, 1997). It is inclusion in this analysis stems from the important fact that it is one of the few, well know plesiosaur specimens known from the Lower Cretaceous (Upper Valanginian-Lower Hauterverian). Originally described as *Plesiosaurus capensis* by Andrews (1922b), its close resemblance to the Jurassic pliosauroid *Leptocleidus superstes* (Andrews, 1922a) was later recognized and it was placed in that genus (Persson, 1963). It is distinguished by its small size, (3 meters or less), a dorsomedian foramen on the midnasal ridge of the premaxillae, expanded lateral rami of the pterygoids, strong descending postorbital flanges and a short rostrum bearing a rosette of procumbent teeth. It is also significant in that it occurs in lagoonal or very close inshore, marine facies.

Brachauchenius lucasi Williston, 1903

Found in the North American Upper Cretaceous deposits from Kansas and Texas is the very large pliosauroid *B. lucasi.* Williston (1903) described this taxon and later, (1907) he surmised its close phyletic link with *Liopleurodon (Pliosaurus) ferox* from the Upper Jurassic of England. Williston (1925) subsequently erected a new family for this unusual plesiosaur, the Brachaucheniidae. Among its many distinctive characteristics are its very shortened neck of 12-13 cervical vertebrae, its large size (approximately 11 meters) and greatly enlarged supratemporal fenestrae. The palate possesses a unique combination of characteristics such as the union of the palatines along the midline anterior to the pterygoids, the lack of an anterior interpterygoid vacuity and the underlapping arrangement of the posterior portion of the pterygoids similar to that seen in Upper Jurassic pliosaurids such as *Liopleurodon*.

Dolichorhynchops osborni Williston, 1902

D. osborni is a polycotylid from the Upper Cretaceous (Campanian) Smoky Hill Chalk of western Kansas and the Pierre Shale of South Dakota and Wyoming. Originally described by Williston (1902), *D. osborni* has also been referred, off and on, to the genus *Trinacromerum*. A complete discussion of the confusing nomenclatural history of *Dolichorhynchops* and *Trinacromerum* has been summarized by Adams (1997). *D. osborni* is known from both juvenile and adult specimens and has a relatively large skull (up to 1 meter in length) with a long, gracile rostrum, numerous long, slender teeth, and a short neck consisting of 19 cervical vertebrae. It also has short and wide supratemporal fenestrae, the suspensorium is oriented vertically and, in contrast to Jurassic pliosaurids, the pterygoids extend as flat plates beneath the basicranium.

Trinacromerum bentonianum Cragin, 1888

T. bentonianum was the first skull of a polycotylid described from North America (Cragin, 1888). It is found in Upper Cretaceous (Cenomanian - Turonian?) deposits of Kansas and Texas. *Ceraunosaurus brownorum* Thurmond (1968) is considered a junior synonym of *T. bentonianum*. *T. bentonianum* differs from *Dolichorhynchops osborni* in having a relatively larger, more robust dentition, a long and narrow supratemporal fenestra, an inclined suspensorium and 20 cervical vertebrae.

MOR 751

MOR 751 is a new large-skulled taxon from the Lower Cretaceous Thermopolis Shale of south-central Montana. It is described in detail above.

Selection of Characters

In this study, 24 skeletal characters were chosen for use in a cladistic analysis. 21 of the characters were selected from the skull and the remaining 3 were selected from the cervical vertebrae. Cranial features were favored over other skeletal characters for several reasons. Firstly, cranial features appear to be more stable indicators of evolutionary relationships than postcranial features (Carpenter, 1997). Published phylogenies, constructed primarily on the basis of overall morphology (relative neck length, skull size and paddle proportions) may be misleading. Secondly, I was unable to personally inspect many of specimens at their respective institutions and relied on excellent, recently published cranial descriptions. Finally, and primarily due to practical considerations, the well-preserved skull and neck of MOR 751 were available for direct comparison to other taxa. Characters taken from the incomplete right forelimb were not included in the analysis.

In keeping with cladistic methodology this analysis has attempted to rely on the use of unique, share derived characters, or synapomorphies, in order to establish evolutionary relationships among the selected taxa. Discrete characters (the absence or presence of a character state) were favored over meristic characters (size and shape) when possible. This methodology was used with the intent to minimize possible affects of ontogeny, character reversal and convergence on the analysis. As new morphological information comes to light this list of characters can be redefined or falsified. It is hoped that these characters may be used in conjunction with a whole suite of other skeletal characters in a more complete phylogenetic review of the entire group. A description of character states and character coding is given below.

Characters Used In Phylogenetic Analysis

1. Relative skull size.

A meristic character that has traditionally been employed to denote an apparent evolutionary trend within the Plesiosauria towards either an increase or decrease in skull size, with respect to trunk length. In this analysis, the ingroup taxa exhibit either conspicuously massive and robust, or small and gracile skulls, in proportion to trunk length. Skeletal proportions in the outgroup taxon, *Pistosaurus*, are incompletely known but have been described by Carroll and Gaskill (1985: 389) as "typically nothosaurian". It is considered here to be of intermediate proportions. It is important to note that the use of skull length to neck length ratios as an indicator of skull size is misleading. The correlation of a decrease in neck length with and increase in skull size is seen in many but not all forms (Brown, 1981). It has been suggested that this character may be subject to reversals (Bakker, 1993; Carpenter, 1997 and Bardet and Godefroit, 1998) Skull size intermediate (0), small (1), large (2).

