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 _____ (Signature) 11/23/98 Date

Approved for the Department of Biology

Ernest Vyse _____ (Signature) 11/23/98 Date

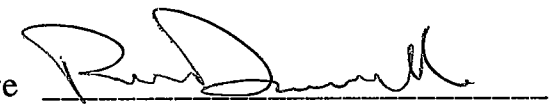
Approved for the College of Graduate Studies

Joseph J. Fedock, PhD _____ (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

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).

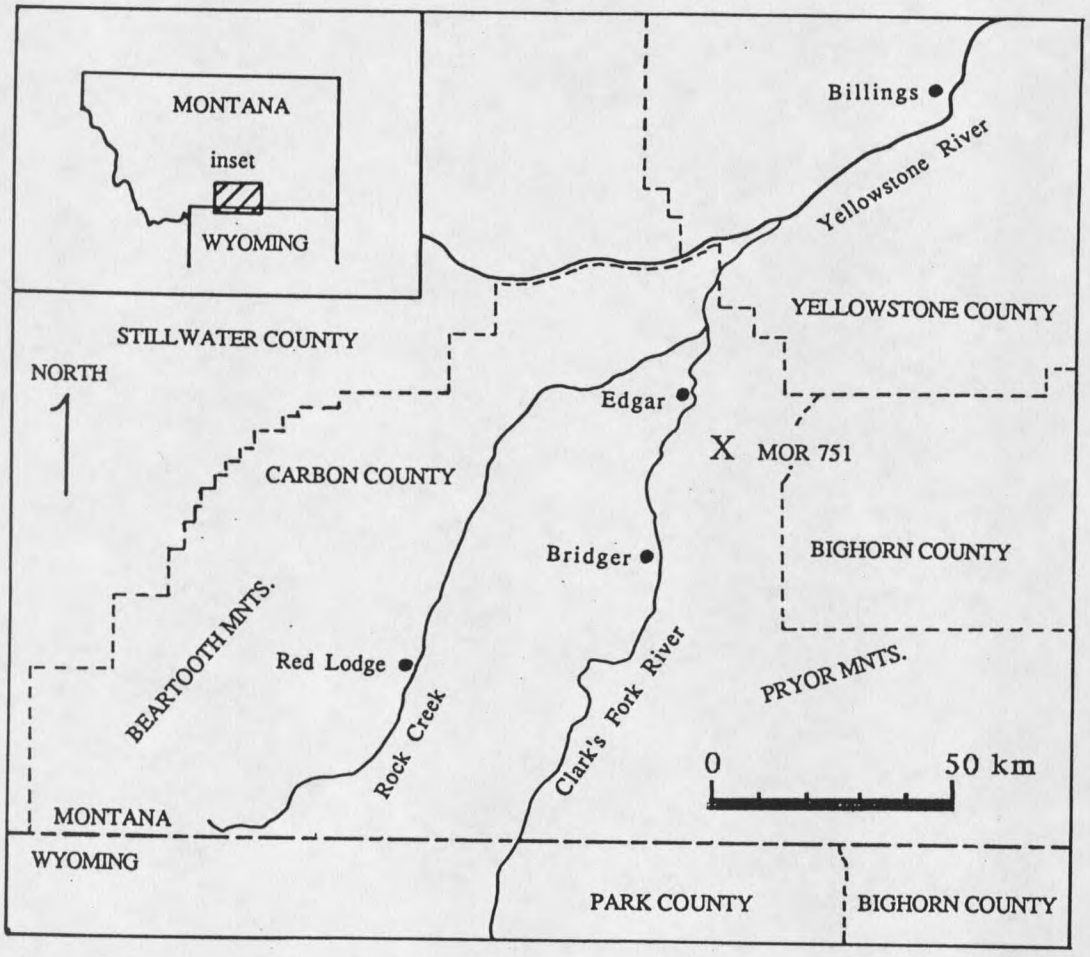


Figure 2. Locality map of MOR 751 in south-central Montana.