2. **Relative skull to rostrum length.**

Rostrum length is defined here as the distance from the tip of the snout to the anterior margin of the orbit. Overall length is measured from the tip of the snout to the posterior margin of the quadrate. Rostrum 40-50 percent total skull length (0), less than 40 percent (1), greater than 50 percent (2).

3. **Dorsal processes of the premaxilla.**

The dorsal processes of the premaxilla of some taxa extend posteriorly along the dorsal midline, separating the frontals and contact the anterior margins of the parietals. Premaxilla does not contact the parietals (0), premaxilla contacts the parietals (1).

4. **Shape of the premaxilla.**

A meristic character that distinguishes a basic difference between the preorbital regions of small and large-skulled forms. Within the ingroup, two distinct morphologies can be observed. In dorsal aspect, small-skulled forms have broad and compact premaxillae (excluding the dorsal processes) whereas large-skulled forms have narrow, laterally compressed premaxillae. Premaxillae long and narrow (0), premaxillae short and wide (1).

5. Presence or absence of a diastema.

This derived character is seen in some large-skulled Jurassic pliosaurids and is probably associated with a particular feeding mode. Diastema absent (0), present (1).

6. Presence or absence of a parietal (pineal) foramen.

The presence of a parietal foramen is considered plesiomorphic for plesiosaurs and *Pistosaurus*. Its loss is considered synapomorphic for upper Cretaceous polycotylids and elasmosaurids by Carpenter (1997). Parietal foramen present (0), absent (1).

7. Ventral margin of the orbit.

In all sauropterygians the jugal remains in contact with the orbit. However, the extent to which the jugal participates in the ventral margin of the orbit varies considerably. In the generalized primitive diapsid condition, from which the sauropterygian cheek evolved, the jugal forms the entire ventral margin of the orbit, a condition seen in many Jurassic pliosaurids and in the Cretaceous elasmosaur, *Libonectes*. In the intermediate state, the ventral margin of the orbit is shared approximately equally by the jugal and maxilla and is present in *Pistosaurus* and *Plesiosaurus dolichodeirus*. In what is interpreted as the most derived condition, the maxilla forms the majority of the ventral orbital rim, as observed in Cretaceous polycotylids and MOR 751. Ventral margin of orbit bound equally by the jugal and maxilla (0), bound primarily by the jugal (1), bound primarily by the maxilla (2).

8. Nature of the postorbital-squamosal contact.

In the ancestral diapsid condition the lateral temporal bar, forming the dorsal margin of the lower temporal arch, is formed through contact of the postorbital anteriorly and the squamosal posteriorly. With loss of the quadratojugal and modification of the jugal the lower temporal arch has been lost in the Sauropterygia (Carroll, 1981). In derived forms, the jugal plays and important roll in the remodeled lateral temporal bar to such an extent that it excludes contact of the postorbital with the squamosal in some forms. Postorbital contacts squamosal (0), postorbital does not contact squamosal (1).

9. **Relative size of the supratemporal fenestra.**

The bones surrounding the supratemporal fenestra serve as sites of origin for the large adductor musculature of the jaw. Large-skulled forms typically have proportionally larger supratemporal fenestrae relative in size to the orbits than small-skulled forms, probably reflecting a difference in feeding habits and prey preferences. Supratemporal fenestra larger than the orbit (0), supratemporal fenestra equal in size or smaller than the orbit (1).

10. **Orientation of the suspensorium.**

The suspensorium, bridging the skull roof to the glenoid fossa may be either vertical or slope at an angle posteriorly. This character may be difficult to determine as a result of preservational distortion. Suspensorium vertical (0), inclined (1).

11. **Formation of the occipital condyle.**

The occipital condyle is formed primarily on the basioccipital in most forms. However in *Plesiosaurus dolichodeirus*, *Cryptoclidus* and apparently some pliosaurids, a portion of the pedicels of the exoccipitals participate in the condyle. The distribution of this character is hard to trace as the condyle of many of the large-skulled forms have been inadequately described or are poorly reserved. Exoccipital contributes to the occipital condyle (0), occipital condyle formed on the basioccipital only (1).

12. **Presence or absence of an anterior interpterygoid vacuity.**

The anterior interpterygoid vacuity forms a narrow cleft along the midline of the palate in most members of the in-group. It is notably lacking in *Pistosaurus* and some Jurassic pliosaurids (e.g., *Simolestes* and *Peloneustes*) and in *Brachauchenius*. Anterior interpterygoid vacuity absent (0), present (1).

13. **The posterior pterygoid structure ventral to the basicranium.**

All plesiosaurs are united by the synapomorphy of an open palate, specifically, a medial cleft formed by the separation of the pterygoids along their posterior midline. Within the Plesiosauria however, the expansion of the pterygoids beneath the braincase is variable. Carpenter (1997) described two different pterygoid structures, types A and B, that apparently arose independently from an open pterygoid structure. Type A pterygoids, seen in pliosaurids, are folded under and meet their opposite along the midline ventral to the braincase. Type B pterygoids occur in elasmosaurid and polycotylids and expand beneath the braincase to form a horizontal plate. Carpenter states that an incipient type A version is seen in *Pistosaurus* while and incipient type B version is seen in *Plesiosaurus dolichodeirus*. For the purposes of this analysis, both incipient types are grouped together and considered the plesiomorphic condition. Because the evolution of different palate types is poorly understood the apparently unique palate found in MOR 751 is coded as type B, which it most closely resembles. Pterygoids do not meet along the posterior midline beneath the basicranium (0), pterygoids fold under the basicranium (1), pterygoids form a horizontal plate beneath the basicranium (2).

14. **Presence or absence of a pterygoid flange.**

In a structural analysis of the skull and mandible of *Rhomaleosaurus zetlandicus*, Taylor (1992a) demonstrates that the presence of a pterygoid flange helps support the jaw ramus against transverse bending and shearing forces associated with subduing large prey items. It is present in most pliosaurids, with the exception of *Pliosaurus*, and is weakly developed in MOR 751. Pterygoid flange present (0), absent (1).

15. **The presence or absence of a suborbital fenestra.**

The anterior pterygoideus, one of the major jaw adductor muscles probably originated in part on the suborbital fenestra (Taylor, 1992a). Its presence is considered an adaptation for the attachment of this muscle and is found in some Jurassic pliosaurids. Its presence in MOR 751 is equivocal, and its distribution in some plesiosaurs is uncertain due to crushing and distortion in the palatal region. Suborbital fenestra absent (0), suborbital fenestra present (1).

16. **Presence or absence of a vomeronasal fenestra.**

The vomeronasal fenestra is present primatively in many tetrapods and in *Pistosaurus*, but was apparently lost early in the evolution of plesiosaurs as it is absent in all known Jurassic plesiosaurs. This character may be subject to reversals as Carpenter

(1997) considers its reappearance in advanced Cretaceous elasmosaurs such as *Libonectes* and polycotylids such as *Dolichorhynchops* as synapomorphic for the two groups. Vomeronasal fenestra present (0), vomeronasal fenestra absent (1).

17. **Tooth form.**

The teeth of plesiosaurs may be grouped into two general categories; large roots and wide-based crowns or small roots and slender crowns. The former are typically associated with large-skulled forms and the latter with small-skulled forms. However, exceptions to the rule are not uncommon. The large-skulled Cretaceous polycotylid *Dolichorhynchops* has numerous, small and slender teeth while the small-skulled Cretaceous elasmosaurid *Libonectes* has developed long, robust teeth suggesting that this character may be subject to reversals. Large roots and wide-based crowns (0), small roots and slender-based crowns (1).

18. **Presence or absence of caniniform teeth.**

Caniniform teeth are defined as those teeth which are significantly larger than surrounding mature teeth. Caniniforms absent (0), present (1).

19. **The character of the mandibular symphysis.**

The jaw symphysis may be described as either long and robust, extending posteriorly to include several pairs of dentary teeth or short and weak, including only one or two anterior most pairs of dentary teeth. Mandibular symphysis long and stout (0), short and weak (1).

20. **The presence or absence of coronoids.**

The coronoids probably help to brace the anterior mandibular elements (splenial and dentary) with the posterior elements (angular and surangular) and are typically present in large-skulled forms. The presence of this element in plesiosaurs is not well documented as a result of poor preservation or difficulty in determining fusion from primary nonexistence (see Storrs, 1996 for *Thalassiodracon hawkinsi*). The presence or absence of the coronoid may be useful in phyletic analyses once the distribution of this character is better understood. Coronoid present (0), absent (1).

21. **Number of pairs of dentary teeth.**

Jurassic and Cretaceous large-skulled forms tend to have 25 or more pairs of dentary teeth (averaging around 30) and show no trend toward increasing or decreasing dentary tooth pair numbers (Brown, 1981). Small-skulled forms however show a tendency to decrease the number of dentary tooth pairs from Jurassic to Cretaceous taxa. Brown (1981) considers 24 pairs to be the primitive number for the elasmosaurids and cryptoclidids. Dentary tooth pairs 25 or greater (0), 24 or less (1).

22. **Atlas centrum.**

Distribution of this character is hard to follow due to fusion of atlas elements during ontogeny. However, in forms for which the atlas has been adequately described two different states for this character exist. In the first condition, found in *Cryptoclidus* and *Muraenosaurus*, the atlas centrum participates in the anterior rim of the atlantal cup, excluding contact between the atlas neural arch and the atlas intercentrum. The alternative condition is seen in Jurassic and Cretaceous large-skulled forms, as well as *Libonectes*, where the atlas centrum is excluded from participation in the anterior rim of the atlantal cup. Atlas centrum participates in anterior rim of atlantal cup (0), does not participate in anterior rim (1).