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

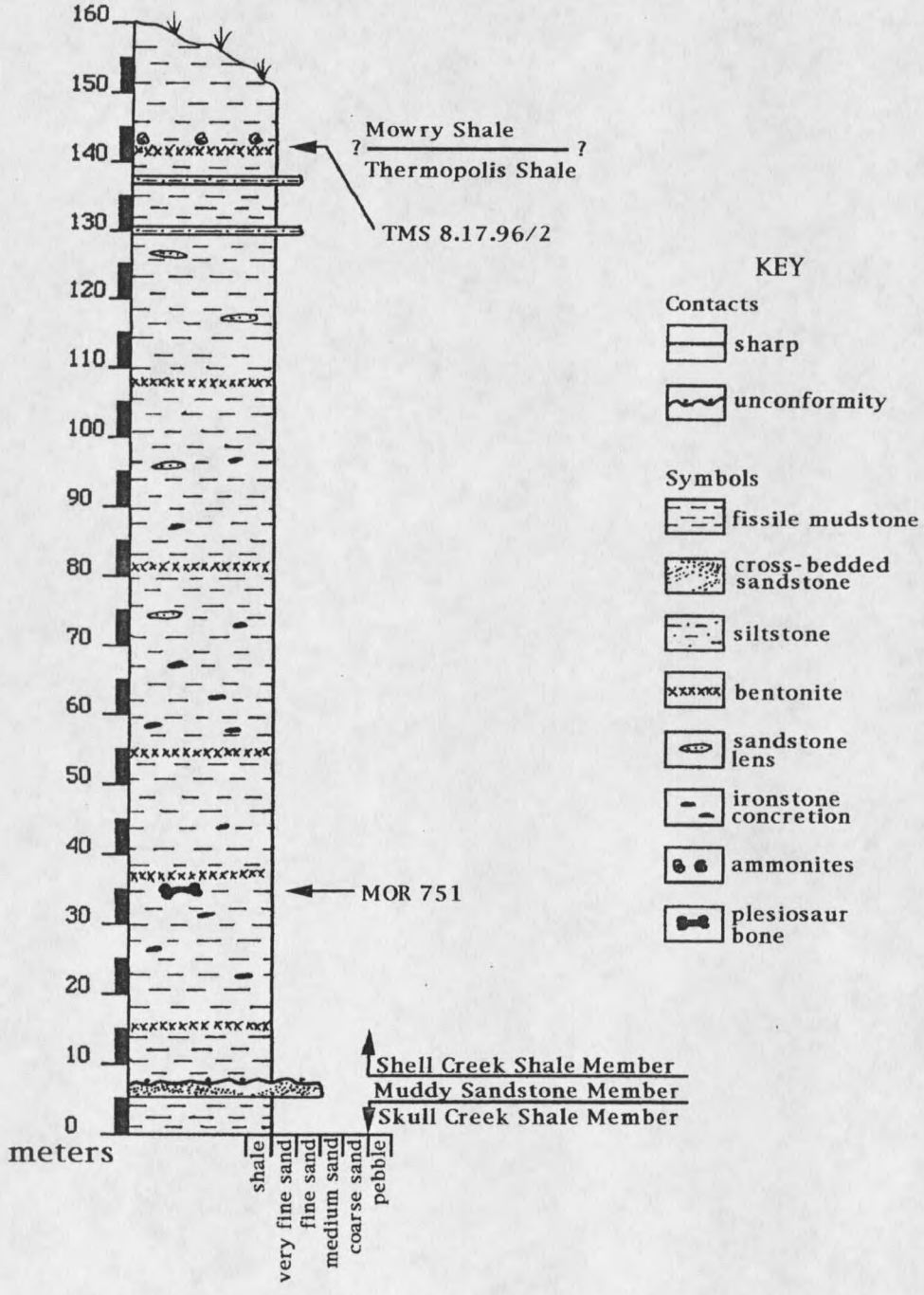


Figure 3. Measured section through the upper Thermopolis Shale (Shell Creek Member equivalent) at the Black Butte locality (T 4 S, R 24 E, Sec. 20), Carbon County, Montana.

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