23. The number of cervical vertebrae.

Brown (1981) considers 28 to 32 to be the primitive number of cervical vertebrae in the Plesiosauria. The presence of an estimated 24 cervical vertebrae in *Pistosaurus* suggests that this range should be revised downward. In this analysis 24-32 cervical vertebrae is considered plesiomorphic. Traditional phylogenies (Welles, 1943) have relied heavily on neck length as an indicator of relatedness, however, recently proposed alternative phylogenies (Carpenter, 1997 and Bakker, 1993) based primarily on cranial character suggest that an increase of decrease in the number of cervical vertebrae may have evolved independently in two or more different clades. Number of cervical vertebrae 24-32 (0), less than 23 (1), more than 33 (2).

24. The number of cervical rib heads.

Cervical vertebrae may bear paired facets on the centrum (dicranopleurous) for the capitulum and tuberculum of the cervical ribs or bear a single facet (cercidopleurous). The plesiomorphic condition is to retain paired facets, as is seen in Jurassic large and small-skulled forms. Rib heads double (0), rib heads single (1).

Methods

A data matrix (Table 5) with 14 taxa and 24 characters was created in MacClade, version 3.03 (Maddison and Maddison, 1992), on a Macintosh Quadra 700. All multistate characters are unordered due to uncertainties of character transformation. Character polarization was determined by outgroup comparison method (Watrous and Wheeler, 1981). The data was transferred into PAUP (Phylogenetic Analysis Using Parismony), version 3.0 (Swofford, 1991) and processed by heuristics search methods (addition sequence: stepwise; closest).

Table 5. Data matrix of plesiosaur character states for 14 taxa used in phylogenetic analysis. Each character is discussed in text. Abbreviations: ?, unknown or missing data.

	Character				
Taxon	5	10	15	20	24
Pistosaurus	00000	00000	?0000	00???	??00
Plesiosaurus	11010	00011	01010	11011	1?20
Cryptoclidus	11010	02010	01?10	11011	0001
Muraenosaurus	11010	02011	110?0	11011	1021
Libonectes	11110	10?01	11210	00110	1?21
Rhomaleosaurus	20001	01101	?1?01	10100	0?00
Peloneustes	22101	01001	0110?	10100	0110
Liopleurodon	22101	0??0?	11101	10100	0110
Pliosaurus	20100	01000	?1111	10100	0?10
Leptocleidus	21111	00001	?1?01	10??0	0??1
MOR 751	22100	02100	1120?	10100	0101
Brachauchenius	22000	0?100	?010?	1010?	1?11
Trinacromerum	22?00	12101	?121?	?000?	0111
Dolichorhynchops	22100	12000	11210	0100?	0111

RESULTS AND DISCUSSION

Results

2 MPR (Most Parsimonius Reconstruction) trees were discovered and summarized into a single strict consensus tree with a tree length of 58, CI (Consistency Index) of .500 and RI (Retention Index) of .646. Support values for the MPR tree were generated by bootstrap (random character sampling) analysis in addition to a decay analysis for tree lengths 59-64. The results are presented in Figure 18.

The analysis suggests the existence of two major clades among the ingroup taxa, in addition to a single basal offshoot, *Brachauchenius*. One clade comprises the traditional Jurassic and Cretaceous, small skulled plesiosauroid taxa *Plesiosaurus*, *Cryptoclidus*, *Muraenosaurus* and *Libonectes*. The Cretaceous polycotylids *Trinacromerum* and *Dolichorhynchops* plus MOR 751 are sister taxa to the plesiosauroid clade. A second clade is comprised of the traditional large-skulled Jurassic pliosaurid taxa *Rhomaleosaurus*, *Pliosaurus*, *Peloneustes* and *Liopleurodon* plus the Early Cretaceous pliosauroid *Leptocleidus*. The relationship between *Peloneustes* and *Liopleurodon* is unresolved.

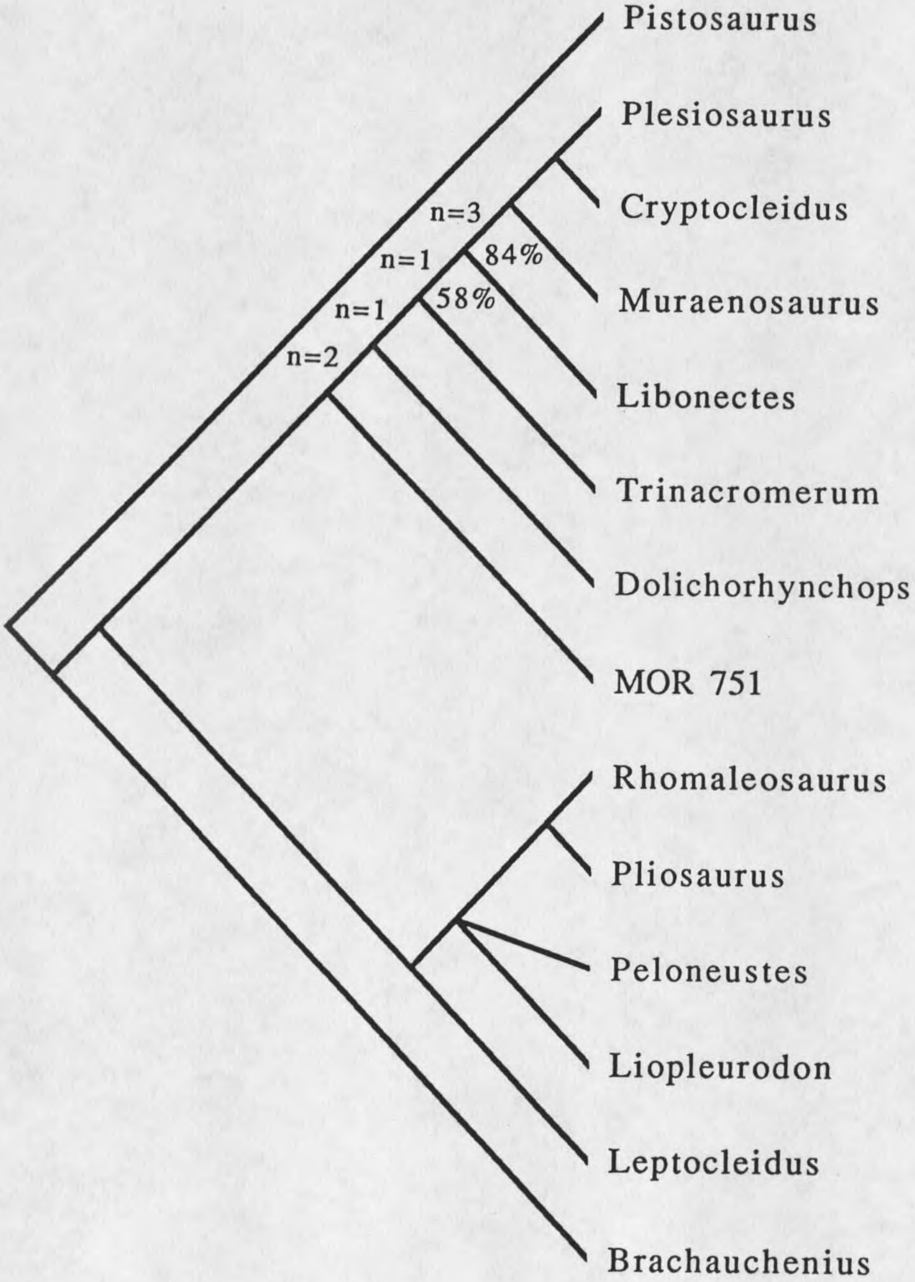

Figure 18. Strict consensus tree (tree length = 58, CI = .500, RI = .646) of two MPR trees obtained from the data matrix shown in Table 5. Abbreviations: n = decay value; % = bootsrap support.

Discussion

The concept of a monophyletic Plesiosauroidea is supported by the following synapomorphies: relative skull size (1, small); relative skull to rostrum length (2, less than 40 percent); shape of premaxillae (4, short and wide); relative size of the supratemporal fenestrae (9, equal in size or smaller than orbit); pterygoid structure ventral to the basicranium (13, form horizontal plate beneath the basicranium); tooth form (17, small roots and slender crowns); character of the mandibular symphysis (19, short and weak); coronoids (20, absent). It is important to note that the two elasmosaurids, *Muraenosaurus* and *Libonectes* clearly group with the two other plesiosauroid genera, in contrast to Bakker's (1993) paraphyletic concept of the Plesiosauroidea.

One of the most interesting outcomes of this analysis is the sister group relationship of the Cretaceous polycotylid genera *Trinacromerum* and *Dolichorhynchops* with the Plesiosauroidea, in particular with the elasmosaurids. While Carpenter (1997) and Bakker (1993) both hypothesize a non-traditional sister group relationship between elasmosaurs and polycotylids, they derive this new clade from different ancestors. This analysis agrees with Carpenter's hypothesis that the Cretaceous short-necked, large-skulled polycotylids share a more recent common ancestor with plesiosauroids than they do with Jurassic pliosaurids. These results suggest a paraphyletic concept for the Pliosauroidea (see below).

MOR 751 is the sister taxon to an unnamed clade including the two polycotylid genera plus plesiosauroids. The results of a decay analysis indicate support for this topology only in the MPR (tree length 58). MOR 751 retains a sister group relationship in a strict consensus tree one step longer than the MPR tree but with *Brachauchenius* at a basal unresolved node. Because *Brachauchenius* and MOR 751 differ radically in palate structure however, a sister group relationship is considered untenable.

A closer relationship of MOR 751 with the two polycotylid genera is more consistent with the data and is well supported by similarities in evolutionarily stable characters such as pterygoid structure ventral to the basicranium and atlas-axis morphology. Postcranial characters such as epipodials which are broader than long help to strengthen this relationship. Although MOR 751 is less derived than other polycotylids in that it retains a pineal foramen, has a more primitive dentition and displays a lesser degree of rostral elongation, it is consistent with Carpenter's (1996,) revised diagnosis for the Polycotylidae, with the exception of MOR 751 having caniniform teeth. The relatively primitive morphology of MOR 751 is also consistent with its stratigraphic occurrence. For these reasons MOR 751 is tentatively placed within the Polycotylidae.

The monophyly of the predominately Jurassic Pliosauridae, including *Leptocleidus* from the Lower Cretaceous, is confirmed by the following synapomorphies: relative skull size (1, large); diastema (5, present); pterygoid structure ventral to the basicranium (13, fold under basicranium); suborbital fenestrae (15, present). Because the interrelationships within the Pliosauridae is beyond the scope of this study, the polytomy between *Liopleurodon* and *Peloneustes* is a result of character selection to reveal broader relationships among all plesiosaur genera, not necessarily relationships within the family.

Brachauchenius appears to represent a basal offshoot from a pliosauroid-like ancestor. Although it is resolved in the strict consensus tree, this taxon finds little bootsrap support. *Brachauchenius* is a spatial and temporal contemporary of Upper Cretaceous polycotylids, however a closer relationship to Jurassic pliosaurids is suggested by similarities in skull morphology, especially in pterygoid structure. A more detailed analysis is required to further characterize its relationships to the Pliosauridae.

The analysis however also suggests that the superfamily Pliosauroidea is paraphyletic as it does not include the Polycotylidae and Brachaucheniidae. This contrasts to the traditional concept of relationships and classification of the Plesiosauria (see Figure1). These results imply that traditionally recognized characters such as a similar neck length and/or skull size may be convergent characters. Specifically, the elongated skulls and shortened necks of polycotylids evolved independent of pliosaurids. Similar selective pressures to feeding on large bodied and/or hard-shelled (cephalopod) prey may have lead to the evolution of similar neck and skull morphologies. Therefore, the use of neck length (number of cervical vertebrae) and skull to torso comparisons must be viewed in a broader context of other cranial and postcranial characters, in particular, palate and atlas-axis structure.

Other work on other new and preexisting European and North American material will undoubtedly help to further our own rapidly evolving understanding of plesiosaur relationships. Future analyses will benefit from the use additional cranial and postcranial characters. Furthermore, a better understanding of character evolution will help to resolve phylogenetic reconstructions and resulting classifications.

CONCLUSIONS

MOR 751 is a large skulled plesiosaur from the Thermopolis Shale of Carbon County, Montana. The specimen is largely articulated and consists of the skull, all cervical, pectoral and five dorsal vertebrae and one pectoral paddle. The very well preserved skull allows a detailed description and interpretation of the relationships of the palate, skull roof and braincase to be made.

The specimen occurs in the lower Upper Thermopolis Shale (Shell Creek equivalent) and is uppermost Albian in age. The Upper Thermopolis Shale represents marine deposits of the Cretaceous Western Interior Seaway and was deposited in the northern arm of the seaway during its second major transgression, prior to the subsequent joining of both arms throughout most of the Upper Cretaceous.

MOR 751 may represent a new taxon which can be diagnosed by the following suite of characters: moderately sized plesiosaur approximately 4 meters in length; large skull relative to trunk length with elongate rostrum; mandibular symphysis bearing at least 6 pairs of caniniform teeth; pineal foramen present; pterygoids unite along the midline ventral to the basicranium in a flat plate and appear to expand ventral and medial to the basipterygoid processes; fenestris ovalis present; neck of moderate length possessing 26 cervical vertebrae; cervical ribs single-headed; epipodials broader than long; phalangeal formula 7-11-10-9-9.

A recently described plesiosaur, *Plesiopleurodon wellesi* (Carpenter, 1996), from the Upper Cretaceous Belle Fourche Shale (lowermost Cenomanian) shares some overall similarities with MOR 751. The published description of *P. wellesi*, however, is based on an incompletely prepared specimen and many important diagnostic characters of the palate, skull roof and cervical region are not visible. Until personal examination of the holotype, CM (Carnegie Museum) 2815, can be made it is not possible to rule out the possibility that they may be congeneric or even conspecific.

A phylogenetic analysis demonstrates that MOR 751 is the sister taxon to a clade comprised of the Cretaceous polycotylids *Trinacromerum* and *Dolichorhynchops* as well as Cretaceous and Jurassic plesiosauroids. This supports a recent hypothesis (Carpenter, 1997) suggesting that Cretaceous elasmosaurs may be the sister group to Cretaceous polycotylids.

REFERENCES CITED

Adams, D. A. 1997. *Trinacromerum bonneri*, New species; Last and fastest pliosaur of the Western Interior Seaway. Texas Journal of Science 49(3):179-198.

Andrews, C. W. 1910-1913. A descriptive catalogue of the marine reptiles of the Oxford Clay. Part I. 205 pp. (1910); Part II. 206 pp. (1913). British Museum of Natural History, London.

Andrews, C. W. 1922a. Description of a new plesiosaur from the Weald Clay of Berwick (Sussex). Geological Society of London Quarterly Journal 78:285-298.

Andrews, C. W. 1922b. Description of a new plesiosaur (*Plesiosaurus capensis*) from the Uitenhage Beds of Cape Colony. Annals of the South African Museum 7:309-322.

Bakker, R. T. 1993. Plesiosaur extinction cycles-Events that mark the beginning, middle and end of the Cretaceous; pp.641-664 *in* Caldwell, W. G. E. and E. G. Kauffman, (eds.), Evolution of the Western Interior Basin. Geological Association of Canada, Special Paper 39.

Bardet, N. and P. Godefroit. 1998. A preliminary cladistic analysis of the Plesiosauria. Journal of Vertebrate Paleontology, Abstracts 18(3):26A.

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

Brown, D. S. 1994. A taxonomic reappraisal of the families Elasmosauridae and Cryptoclididae (Reptilia: Plesiosauroidea). Revue de Paleobiologie, Volume special (for 1993), 7:9-16.

Brown, D. S., and A. R. I. Cruickshank. 1994. The skull of the Callovian plesiosaur *Cryptoclidus eurymerus*, and the sauropterygian cheek. Paleontology 37(4):941-953.

Carpenter, K. 1996. A review of short-necked plesiosaurs from the Cretaceous of the Western Interior, North America. Neues Jahrbuch Geologie und Palaentologie Abhandlungen 201(2):259-287.

Carpenter, K. 1997. Comparative cranial anatomy of two North American Cretaceous plesiosaurs (Reptilia: Sauropterygia); pp. 191-216 *in* Callaway, J. M., and E. L. Nicholls, (eds.), Ancient marine reptiles. Academic Press, San Diego.

Carroll, R. L. 1981. Plesiosaur ancestors from the Upper Permian of Madagascar. Philosophical Transactions of the Royal Society of London B 293:315-383.

Carroll, R. L., and P. Gaskill. 1985. The nothosaur *Pachypleurosaurus* and the origin of the plesiosaurs. Philosophical Transactions of the Royal Society of London B 309(1139):343-393.

Cragin, F. W. 1888. Preliminary description of a new or little known saurian from the Benton of Kansas. American Geologist 2:404-407.

Cruickshank, A. R. I. 1994. Cranial anatomy of the Lower Jurassic pliosaur *Rhomaleosaurus megacephalus* (Stuchbury) (Reptilia: Plesiosauria). Philosophical Transactions of the Royal Society of London B 343:247-260.

Cruickshank, A. R. I. 1997. A lower Cretaceous pliosauroid from South Africa. Annals of the South African Museum 105(2):207-226.

Dolson, J., D. Muller, M. J. Evetts, and J. A. Stein. 1991. Regional paleotopographic trends and production, Muddy Sandstone (Lower Cretaceous), central and northern Rocky Mountains. Bulletin of the American Association of Petroleum Geologists 75(3):409-435.

Dyman, T. S., K. W. Porter, R. G. Tysdal, W. A. Cobban, J. E. Fox, R. H. Hammond, D. J. Nichols, W. J. Perry, D. D. Rice, D. R. Setterholm, G. W. Shurr, J. C. Haley, D. E. Lane, S. B. Anderson, and E. B. Campen. 1995. West-east stratigraphic transect of Cretaceous rocks in the northern Rocky Mountain and Great Plains region, southwest Montana to southwest Minnesota. Geological Society of America Miscellaneous Investigation Series, Map I-2474-A.

Eicher, D. L. 1960. Stratigraphy and micropaleontology of the Thermopolis Shale. Bulletin of the Peabody Museum of Natural History, Yale University15:1-121.

Hampe, O. 1992. Ein grosswuechsiger Pliosauridae (Reptilia, Plesiosauria) aus der Unterkreide (oberes Aptium) von Kolumbien. Courier Forschung Institut Senckenberg 145:1-32.

Kauffman, E. G., B. B. Sageman, J. I. Kirkland, W. P. Elder, P. J. Harries, and T. Villamil. 1993. Molluscan biostratigraphy of the Cretaceous Western Interior Basin, North America; pp. 397-434 *in* Caldwell, W. G. E. and E. G. Kauffman, (eds.), Evolution of the Western Interior Basin. Geological Association of Canada, Special Paper 39.

Maddison, W. P., and D. R. Maddison. 1992. MacClade, version 3. Sinauer Associates, Inc., 398 pp.

Martill, D. M. 1992. Pliosaur stomach contents from the Oxford Clay. Mercian Geologist 13(1):37-42.

Massare, J. A. 1988. Swimming capabilities of Mesozoic marine reptiles: Implications for method of predation. Paleobiology 14(2):187-205.

Nicholls, E. L., and A. P. Russell. 1991. The plesiosaur pectoral girdle: The case for a sternum. Neues Jahrbuch Geologie und Paleontologie Abhandlung 182(2):161-185.

Obradovich, J. D. 1993. A Cretaceous time scale; pp.379-396*in* Caldwell, W. G. E. and E. G. Kauffman, (eds.), Evolution of the

Western Interior Basin. Geological Association of Canada, Special Paper 39.

Persson, O. 1963. A revision of the classification of the Plesiosauria, with a synopsis of the stratigraphical and geographic distribution of the group. Lunds Universitets Arsskrift 59(2):1-60.

Porter, K. W., T. S. Dyman, and R. G. Tysdal. 1993. Sequence boundaries and other surfaces in Lower and Upper Cretaceous rocks of central and southwest Montana - A preliminary report; pp. 45-60 *in* Hunter, L. D. V., (ed.), Energy and Mineral Resources of central Montana, 1993 Field Conference Guidebook. Montana Geological Society, Billings, MT.

Sander, P. M., O. C. Rieppel, and H. Bucher. 1997. A new pistosaurid (Reptilia: Sauropterygia) from the Middle Triassic of Nevada and its implications for the origin of the plesiosaurs. Journal of Vertebrate Paleontology17(3):526-533.

Storrs, G. W. 1991. Anatomy and Relationships of *Corosaurus alcovensis* (Reptilia: Sauropterygia) and the Triassic Alcova Limestone of Wyoming. Bulletin of the Peabody Museum of Natural History 44:1-151.

Storrs, G. W. 1993a. Function and phylogeny in Sauropterygian (Diapsida) evolution. American Journal of Science 293-A:63-90.

Storrs, G. W. 1997. Morphological and taxonomic clarification of the genus *Plesiosaurus*; pp. 145-190 *in* Callaway, J. M., and E. L. Nicholls, (eds.), Ancient marine reptiles. Academic Press, San Diego.

Storrs, G. W., and M. A. Taylor. 1996. Cranial anatomy of a new plesiosaur genus from the lowermost Lias (Rhaetian/Hettangian) of Street, Somerset England. Journal of Vertebrate Paleontology 16(3):403-420.

Sues, H.-D. 1987. Postcranial skeleton of *Pistosaurus* and interrelationships of the Sauropterygia (Diapsida). Zoological Journal of the Linnean Society 90:109-131.

Swofford, D. L. 1991. Phylogenetic Analysis Using Parsimony (PAUP) version 3.0s. Illinois Natural History Survey, Champaign.

Tarlo, L. B. 1960. A review of the Upper Jurassic pliosaurs. Bulletin of the British Museum of Natural History, Geology 4(5):147-207.

Taylor, M. A. 1981. Plesiosaurs - Rigging and ballasting. Nature 290:628-629.

Taylor, M. A. 1992a. Functional anatomy of the head of the large aquatic predator *Rhomaleosaurus zetlandicus* (Plesiosauria, Reptilia) from the Toarcian (Lower Jurassic) of Yorkshire, England. Philosophical Transactions of the Royal Society of London Series B 335:247-280.

Taylor, M. A. 1992b. Taxonomy and taphonomy of *Rhomaleosaurus zetlandicus* (Plesiosauria, Reptilia) from the Toarcian (Lower Jurassic) of the Yorkshire coast. Proceedings of the Yorkshire Geological Society 49(1):49-55.

Taylor, M. A., and A. R. I. Cruickshank. 1993. Cranial anatomy and functional morphology of *Pliosaurus brachyspondylus* (Reptilia: Plesiosauria) from the Upper Jurassic of Westbury, Wiltshire. Philosophical Transactions of the Royal Society of London B 341:399-418.

Thomas, L. E. 1965. Sedimentation and structural development of the Big Horn Basin. Bulletin of the American Association of Petroleum Geologists 49(11):1867-1877.

Thurmond, J. T. 1968. A new polycotylid plesiosaur from the Lake Waco Formation (Cenomanian) of Texas. Journal of Paleontolgy 42(5):1289-1296.

Tschanz, K. 1989. *Lariosaurus buzzii* n. sp. from the Middle Triassic of Monte San Giorgio (Switzerland) with comments on the classification of nothosaurs. Paleontographica A 208:153-179.

Vuke, S. M. 1984. Depositional Environments of the Early Cretaceous Western Interior Seaway in southwestern Montana and the Northern United States, 127-144 *in* The Mesozoic of Middle

North America, D. F. Stott and D. J. Glass (eds.), Canadian Society of Petroleum Geologists Memoir 9.

Watrous, L. E., and Q. D. Wheeler. 1981. The out-group comparison method of character analysis. Systematic Zoology 30(1):1-11.

Welles, S. P. 1943. Elasmosaurid plesiosaurs with description of new material from California and Colorado. Memoirs University of California, Berkeley 13(3):125-215.

Welles, S. P. 1949. A new elasmosaur from the Eagle Ford Shale of Texas. Fondren Science Series 1:1-28.

Welles, S. P. 1962. A New species of elasmosaur from the Aptian of Colombia and a review of the Cretaceous plesiosaurs. University of California Publications in Geological Science, Berkeley 44(1):1-96.

Williston, S. W. 1902. Restoration of *Dolichorhynchops osborni*, a new Cretaceous plesiosaur. Kansas University Science Bulletin 1(9):241-245.

Williston, S. W. 1903. North American Plesiosaurs. Part 1. Field Columbian Museum Publication 73. Geological Series 2:1-77.

Williston, S. W. 1907. The skull of *Brachauchenius,* with observations of the relationships of the plesiosaurs. Proceedings of the National Museum 32(1540):477-493.

Williston, S. W. 1925. The osteology of the reptiles. Cambridge, Massachusetts 300pp.